Enrique Murgui · Marcus Hedblom
Editors

Ecology and Conservation of Birds in Urban Environments

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Foreword

Urbanization is one of the most transformative human land-use processes on our globe and will increase in the coming years. Today, more than half of the world's population resides in urban areas and it is projected that by 2050 at least two-thirds of the world's population will be urban. Urbanization has an enormous impact on natural habitats and resources, and urban growth is responsible for major losses in biodiversity. However, urbanized areas can offer a wide variety and mosaic of habitats and structures, from almost vegetation-free city centers to various kinds of gardens in the suburbs and residential areas, including city parks, cemeteries, forest remnants, and fallow land with ruderal vegetation. A core question relating to urban landscapes is, therefore, to what degree urban habitats can contribute to biodiversity, because it is not just man that urbanizes but wildlife also. Birds are among the most conspicuous urbanizers and are the best studied. Birds often serve as model organisms for many studies of how wildlife copes with and adapts to urban life. Consequently, bird studies are at the forefront of research aiming to understand the role and consequences of urbanization on wildlife.

Birds have various abilities that enable them to cope with urbanization and the rural-to-urban gradient. Some avoid urban areas, others exploit the new environment, and others adapt to the urban landscape and become common in cities. Consequently, the composition of bird communities, species richness, and abundance of birds along an urbanization gradient are variable in space and time but may also have some features in common.

Numerous studies have shown the structural properties of bird communities in cities and revealed habitat–bird relationships in urban landscapes. However, it is not just the occurrence and abundance of birds in cities that is important. It is also necessary to know whether birds, and wildlife in general, in urban habitats reproduce and survive to serve and maintain viable self-sustaining populations or whether they are "sink" populations that are unable to do so and are composed mainly of immigrants from nearby rural habitats. Consequently, understanding wildlife in urban habitats and the consequences of urbanization on wildlife also requires an understanding of functional properties. Key to understanding ecological functionality are studies evaluating the demography of urban versus rural

populations and connectivity in urban landscapes, which is the degree to which a landscape and its habitats enable the movement and gene flow of organisms. Because human activities affect the behavior of animals and their ability to move freely, movement studies from rural landscapes cannot simply be translated to the urban landscape but require specific "urban" approaches.

At the same time, we need to quantify the increase in biodiversity in urbanized areas versus the loss of biodiversity as a result of urbanization. Specialized and, thus, often rare species from natural landscapes are very likely to be heavily affected by loss of natural and rural habitats, whereas generalists benefit from urban landscapes. Consequently, evaluation of the conservation value of urban habitats and urban biodiversity requires a more differentiated approach than study of species richness and biodiversity in cities.

With increasing urbanization, conservation of wildlife in urban areas also becomes a matter of interest, although it sounds contradictory, and urban biodiversity must never distract from conservation of natural habitats. However, the mosaic of habitats in urban landscapes offers new opportunities for conservation and modern urban landscape planning. Preservation of as much as possible of remnant natural habitats of appropriate area size is certainly the most effective and sustainable strategy. Restoration of habitats, re-vegetation of sites with a variety of native plants, and natural undisturbed succession sites, corridors, and under-road wildlife passages can also offer a wide array of support for wildlife in urban areas to maintain or restore functional connectivity. By doing so, urban habitats and their populations of native wildlife can supplement biodiversity conservation in the wider countryside.

Conservation activities in urban landscapes should not only be considered in the light of wildlife conservation per se. They also have a huge potential for public biodiversity education. In no other landscape are man and biosphere as tight as in cities. Attracting public attention to city-dwelling wildlife (e.g., by citizen science projects) offers great opportunities for education on the importance of conservation to society and to improve social support for conservation of wildlife and biodiversity in general.

Therefore, I very much hope that this book achieves its aims for the development of urban wildlife research and science, for effective knowledge transfer between biodiversity sciences and urban landscape planning practice, for conservation, and for the education of society.

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Preface

In the period when we were planning the scope and content of this book, two other titles on urban bird ecology were published. This entailed two consequences for our task as editors of this volume: on the one hand, it forced us to discard some of the intended chapter topics that already had been recently examined (in a very brilliant way) in those books; on the other hand, it confirmed that there were many other issues of urban bird ecology that deserved attention. Above all, far from feeling discouraged by the coincidence in time of seemingly similar projects, we were truly pleased that the interest in bird fauna in cities and of urban ecology as a whole were growing and that the pioneering books *Urban Bird Ecology* (Marzluff et al. 2001) and *Birds in European Cities* (Kelcey and Rheinwald 2005) were followed by such outstanding examples. We hope that this volume will be comparable.

The growing interest in urban ornithology mentioned above is not a fortuitous circumstance. All around the planet we are witnessing an unprecedented expansion of urban areas, not only over land already transformed for agricultural purposes but, especially in developing countries, over relatively untouched types of ecosystems. Unavoidably, this provokes changes in ecological patterns and processes that can rarely be defined as positive for biodiversity conservation at a global scale. For investigation of the consequences of urbanization, as has previously occurred in ecological research, birds may play an important role. Indeed, the considerable literature on urban bird ecology provides crucial information about how urbanization impacts many aspects of bird ecology and behavior, along with useful guidelines on how to minimize the deleterious effects of urban development. Furthermore, the literature shows how urban bird fauna (even the "dull" bird species) can contribute to increased ecological awareness in citizens that experience little daily contact with nature. Of course, this picture is not free of uncertainties (we probably know rather less about urban bird ecology than we think) and controversy, but these are powerful engines for good science.

Our own research on urban bird ecology comes from quite different experiences (acquired at, respectively, the northern and southern extremes of Europe) of bird fauna, urban development, and their interactions. We have tried to incorporate such

different perspectives in our contributions to the book as well as in the selection of chapters.

As editors, we truly enjoyed the great number of talented people who dared to join us for this exciting journey towards the making of this book. By contacting and discussing topics on urban bird ecology, we undertook a global journey that led us through urban areas in different geographical regions. It was a privilege and great fun to obtain a first glimpse of new research findings and methodology in current urban bird ecology and to see the patterns made apparent through review of published works. We can only hope that you as a reader will share this excitement and fascination for the new advances in urban bird ecology.

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Acknowledgements

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Part I
Introduction

Chapter 1
Urban Bird Research in a Global Perspective

Marcus Hedblom and Enrique Murgui

Abstract More than half of the world's human population lives in cities in which birds constitute the major, or only, contact people have with wildlife. The vast amount of predicted urbanization in the coming years will, however, consume habitats and reduce the possibilities for birds to thrive in cities and thus also reduce people's potential to detect birds. The scientific literature is presently dominated by studies from Europe and North America although the largest occurring urbanization processes occur in South East Asia and Africa. Further, these understudied continents, together with South America, harbor some of the most important areas of urban bird biodiversity and are thus of special importance to study. The last 15 years of urban bird ecology research have been exponential and now enables amalgamations and reviews of research. Here, in this volume, we try to overview these present findings in urban bird research from all continents. We illustrate this by overviewing patterns and processes, spatial and temporal scales and methodological approaches, pollution effects on birds, bird's effects on human well-being, and how urban habitats are conserved and managed for birds. The patterns of how urban birds are affected by urbanization processes are similar globally, with decreasing habitats and change of habitat qualities and pollution effects. However, increasing number of areas for urban bird conservation are being recognized and habitats managed to provide urban bird populations are increasing. In a global perspective, cities do still provide habitats to allow a diverse bird fauna.

Keywords Anthropogenic • Management • Reviewing urban bird research • Urban bird conservation • Urban bird ecology • Urban greenery

Birds have fascinated and attracted humans throughout history by their colorful appearance, flight, and song (Cocker and Tipling 2013). However, they have also

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shown to be considered disturbing because of their noise, feces, and high population densities Nevertheless, in the era of urbanization, where more than half of the world's population lives in cities (UN 2015), birds are probably the main everyday experience of wildlife for people globally (US Department of the Interior et al. 2011). Children of today will spend a major part of their lives in cities. Thus, to pick up a small bird in one's hand or to hear a bird sing on the way to work are valuable experiences and important links to nature for city dwellers. These experiences may also promote a deeper understanding of other habitats outside the urban fringes (Myer and Franz 2004; Miller 2005). City planners do not generally focus on urban nature or birds when planning, but instead concentrate on housing, roads, and industry, which continue to consume habitats. However, cities *can* be planned to permit birds to thrive and thus increase the potential for positive experiences of birds and nature. Cities harbor unique habitats that allow the presence of red-listed species, endemic species, and a large diversity of birds (Aronson et al. 2014). However, conservation of areas for birds in cities not only needs effective dialogue between nature conservationists, ornithologists, city planners, and decision makers but also requires an understanding of what makes birds flourish in cities and what makes them avoid cities or perish there. Thus, conservation of birds in cities needs knowledge of their ecology.

Urban bird ecology has transformed from a rather diffuse topic on the periphery of traditional ecology, conducted in more "natural" habitats, to an established research field in its own right. This is illustrated by the increasing number of publications and books on urban bird ecology (Dinetti and Fraissinet 2001; Marzluff et al. 2001; Kelcey and Rheinwald 2005; Lepczyk and Warren 2012; Gill and Brumm 2014; see also Fig. 1), and a large and growing number of papers (see Warren and Lepczyk 2012), reviews on the subject (e.g., Chace and Walsh
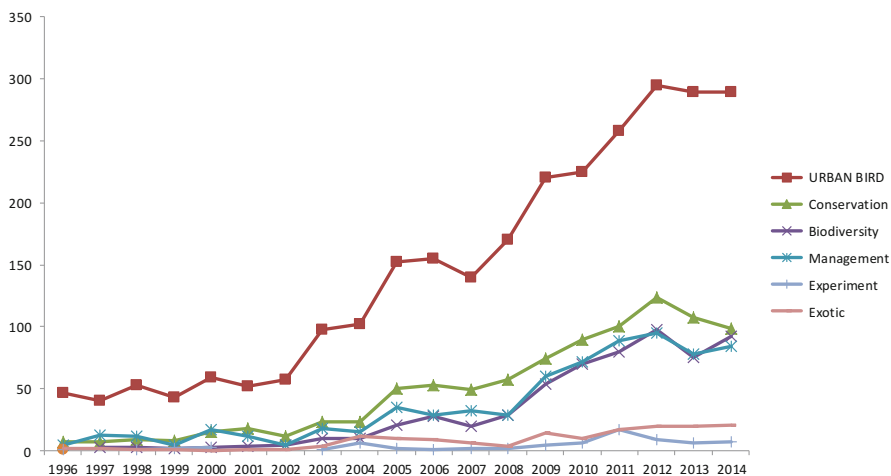
Fig. 1 Articles published in the ISI Web of Knowledge from 1996 to 2014 using the search terms "urban" and "bird" and distinguished by topic
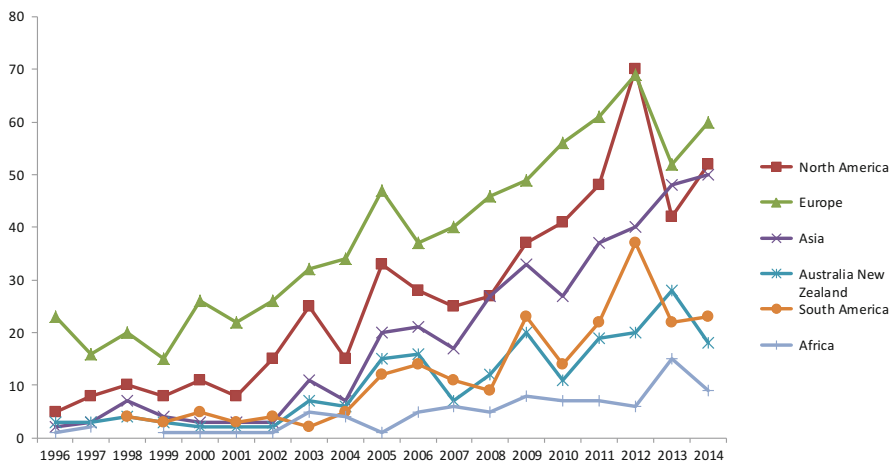
Fig. 2 Articles published in the ISI Web of Knowledge from 1996 to 2014 using the search terms "urban" and "bird" and distinguished by continent

2006), popular science books (Marzluff 2014), and books on urban birdwatching (e.g., Milne 2006; Lindo 2015).

Current literature is dominated by studies from the northern hemisphere (Europe and USA) and Australia, although some of the biggest urbanization processes are presently occurring in Southeast Asia, Africa, and South America. This is a *major* bias in the research field of urban bird ecology (Warren and Lepczyk 2012; see also Fig. 2).

It is thus important to highlight these other parts of the world and their cities because many are presently expanding in tropical areas or in areas with high endemism, which makes mapping of species and ecological knowledge for potential conservation urgent. In this volume, we approach urban ecology from a global perspective, including all continents except Antarctica.

Previous studies concerning ecological theories and patterns for cities have been rather scattered, but the current high number of publications on urban birds allows review and amalgamation of results. This volume presents numerous topics, such as species abundance in cities, adaptation, effects of temporal and spatial scales, and how birds are affected by anthropogenic factors such as different types of pollution. Because cities are diverse in size, location, and types of habitat (urban greenery and water) yet fall under the same umbrella of urbanization, these reviews can reveal potential patterns of effects on urban bird fauna globally. Present knowledge of urban birds is varied, where some nations lack basic knowledge of existing bird species abundance in their cities and others have monitored birds for years, allowing sophisticated research on the mechanisms behind, for example, urban adaptation or abundance.

Conservation in cities is challenging and maybe more so than in non-urban landscapes because the value of birds and nature in general is set against property values and an ever-increasing need for infrastructure. Seemingly, once nature is

transferred into infrastructure it is to a large extent irreversible; very few roads, houses, and squares are returned to nature-like conditions. Furthermore, many cities are located in global urban biodiversity hotspots (Cincotta et al. 2000) that, in the coming years, will have a large impact on urban surroundings (Seto et al. 2012).

Urban areas are predicted to increase threefold by 2050, reaching a global cover of 3,180,000 km^2 (Angel et al. 2012) and thus becoming landscapes themselves. Therefore, there is an urgent need to discuss how these urban conglomerations, covering large landscapes, can also promote conservation of bird species. In China alone the present number of people in cities is 758 million and will increase by an additional 292 million by the year 2050. However, the highest percentage increase in urban populations is expected in Africa, where it is predicted that the rate of increase in urban land cover will be 590 % above 2000 levels by 2030 (Seto et al. 2012).

The first section of this volume *General patterns and processes* (Chaps. 2–7) reveals global and large spatial scale patterns of abundance, evolution, and adaptation to cities by urban bird species. Lepczyk et al. (Chap. 2) show that the general portrait of urban areas as species-poor, with a dominance of omnivorous and granivorous species, does not reflect reality. By comparing cities globally they illustrate that the most common families are Accipitridae, Anatidae, and Scolopacidae. Although the diversity of birds in cities is relatively high from a global perspective (Aronson et al. 2014), 31 of the world's most invasive species are found in cities (Lepczyk et al. Chap. 2). Belloq et al. (Chap. 3) narrow the global perspective to a 1400-km gradient of South America and reveal that, although less urbanized than many other regions of the world, the urbanization process affects birds in similar patterns as elsewhere. The size of city had a threshold effect on species composition, with no effect in cities of less than 7000 inhabitants. According to Belloq et al., this contradicts previous European studies in that bird species richness declined with increasing latitude in rural areas.

China is going through the biggest urbanization process ever seen in history, according to the number of people moving from rural to urban areas. Chen and Wang review for the first time existing studies on urban birds in China (Chap. 4). They show that cities close to each other have similar bird species (indicating similar vegetation) but also that cities in different biogeographic regions have similar species, indicating a potential homogenization process. Some bird species apparently become more successful in urban areas than others. There is no single explanation for this but instead the research fields of bird adaptation (evolutionary processes) and adjustment (plasticity in existing populations) to urban areas have multiple alternative hypothesis rather than pointing in one direction. In this volume, three chapters (Chaps. 5–7) approach this issue from different angles using some common denominators. Sol et al. (Chap. 5) highlight the paradox that exotic species (non-native) have had little opportunity to adapt to the novel environment of cities but are still able to proliferate there (and even become more abundant than many native species). Sol (Chap. 5) proposes that exotic species occupy novel ecological niches that most native species are unable to use and that exotic species possess the necessary adaptations to invade these niches. Garcia et al. (Chap. 6) further argue

that possession of phenotypic plasticity or behavioral plasticity is one of the major differences between rural and urban bird species. They argue that some species can keep pace in adapting to ever-changing urban areas (e.g., as house sparrows have done) whereas other urban species cannot maintain these rapid changes and are forced to leave the urban environment. This is partly confirmed by Miranda (Chap. 7), who states that further research is needed, especially in southern regions in areas with recent urbanization. Miranda (Chap. 7) has added yet another aspect to urban adaptation by comparing plasticity and microevolutionary changes in behavior in urban species. Both Miranda (Chap. 7) and Garcia et al. (Chap. 6) suggest that genetic and environmental components should be separated to understand the role of evolutionary changes versus phenotypic plasticity in future studies.

The urbanization process affects available habitats for birds in cities globally through densification, where urban green habitats are reduced, and through fragmentation of habitats by expansion of cities into the peri-urban surroundings (often referred to as sprawl). How these processes affect birds is linked to two fundamental factors of ecology: scale and time. The section *Spatial and temporal scale and methodological approaches* (Chaps. 8–11) discusses methods used to investigate these effects.

The issue of scale is raised directly and indirectly in many of the chapters in this volume, but Litteral and Shochat (Chap. 8) specifically discuss and review landscape scale factors and their influence on the shaping of urban bird communities. The importance of long-term ecological studies is well recognized but there are few studies of urban bird ecology in general and almost none outside North America and Europe. Fidino and Magle (Chap. 9) review long-term urban bird research and show that most urban bird studies only span one or two years and that very few studies date back longer than 30 years. Fidino and Magle (Chap. 9) emphasize that that the potential for long-term studies is infinite but describe some challenges in sampling and in ensuring standard protocols. They also suggest alternative sources of data for dating back in time, such as newspaper articles and museum collections. Van Heezik and Seddon (Chap. 10) review the methodology of bird counts, which complements the findings of Fidino and Magle (Chap. 9) concerning shortcomings in methodologies. They provide a framework for estimating bird abundance in cities and discuss the strengths and weakness of different approaches relating to an urban context. Luniak (Chap. 11) reviews the ornithological atlases currently existing in Europe. The urban atlases highlighted in the chapter by Luniak could also contribute to dating back in time.

Some birds respond rapidly to changes in the physical environment by management changes in habitat, but also respond to other types of anthropogenic effects such as pollution. In the section *Anthropogenic factors* (Chaps. 12–15), the indirect and direct effects of humans on birds are reviewed and also the "opposite" effect of birds on human well-being. It is possible to use birds as indicators of a healthy human environment; therefore, investigation of their general condition, breeding success, and uptake of anthropogenic pollutants can give an indication of conditions for human well-being. Kekkonen (Chap. 12) reviews the effects of heavy metals and organic pollutants on urban bird populations. It is largely a dystopic picture,

illustrating that, despite the many restrictions already in force to discourage harmful substances, many heavy metals and persistent organic pollutants will remain in the urban environment for a very long time. These pollutants have direct physiological effects on urban birds and also indirect effects such as decreased food availability. Another pollutant, quite unique for urban habitats, is night light. Dominoni (Chap. 13) reviews this topic, revealing that light directly affects mortality by causing collisions against lit towers but also changes the daily and seasonal biology of species. Dominoni used light loggers (miniature loggers glued onto the back of blackbirds) to reveal their exposure to artificial night light in the field. He further extended this work to experiments in cages, revealing that increased exposure to night light affects reproductive physiology. Tomiałojć (Chap. 14) overviews the effects of human intervention on urban bird species in cases where exotic birds escaped from captivity and later became part of the urban bird fauna. He reveals a long history of human interference with tame and wild birds in Europe. Hedblom et al. (Chap. 15) review the new and highly transdisciplinary field of cultural ecosystem services, which concerns the cultural value that birds provide humans through positive experiences by increasing well-being and potentially reducing stress for urban residents.

Humans affect the existing habitats of birds by transforming the landscape through infrastructure but also by replacing natural habitats with other more human-related, non-indigenous habitats. The section *Urban bird habitats: conservation and management* (Chaps. 16–23) reviews different urban habitats and their prerequisites and discusses their influence on bird abundance, conservation, and management. Symes et al. (Chap. 16) investigate a region in South Africa where urbanization changed the prerequisites of bird fauna dramatically from a savanna–grassland ecosystem to a woody habitat through bush encroachment and planting of exotic and native trees. These changes transformed the previous original grassland bird fauna to a more exotic and wood-dependent fauna. In Australia, similar to South Africa, the landscape has been transformed from native trees that let through half of the incident light into dense crowned European forests, which changed the prerequisites for native urban bird fauna (Daniels and Kirkpatrick; Chap. 17). Daniels and Kirkpatrick reveal that it is the beta diversity in exurban habitats that provides opportunities both for native and exotic species. In both South Africa and Australia these major changes occurred over less than 200 years. Goddard et al. (Chap. 18) deepen our knowledge of residential gardens, which are a rather unstudied urban habitat although covering substantially large areas of cities. They emphasize that this habitat offers considerable opportunities for bird conservation and that, in contrast to urban planning that is often top-down, private urban gardens can be managed through personal initiative and designed to enhance bird populations. Meffert (Chap. 19) describes the state of knowledge of birds in the rarely examined and unique habitat of wastelands. This habitat, which only exists in cities, has important value for endangered species.

Gleditsch (Chap. 20) illustrates the positive and negative, indirect and direct effects of exotic plants on urban birds. Furthermore, Sorace and Gustin (Chap. 21) compare parks with surrounding urban areas as habitats for species requiring

conservation, revealing potential homogenization effects. Herrando' et al. (Chap. 22) take a step further towards provision of an indicator for monitoring programs by relating urban green infrastructure to current data on bird abundance. The indicator is based on species response to green infrastructure at the population level. Through this indicator it is possible to track temporal changes in bird populations linked to an increase or decrease in urban green areas. Despite increasing attention to practical suggestions for conservation (often at the end of papers summarizing the need for change), few examples of true implementation are found. Heyman et al. (Chap. 23) put theory into practice with their large-scale experiment on managing urban woodlands to both optimize urban bird species richness and create woodlands that are recreational friendly for humans. They also review how management affects urban bird populations.

To summarize, this volume opens up questions concerning urban ecology and conservation. In the final chapter, we try to reveal some of the shortcomings of current research and implementation and indicate future needs (Chap. 24; Murgui and Hedblom).

The conclusion, in short, is that the effects of urbanization on urban birds are similar worldwide, where existing habitats are reduced in size (or totally removed), natural habitats are turned into more human-influenced habitats such as parks and lawns, green areas are managed to suit human purposes such as leisure and safety, and different pollutants are constantly added. Despite this seemingly large number of negative influences on urban birds, cities globally still *do* provide habitats that allow a diverse and flourishing bird fauna (Aronson et al. 2014), although it is necessary to take action to enable birds to thrive in cities. Hopefully, increased global awareness of the present situation of urban birds illustrated by this volume will add to overall knowledge and have an effect on future decisions in city planning. We believe that providing urban bird habitats in cities, such as urban greenery and open waters, not only creates healthy and diverse bird populations but also provides cities that are attractive and healthy for humans.

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Part II
General Patterns and Processes

Chapter 2
Global Patterns and Drivers of Urban Bird Diversity

Christopher A. Lepczyk, Frank A. La Sorte, Myla F.J. Aronson, Mark A. Goddard, Ian MacGregor-Fors, Charles H. Nilon, and Paige S. Warren

Abstract The rapid urbanization of the world has profound effects on global biodiversity, and urbanization has been counted among the processes contributing to the homogenization of the world's biota. However, there are few generalities of the patterns and drivers of urban birds and even fewer global comparative studies. Comparable methodologies and datasets are needed to understand, preserve, and monitor biodiversity in cities. We explore the current state of the science in terms of basic patterns of urban birds in the world's cities and lay out a research agenda to improve basic understanding of patterns and processes and to better inform conservation efforts. Urban avifaunas are often portrayed as being species poor and dominated by omnivorous and granivorous species that tend to be nonnative. Common families in cities include Accipitridae, Anatidae, and Scolopacidae, all

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of which have more species than expected in cities compared to the global distribution of species in these families. Recent research shows that cities support an avifauna dominated by native species and that cities are not homogenized at the global level. However, cities have lost substantial biodiversity compared to predicted peri-urban diversity, and 31 of the world's most invasive bird species are found in cities. Future research is needed to better characterize the anthropogenic, environmental, and ecological drivers of birds in cities. Such mechanistic understanding is the underpinning of effective conservation strategies in a human dominated world.

Keywords Homogenization • Invasive species • Land cover • Species traits

2.1   Introduction

The world of the twenty-first century is an urban one, with the majority of people now settled in some type of city, town, or other urban areas. At present 0.5–3.0 % of the globe's terrestrial land surface is in some form of urban land cover (see Liu et al. 2014 for discussion), and urban land cover is expected to continue growing concomitant with the human population over the twenty-first century (Seto et al. 2012). The rise in urban areas ultimately translates to habitat alteration, fragmentation, and loss for many species of flora and fauna. Because of urbanization's effects on habitat and species, it is often assumed that such wholesale transformation of the land has resulted only in ecological outcomes that might be considered detrimental, such as homogenization of species among cities (McKinney 2006). However, comparable data on species are needed across the urban areas of the world in order to assess what processes are leading to the patterns we observe and if there are commonalities among them.

Birds offer an ideal taxonomic group from which to understand the effects of urbanization on species using comparative approaches as more than 2,000 species (of the approximately 10,000 described species of birds globally) occur in urban areas (Aronson et al. 2014). Beyond the sheer number of species observed in urban areas, birds are well studied, easily observable, and important for the ecosystem services they provide. Additionally, birds can act as indicator species of habitats that support numerous other taxa. Hence, using birds as model taxa, we consider both what is currently understood about birds in cities and what are the next steps needed for both research and conservation.

Urban areas worldwide contain similar physical features and environmental conditions, and urban areas act as a focal point for the introduction of nonnative species and the extinction of native species (Sol et al. 2016; Tomiałojć 2016). As such, urban areas offer a unique opportunity to investigate the ecological consequences, as they develop globally, of intensive land-use change and human-mediated biotic interchange. Birds have played an important role advancing this global perspective, primarily through the prevalence of data on urban bird

communities. Avian communities in North America and European cities are currently the best sampled and studied. However, efforts are increasingly being directed to developing data resources for cities outside these regions.

2.2 The Types of Birds Found in Cities

Geographically, cities form complex systems that differ markedly from those systems present before the urbanizing process began (Berkowitz et al. 2003; McKinney 2006). Such changes can present an ecological barrier for some animal species who are unable to traverse an urban area or utilize it, whereas other species are able to use some urban resources, and a few are highly successful at exploiting urban resources and conditions (Croci et al. 2008; MacGregor-Fors et al. 2010; Puga-Caballero et al. 2014). Because animals respond differentially to urbanization, they are often classified into the following categories: (1) *urban avoiders*, which are species that are generally absent in highly developed areas, but can be present in natural areas embedded in urban area; (2) *urban utilizers*, which are species that use urban resources and conditions but whose populations require immigration from natural areas; and (3) *urban dwellers*, which are species that reproduce and persist in urban areas (Fischer et al. 2015).

The presence and distribution of bird species inside a city depend, among other factors, on the biogeographic species pools, the natural history of species, and the nature and distribution of habitat-related traits (Lepczyk et al. 2008; MacGregor-Fors and Scondube 2011; McCaffrey et al. 2012). In general, omnivorous, granivorous, and cavity-nesting species have shown the strongest associations with urban areas in temperate areas (Chace and Walsh 2006). However, insectivorous, frugivorous, and nectarivorous species are also predominant in some tropical and subtropical urban areas (Brazil and Mexico, Singapore, Australia, respectively; Ortega-Álvarez and MacGregor-Fors 2011a, b). Regarding the traits related to birds able to use the unique array of resources and survive the hazards of urbanization (Emlen 1974), sociability, sedentary, broad diet, longevity, and widespread distribution head the list (Croci et al. 2008; Kark et al. 2007).

Based on a global study of 54 cities, the most common species in cities globally included *Columba livia*, *Passer domesticus*, *Sturnus vulgaris*, and *Hirundo rustica* (Aronson et al. 2014). Across these same cities, the most common bird family was Accipitridae (Table 2.1), not Columbidae, the family containing the ubiquitous rock pigeon (*Columba livia*). In comparing the representation of species within families, we continued our analysis from Aronson et al. (2014) and found that Psittacidae were underrepresented in cities, whereas the families Accipitridae, Anatidae, and Scolopacidae were overrepresented (permutations tests; 9999 samples with replacement; $P < 0.001$). Further, cities harbored the majority of species-level diversity of Anatidae and Scolopacidae (48 % and 59 %, respectively).

Table 2.1 Top ten most common bird families found in the 54 cities of Aronson et al. (2014)

	54 cities		Worldwide		
Family	Number	Proportion	Number	Proportion	% of total
Accipitridae	99	0.049[a]	283	0.025	35.0
Anatidae	87	0.043[a]	183	0.016	47.5
Emberizidae	76	0.037	347	0.031	21.9
Sylviidae	75	0.037	342	0.031	22.0
Tyrannidae	71	0.035	442	0.040	16.1
Muscicapidae	65	0.032	326	0.029	20.0
Scolopacidae	57	0.028[a]	96	0.009	59.4
Columbidae	52	0.025	336	0.030	15.2
Picidae	51	0.025	220	0.021	22.2
Psittacidae	49	0.024[b]	406	0.036	12.1

[a]Bird families with a significantly greater number of species ($P < 0.05$) than expected by chance alone based on the distribution of species within all bird families worldwide
[b]Bird families with a significantly fewer number of species ($P < 0.05$) than expected by chance alone based on the distribution of species within all bird families worldwide

Cities also support threatened and endangered species. Specifically, 14 % of the 54 cities studied housed threatened and endangered species (Aronson et al. 2014). On the other hand, cities are also focal points of species introductions. Of the world's 31 most invasive bird species, 97 % ($n = 30$) were found in cities (Table 2.2). Australasian cities harbor the greatest number of invasive bird species ($n = 176$), followed by cities in the Palearctic ($n = 157$), Nearctic ($n = 127$), Indo-Malay ($n = 108$), and Afrotropic ($n = 65$).

2.3 Patterns and Drivers of Urban Birds

2.3.1 Global and Regional Drivers

Current research has found that urbanization has had a profound effect on the structure of native bird communities at the global scale. In a recent evaluation of 54 cities from around the world (Fig. 2.1), Aronson et al. (2014) found that they housed ~20 % of the world's bird species. Though important, these estimates are clearly not comprehensive for global urban biodiversity as our species accumulation curves that extend Aronson et al.'s (2014) results failed to reach an asymptote (Fig. 2.2), showing that the contribution of cities to global biodiversity is even higher than suggested. In fact we lack knowledge of urban birds from many cities around the world, particularly those in tropical regions and the Southern Hemisphere (but see Bellocq et al. 2016; Chen and Wang 2016).

Across the 54 cities, Aronson et al. (2014) compared different models to explain bird species density in terms of both anthropogenic and non-anthropogenic factors using robust linear regression and an information-theoretic approach with nested

Table 2.2 Prevalence of invasive bird species found in 54 cities

Species	# Cities
Acridotheres fuscus	1
Acridotheres tristis	9
Alectoris chukar	1
Anas platyrhynchos	35
Anser anser	14
Branta canadensis	16
Bubo virginianus	2
Bubulcus ibis	14
Carpodacus mexicanus	10
Circus approximans	3
Columba livia	51
Corvus splendens	3
Cygnus olor	20
Estrilda astrild	5
Gallus gallus	1
Gymnorhina tibicen	4
Leiothrix lutea	1
Molothrus ater	9
Molothrus bonariensis	2
Myiopsitta monachus	3
Oxyura jamaicensis	2
Passer domesticus	48
Pitangus sulphuratus	3
Porphyrio porphyrio	5
Psittacula krameri	16
Pycnonotus cafer	2
Pycnonotus jocosus	4
Streptopelia decaocto	30
Sturnus vulgaris	44
Zosterops japonicus	2

Invasive birds were defined by the IUCN Global Invasive Species Database (http://www.issg.org/database). Across the 54 cities examined 30 of the 31 species were found, with only *Gallus varius* was not found

models (Burnham and Anderson 2002). Following the approach used in Aronson et al. (2014), we found that bird species richness was better predicted by anthropogenic than non-anthropogenic factors (Table 2.3). Human population size and land-cover class had the strongest correspondence with the number of bird species. The age of the cities played a tertiary role suggesting human history has a much more limited role relative to the physical features of the city.

Land cover was expected to be an important predictor of species richness as it defines the quantity and quality of suitable habitats within the city. For the two land cover classes we considered in the current analysis, the number of bird species was
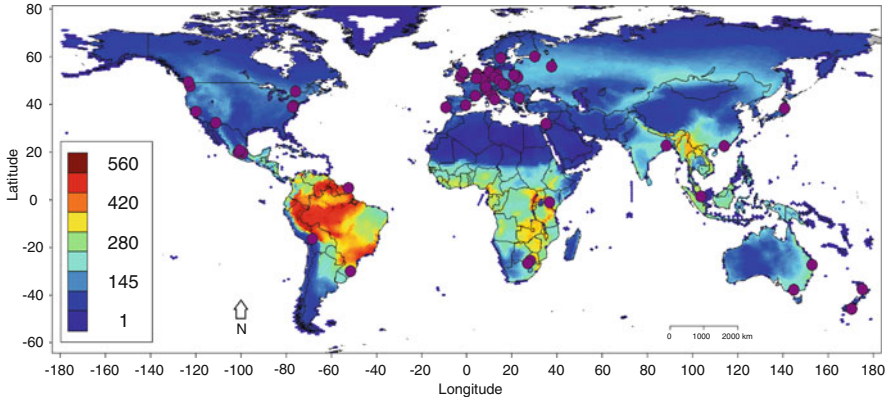
Fig. 2.1 Breeding season species richness for the world's terrestrial birds (10,081 species) summarized within equal-area hexagons (12,452 km²) of a global icosahedron. The *purple dots* are the locations of 54 cities from Aronson et al. (2014) with richness ranging from 1 (*blue*) to 560 (*dark red*) species per hexagon
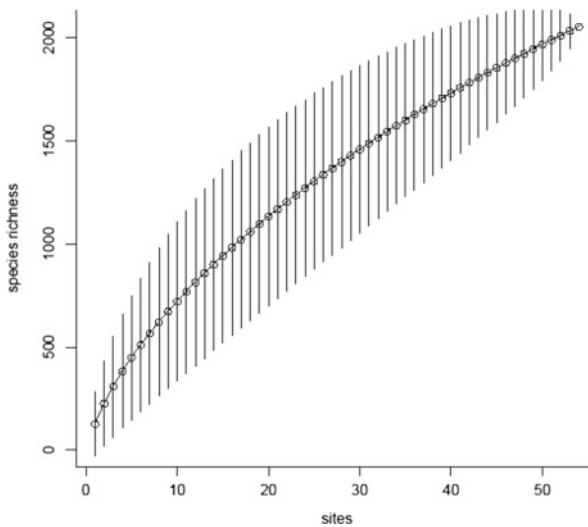
Fig. 2.2 Species accumulation curve based upon the number birds documented from the 54 cities of Aronson et al. (2014). The *vertical lines* are ±2SD where SD were estimated from 100 random permutations of the data

associated with urban land cover and negatively associated with intact vegetation (Table 2.4). These findings may be explained by a variety of factors. First, increasing habitat heterogeneity with urbanization (Desrochers et al. 2011) which leads to higher species richness. Second, the inability of land-cover data to capture small patches of remnant vegetation (300 m resolution). Third, the species-area

Table 2.3 Robust regression models contrasting anthropogenic and non-anthropogenic correlates of bird species richness in cities worldwide

Model	Bird richness		
	AIC_c	$\Delta_i AIC_c$ [a]	w_i [b]
Full	132.0	40.3	0.00
Anthropogenic	91.7	0.0	0.74
Population size	94.1	2.4	0.22
City age	104.1	12.4	0.00
Land cover	97.9	6.2	0.03
Non-anthropogenic	160.7	69.0	0.00
Geography	110.8	19.1	0.00
Climate	112.7	21.0	0.00
Topography	102.7	10.9	0.00

[a]Change in model AIC_c ($\Delta_i AIC_c$) represent the difference between model i and the model with the lowest AIC_c score
[b]AIC_c weight (w_i) is the level of evidence for model i based on the entire set of models

Table 2.4 Robust regression coefficients for 12 predictors of bird species richness and proportion of nonnative plants. The predictors are contained within three anthropogenic and three non-anthropogenic models

Model	Predictors	Bird richness	
		Coefficient	F
Anthropogenic			
Population size	Population size	0.243	20.05[****]
Land cover	Urban extent	1.153	10.58[***]
	% intact vegetation	−0.912	9.22[***]
City age	Establishment date	0.170	5.28[**]
Non-anthropogenic			
Geography	Realm	0.207	1.74
	Latitude	−0.304	7.82[***]
Climate	Temperature	0.032	3.86*
	Temperature seasonality[a]	−0.002	0.17
	Precipitation	0.000	0.04
	Precipitation seasonality[a]	0.003	0.73
Topography	Elevation	0.016	0.12
	Elevation variation	−0.124	2.60

Significant differences for robust F-tests are indicated: *$P < 0.1$, **$P < 0.05$, ***$P < 0.01$, and ****$P < 0.001$
[a]Temperature seasonality is the standard deviation of annual temperature *100 from BIOCLIM, and elevation variation is the standard deviation of elevation within a 15 km radius of the city center, a metric of topographic heterogeneity

relationship (Pautasso et al. 2011). Urban land cover and human population size were positively correlated (Pearson $r = 0.58$, $t = 8.68$, $P < 0.001$), whereas intact vegetation and human population size were negatively correlated (Pearson

$r = -0.27$, $t = -3.38$, $P < 0.001$). Cities with larger human populations were also the largest cities in area (Pearson $r = 0.74$, $t = 13.11$, $P < 0.001$).

The transition from native to urban environments resulted in dramatic losses in the density of species found in cities compared to nonurban areas (Aronson et al. 2014). Unlike urban plant communities, the loss for urban bird communities is not compensated through the introduction of nonnative species. Avian assemblages in the 54 cities contained a median of only 3 % nonnative species, which is in strong contrast to the 28 % displayed by urban plant assemblages (Aronson et al. 2014). When considering potential explanations for the current density of native breeding bird species within cities worldwide, anthropogenic features such as land cover and city age were found to be better predictors than the geographical, climatic, and topographic factors typically identified as important predictors of global patterns of diversity (Aronson et al. 2014). These findings suggest anthropogenic drivers take precedence in defining patterns of urban diversity worldwide. When these findings are considered in combination with those from other global urban bird studies, clear management, planning, and conservation recommendations emerge. For example, there is evidence that remnant patches of intact vegetation within urban areas retain macroecological patterns similar to those found in patches of intact vegetation outside urban areas (Pautasso et al. 2011), and large and interconnected patches of intact vegetation are important in maintaining levels of urban bird diversity (Beninde et al. 2015). Thus, the remnant native bird assemblages that occur in urban areas worldwide can be maintained through the development and preservation of interconnected patches of intact vegetation within cities (Daniels and Kirkpatrick 2016).

When examining patterns of urban biodiversity, occurrence information is often more prevalent than abundance information. This deficiency has the potential to obscure the full ecological implications of urbanization. Using North American urban areas as a test case, we present a preliminary analysis exploring the basic associations between patterns of occurrence and patterns of abundance within urban areas. Based on the positive correlation that has often been identified between occurrence and abundance (Gaston et al. 2000), we would expect the most broadly distributed species in North America to also occur with the highest abundance. Moreover, we would expect these patterns to be the most pronounced for broadly distributed nonnative human commensal species, such as the house sparrow (*Passer domesticus*), house finch (*Haemorhous mexicanus*), and European starling (*Sturnus vulgaris*).

Using eBird checklists compiled within North America between 24° and 50° N latitude during the breeding season (June–July) for the years 2002 to 2014 combined, we examined patterns of occurrence and abundance for the ten most commonly occurring urban bird species in two land-cover categories: urban and intact vegetation. Following the methods described in La Sorte et al. (2014), we classified land cover for each eBird checklist using the second edition of the North American Land Cover (NALC) map for 2005 produced by the North American Land Change Monitoring System (NALCMS).

Table 2.5 The ten most commonly occurring bird species in urban areas in North America and the percent of eBird checklists the species was observed in two land-cover categories: urban and intact vegetation

Common	Scientific	Urban	Intact vegetation
American robin	*Turdus migratorius*	48 (5.6)	38 (4.2)
Mourning dove	*Zenaida macroura*	47 (4.0)	31 (3.7)
Northern cardinal	*Cardinalis cardinalis*	44 (3.2)	25 (3.3)
House sparrow*	*Passer domesticus*	39 (8.2)	9 (5.7)
House finch*	*Haemorhous mexicanus*	37 (6.1)	16 (5.6)
American goldfinch	*Spinus tristis*	32 (3.7)	24 (4.0)
Blue jay	*Cyanocitta cristata*	32 (2.6)	22 (2.6)
European Starling*	*Sturnus vulgaris*	31 (11.8)	11 (10.0)
Common grackle	*Quiscalus quiscula*	30 (6.5)	13 (5.9)
Song sparrow	*Melospiza melodia*	30 (3.4)	25 (3.4)

Average abundance is shown in parentheses. Asterisks identify species that are nonnative human commensal

The ten most common urban bird species were widespread North American bird species that occurred in lower proportions in areas of intact vegetation (Table 2.5). Among these ten species were three nonnative human commensals, which were two to three times more prevalent in urban areas (Table 2.5). These three species also tended to be more abundant on average in urban areas (Table 2.5). Our findings suggest urban areas host a greater proportion of commonly occurring North American bird species, and patterns of abundance for these species are skewed toward those having the strongest affinities to human activities and human manufactured environments.

2.3.2 Seasonal Drivers

The primary research focus when considering urban bird diversity has been to examine the structure and composition of breeding bird communities during the breeding season. The breeding season is a critical phase of the annual cycle, and breeding communities are typically the easiest to survey. However, in temperate regions of the Northern Hemisphere, the breeding season lasts only a month or two of the year, and a large proportion of the breeding communities are composed of migratory species (Somveille et al. 2013). How urban bird diversity is defined during other phases of the annual cycle is less common (e.g., Murgui 2010). In particular winter urban bird diversity studies occur less frequently (Jokimäki and Kaisanlahti-Jokimäki 2012; Tryjanowski et al. 2015), and during migration urban bird diversity has rarely been considered.

When species richness and within-year temporal turnover in species composition have been examined across an urban land-use gradient in North America during the full annual cycle (La Sorte et al. 2014), species richness was found to

peak across all components of the land-use gradient during spring and autumn migration. However, urban areas tended to have the lowest species richness on average, and urban areas tended to have the lowest within-year temporal turnover in species composition, suggesting that bird diversity within urban areas has been degraded and simplified across all phases of the annual cycle. Another finding to emerge from this work is that these patterns varied geographically, reflecting the influence of different land-cover characteristics and land-use change histories.

However, urban areas do retain a surprisingly high level of relevance for bird communities during migration events. This outcome may simply be due to the high prevalence of urban landscapes within existing migration flyways. Nevertheless, activities directed toward improving the quantity and quality of stopover habitat within urban areas may provide critical support to migratory bird populations during the most vulnerable period of their life cycle.

2.3.3   Local Scale Drivers

Despite the significant contribution of global and regional scale factors, the ability of a bird species to maintain a viable population within a city is ultimately driven by the availability of habitat at the local scale (Evans et al. 2009). As predicted by the species-area relationship, urban bird species richness is strongly correlated with area, both at the scale of the entire city (MacGregor-Fors et al. 2011; Ferenc et al. 2014a) and within individual urban habitat patches (Fernandez-Juricic and Jokimaki 2001; Mörtberg 2001; Chamberlain et al. 2007; Murgui 2007; van Heezik et al. 2013). Within cities, bird species density was highest in cities with the lowest proportion of urban land cover (Aronson et al. 2014), indicating that the provision of green space at the city scale is crucial to bird species conservation in cities (Chace and Walsh 2006; Evans et al. 2009). Similar to whole city studies, urban-rural gradient research has shown that increased urbanization leads to decreased species richness (Lepczyk et al. 2008) but an increase in total avian biomass due to the dominance of a few urban dwelling species (Clergeau et al. 2006; Garaffa et al. 2009).

Within cities a number of factors have been suggested that determine their suitability for birds. These factors include (1) the presence and size of remnant (native) vegetation patches, (2) the presence of nonnative predators, (3) the structure and floristic attributes of planted vegetation, and (4) supplementary feeding by humans (Chace and Walsh 2006). A useful framework for understanding the underlying drivers of these factors is considering urban biodiversity as controlled by either city-level top-down or household-level bottom-up processes (Kinzig et al. 2005). For instance, the extent of green space in cities is largely driven by top-down processes such as government policy (Dallimer et al. 2011), and a challenge to policymakers and conservationists is that the response of urban bird species to the provision of green space can be time-lagged such that contemporary species richness is best explained by historical land cover (Dallimer et al. 2015). In

addition to the extent of urban habitat, birds also respond to the connectivity and configuration of urban green space(e.g., Fernandez-Juricic 2000; Pellissier et al. 2012) suggesting an important role for urban planners in the design of green infrastructure strategies.

Bottom-up processes that reflect the collective decisions of individual households and communities can lead to both positive and negative outcomes for birds. For example, the decision to keep an outdoor domestic cat can have major negative implications for urban bird communities (Lepczyk et al. 2004b; Sims et al. 2008; van Heezik et al. 2010; Bonnington et al. 2013; Belaire et al. 2014). On the other hand, vegetation composition and structure can positively influence bird diversity in a wide variety of urban habitats, including parks and public gardens (Shwartz et al. 2008; Paker et al. 2014), domestic gardens (Daniels and Kirkpatrick 2006; Belaire et al. 2014), remnant native vegetation (Palmer et al. 2008; Davis et al. 2013), and business parks (Hogg and Nilon 2015). Notably, there is evidence that native vegetation is important for supporting native avifauna (Daniels and Kirkpatrick 2006; Burghardt et al. 2009; Lerman and Warren 2011). Although planting and landscaping in public parks are largely the product of top-down decisions (Kinzig et al. 2005), the ability for householders to buy and maintain vegetation is driven by socioeconomic and personal choices (e.g., Hope et al. 2003; Lepczyk et al. 2004a; Martin et al. 2004; Lubbe et al. 2010). In fact, a positive relationship between householder neighborhood socioeconomic status and bird diversity has been widely documented (Kinzig et al. 2005; Melles 2005; Strohbach et al. 2009; Lerman and Warren 2011; Luck et al. 2013). Besides planting and landscaping decisions, people also directly influence the provision of food for birds in cities through supplementary feeding, and this has been shown to effect bird populations at multiple spatial scales (Robb et al. 2008; Fuller et al. 2008, 2012). In the USA and UK, the decision to feed birds is driven by a complex range of socioeconomic and demographic factors (Lepczyk et al. 2012; Goddard et al. 2013).

2.4 Next Steps in Urban Bird Ecology

2.4.1 Questions in Basic Ecology

Although our understanding about the urban ecology of birds has advanced markedly in recent years, there remain several key areas in need of further research, including demography, disease, behavior, and species interactions. We highlight demography and disease ecology as being among the two areas most critically in need of investigation. However, behavioral studies are proliferating rapidly, revealing the simultaneous capacity of birds to adapt to the novel conditions found in cities (reviews in Gil and Brumm 2014) as well as the impacts of behavioral constraints in limiting species distributions. Unresolved debates over the role of species interactions in structuring urban bird communities illustrate the need for

additional mechanistic studies of predation (Rodewald and Kearns 2011; Stracey 2011; Fischer et al. 2012) and competition (Rodewald and Shustack 2008; Shochat et al. 2010; Farwell and Marzluff 2013).

Demographic studies are urgently needed to complement the many occupancy and abundance studies of birds in urban areas. Without demographic data and analyses, it is impossible to determine the likelihood of persistence for species present in urban areas. One meta-analysis found reduction in clutch sizes, nestling weight, and productivity per nesting attempt in urban relative to paired nonurban bird populations (Chamberlain et al. 2009). These differences might be counterbalanced, however, by earlier and/or longer breeding seasons and increased numbers of nesting attempts (Reale and Blair 2005; Deviche and Davies 2014). As a result, the net effect of urbanization on population trends is unclear for most species. Furthermore, some urban land-use types support higher levels of reproductive success than others (e.g., Marzluff et al. 2007; Stracey 2011). Thus, studies are needed that address heterogeneities in avian productivity within urban areas.

Diseases can fundamentally alter urban bird communities, as exemplified by the high-profile West Nile virus which has the potential to dramatically impact avian populations (Kilpatrick et al. 2007). There are many other less well-known pathogens affecting urban birds (Robinson et al. 2010; Martin and Boruta 2014), such as intestinal coccidians (Giraudeau et al. 2014), which may be implicated in reductions in plumage coloration with urbanization (Giraudeau et al. 2015). Within cities, lower income areas may receive the brunt of disease outbreaks when economic declines and disinvestment are associated with habitat for pathogen hosts (e.g., Davis 1953; Harrigan et al. 2010). In addition, supplementary feeding has been cited as a potential factor in outbreaks of a wide variety of avian diseases (Martin and Boruta 2014). But insufficient information exists as yet to predict how feeders affect rates of infection and disease outbreaks. Interestingly, though, a variety of studies have found that urbanization may actually *reduce* the spread or impact of disease, while in other cases, it appears to exacerbate rates of infection (Bradley and Altizer 2007; Martin and Boruta 2014). Such differences in relationships suggest that the kind of host and mode of transmission may be important in determining how urbanization affects the prevalence of avian diseases. Finally, there are important potential feedbacks between avian health and human health related to disease that need further exploration (Strohbach et al. 2014).

2.4.2   Managing for Birds in Cities

Research conducted at multiple scales has important repercussions for managing birds in cities. Global-scale data are important because they allow us to understand how large-scale factors affect bird distributions and how cities differ or are similar in how they support bird diversity. Furthermore, global data analyses allow for generalizations on landscape-scale characteristics that are important for birds. On

the other hand, local-scale data allows us to understand what factors are important for particular species or populations of particular species.

At the local scale, urban bird species appear more sensitive to local habitat features than landscape factors (Evans et al. 2009), providing considerable opportunities for enhancing avian diversity through management. Management recommendations based on associations between vegetation variables and bird species richness and diversity in urban green spaces have often been made at the city scale (e.g., Palmer et al. 2008; Belaire et al. 2014; Ferenc et al. 2014b), but to make robust generalizations requires standardized data on bird-habitat associations from multiple cities (Fontana et al. 2011; Lerman et al. 2014). Furthermore, such data are needed from cities occurring in areas of high regional biodiversity, such as tropical cities and cities within biodiversity hotspots (Aronson et al. 2014), as urbanization is occurring at a rapid pace (Fragkias et al. 2013).

Even with additional data, management recommendations may not be universally applicable. For example, supplementary feeding has been shown to have positive effects in the UK (Fuller et al. 2008, 2012), but detrimental effects in Australia where bird feeding is discouraged (Jones and Reynolds 2008). Other management recommendations, such as increasing the amount of dead wood (Sandstrom et al. 2006), the addition of standing water (Ferenc et al. 2014a), and reduced management of urban parks (Shwartz et al. 2008), will require reconciling human safety and public perception with the needs of the urban avifauna. Furthermore, work from Australia, the USA, and Israel suggests that the presence of native vegetation in urban yards benefits the bird community (Daniels and Kirkpatrick 2006; Burghardt et al. 2009; Lerman and Warren 2011; Paker et al. 2014), but there are no corroborating results from Europe to date. With the exception of Burghardt et al. (2009), who were careful to select pairs of yards that differed only in the proportion of shrub and groundcover that consisted of native plants, no studies have been designed to explicitly test for the effect of native versus nonnative vegetation on bird diversity. Likewise, many of the other management recommendations would benefit from experimental manipulations to deepen our understanding of the mechanisms that structure urban bird communities (Shochat et al. 2006). For example, Lerman et al. (2012b) used artificial food patches to examine differences in foraging behavior between mesic (lush, exotic vegetation) and xeric (drought-tolerant, native vegetation) yards in Phoenix, USA, and showed that xeric yards constituted a superior avian habitat. Larger-scale experiments across multiple cities are emerging for other taxa such as pollinators (e.g., the UK Urban Pollinators Project: http://www.bristol.ac.uk/biology/research/ecological/community/pollinators/background/question3/), but comparable avian studies are lacking.

Effective management of urban ecosystems requires coordination across multiple spatial scales and across multiple stakeholders (Goddard et al. 2010; Gaston et al. 2013). Most bird species cannot maintain a viable population within a single habitat patch, but instead utilize urban green spaces at relatively broad spatial scales (Hostetler and Holling 2000) and will therefore respond to habitat heterogeneity at the landscape scale (Litteral and Shochat 2016). How best to manage a network of green spaces (the vast majority of which are owned and managed by many different

stakeholders) to maximize bird diversity within a given city remains a key challenge. One possibility is the creation of a mosaic of habitat zones across a city, wherein private gardens and other urban green spaces are managed under a common theme (Goddard et al. 2010). Such an approach would be most effective if implemented as new housing schemes are planned and designed, perhaps as part of conservation development (Reed et al. 2014) and could also include a mechanistic component by embedding a designed experiment within the new development (Felson and Pickett 2005). In addition to working with city planners and housing developers, ecologists also need to engage with social institutions operating at relevant scales for coordinated biodiversity management. For instance, Lerman et al. (2012a) show that neighborhoods belonging to a homeowner association had significantly greater bird diversity than other neighborhoods, which could potentially be explained by the presence of top-down sanctions enforcing certain landscaping designs.

Managing for birds could also spread through bottom-up processes, such as neighbor mimicry (Warren et al. 2008; Goddard et al. 2013). Such social processes could be facilitated by citizen science programs that provide residents with positive feedback about management activities that benefit birds (Cooper et al. 2007; van Heezik et al. 2012). Likewise, educational outreach programs could also target urban planners and policymakers (Hostetler 2012). However, it remains the case that more sociological-based studies are required to understand how best to incentivize householders and other urban land managers into a bird-friendly management. These studies should address further how urban habitat management attitudes and behavior vary with culture, socioeconomic, and demographic factors (Kirkpatrick et al. 2012; Lepczyk et al. 2012). Subsequent recommendations will be most effective when they are specifically geared to different stakeholders (Snep et al. 2015).

2.4.3   Cities and Climate Change

Though climate change has been a central topic of concern in ecology and conservation biology, our understanding of how it may affect birds in cities remains elementary. Bird diversity does relate directly to how variable the energy from year to year is at given location on earth (Rowhani et al. 2008), and urban areas in the USA show much less interannual variability than rural areas (Linderman and Lepczyk 2013). Such findings suggest that cities may represent relatively more stable systems than those surrounding the city and could thereby provide some refuge for urban birds. However, climate change is altering both temperature and precipitation patterns, both of which have well-established relationships with survival and reproduction in birds as measured in local weather patterns (Chase et al. 2005; Preston and Rotenberry 2006; Wright et al. 2009; Skagen and Adams 2012). Thus, understanding how changes in local-scale weather will influence urban birds is needed.

Climate change has already been related to changes in bird phenology (Root et al. 2003) and changes in bird diversity in cities (La Sorte and Thompson 2007). Furthermore, because species respond differentially to climate change (Wiens et al. 2009), how geographic ranges will change in relation to one another, particularly in relation to urban areas, remains to be seen. As many cities are now working on developing climate change adaptation plans, it will be important to link such plans with how they affect both bird habitat and the birds themselves.

2.4.4 Monitoring

In order to have full understanding of species and their populations over space and time requires sound monitoring (for the necessity of a temporal perspective in bird urban ecology see Fidino and Mason 2016). Though several well-established monitoring programs (e.g., the North American Breeding Bird Survey, Audubon's Christmas Bird Count) and international surveys (e.g., BirdLife International Global Survey on the Status of Urban Bird Conservation) have proved key in our understanding of avian ecology (e.g. Fergus et al. 2013; La Sorte and Thompson 2007; Lepczyk et al. 2008; Pidgeon et al. 2014), we lack in having monitoring programs that are unified in methodology across cities of the world. Furthermore, we simply lack monitoring of any type for many locations previously highlighted, making not only comparative questions challenging, but resulting in a lack of knowledge about the fates of many species. What would be beneficial is a global monitoring program, perhaps akin to eBird, that could account for habitat/environmental conditions and would be feasible to use in the tropics and Southern Hemisphere, where we lack knowledge on urban systems.

2.5 Conclusions

The resurgence of urban ecology in the past several decades has greatly advanced our knowledge of urban avian ecology from local to global scales. However, as urbanization continues, the human population grows, and climate changes, we have many remaining challenges in understanding relationships between birds and cities. In order to effectively preserve bird diversity in cities, the following research and management efforts are needed. First, we lack monitoring programs that are unified in methodology across cities of the world (see van Heezik and Seddon 2016 for a review on censusing birds in urban areas). A number of cities do have urban bird monitoring programs (e.g., Turner 2003; Murgui 2014) and elements of such programs could be utilized to develop a robust urban bird monitoring program across the cities of the world. Such a unified methodology is needed if we are to have a more complete understanding of urban birds and develop appropriate management guidelines at the correct scales. Second, we lack information about birds from much

of the Southern Hemisphere's cities, particularly those in lesser developed nations, the tropics, and urban areas on islands. As a result, our present understanding is dominated by Northern Hemisphere temperate systems, which may differ from urban areas in other parts of the world. Third, we need to focus attention on urban birds in and near biodiversity hotspots and locations experiencing rapid rates of urbanization. Finally, we need to continue researching basic ecological aspects of urban birds.

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Chapter 3
Urbanization and Bird Communities: Spatial and Temporal Patterns Emerging from Southern South America

M.I. Bellocq, L.M. Leveau, and J. Filloy

Abstract Urbanization is an expanding process worldwide, and South America seems to follow the general pattern observed in more urbanized regions of the world. Most conceptual models on the response of biodiversity to urbanization, however, are based on the experience in developed economies. In this chapter, we summarize patterns of bird communities found at different spatial and temporal scales in southern South America. Along a 1400-km latitudinal gradient, we found that urbanization (1) obscured the latitudinal pattern of bird species richness, (2) had a stronger negative effect on bird richness in tropical than in temperate or arid regions, and (3) resulted in more similar communities than the seminatural or rural areas, suggesting a process of biotic homogenization. The analysis of urban centers of different sizes indicated that bird richness and abundance were negatively affected by urbanization only in cities above 7000 and 13,000 inhabitants, respectively. In the Pampean region, urbanization affected negatively birds that nest on the ground, with insectivorous and carnivorous diets, feeding on the air and on vegetation and with solitary and migratory behaviors. Urbanization decreased the seasonal and interannual variability of bird species composition. We suggest future directions of research on the influence of latitude on temporal dynamics of bird communities in urban areas, comparison of bird responses to urbanization among biogeographical regions using a mechanistic approach, and including functional and phylogenetic diversity as response variables in the analyses.

Keywords Argentina • Biotic homogenization • Community similarity • Neotropics • Species richness

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3.1 Introduction

Human land use changes native ecosystems and, when globally expanded, contributes to biodiversity loss, climate change, and environmental degradation (Lambin et al. 2001). From the perspective of biodiversity conservation, urbanization is considered a major cause of species extinction (i.e., Czech et al. 2000). It promotes the replacement or impoverishment of native communities and the arrival of cosmopolitan species (loss of beta diversity); consequently, it is expected that taxonomic similarity between communities increases in this process of biotic homogenization (McKinney 2006). Furthermore, given that species able to exploit human-modified habitats tend to be ecologically redundant and/or phylogenetically close related, functional and phylogenetic diversities would also be lost (Olden et al. 2004).

Urbanization is an expanding process worldwide (see Lepczyk et al. 2016; Chen and Wang 2016), and South America seems to follow the general pattern observed in developed economies (Pimentel et al. 1998). In Europe and the United States (to a less extent), however, landscape is highly fragmented by urbanization, whereas in South America, urban centers are still growing over rural or seminatural areas (McGranahan and Satterthwaite 2003; Pauchard et al. 2006; Garaffa et al. 2009). The great majority of the studies on bird assemblages in urban areas were conducted in Europe and the United States where urbanization is most developed, and much less were conducted in South America, Africa, and Asia (i.e., in most of the Earth). For example, the geographical distribution of bird surveys used by Pautasso et al. (2011) to describe the global macroecology of bird assemblages in urbanized ecosystems accounts for that spatially unbalance number of studies.

In this chapter, we analyze some spatial and temporal patterns of bird assemblages that emerged from urban areas developed in southern South America. First, we examine changes in species richness and composition similarity along a latitudinal gradient, relating variations to environmental variables (associated with causal hypothesis) and comparing the patterns between urban and nonurban areas. Second, we analyze the response of bird species richness to urbanization gradients from the core-urban area to the rural zone, in urban centers located in the Pampean region of Argentina. Third, we analyze the influence of town size on the response of bird species richness and total abundance to urbanization gradients. Fourth, we compared bird functional groups between urban and nonurban areas in several cities of the Pampean region. Fifth, we show seasonal and year-to-year variability in bird community attributes recorded in a coastal city. Finally, we suggest directions for future research.

3.2   Spatial Patterns of Diversity

Patterns of community attributes, such as species composition, richness, and diversity, occurring at large geographical scales are explained by factors acting at large scales, such as climatic factors. Similarly, local diversity patterns are usually explained by the variation of local environmental factors such as habitat heterogeneity. There is evidence that bird communities responded to urbanization along both climatic and land cover gradients in the southern Neotropics.

3.2.1   Latitudinal Patterns and Diversity–Environment Relationships

Species richness in general and bird richness in particular decline from the equator to the poles (Hawkins et al. 2006). It is widely accepted that broad-scale latitudinal changes in bird richness are explained by the flow of energy and water showing a positive association between richness and temperature or rainfall (Mittelbach et al. 2001; Hawkins et al. 2003), a pattern also observed in the southern Neotropics (Rabinovich and Rapoport 1975; Bellocq and Gómez-Insausti 2005). Studies conducted in Argentina, however, showed that urbanization obscured the latitudinal pattern of bird species richness from 26° to 38°S and 59° to 61°W that includes subtropical forests, shrublands, and grasslands (Fig. 3.1). Bird richness declined with increasing latitude in rural areas but remained relatively constant in urban centers; in rural areas, mean annual temperature and mean annual precipitation accounted for the latitudinal pattern (Filloy et al. 2015). That indicates urban centers held a constant number of species independently of town climatic location, probably due to changes in temperature and water inputs and to sustained resource availability (compared to the surroundings) as a consequence of human management of urban areas. In contrast to the pattern observed in southern South America, along a latitudinal gradient in Europe (from 41° to 53°N, a similar length to our study), there were significant positive correlations between latitude and bird species richness in urban areas (Ferenc et al. 2014); that is, species richness surprisingly increased with latitude (that the authors hypothesized due to climatic variability promoting generalist species). The latitudinal patterns observed in nonurban areas also differed between southern South America (richness declined with increasing latitude, explained by temperature and precipitation) and Europe (richness peaked at intermediate latitudes within the study range, explained by potential sampling biases and patterns occurring at larger scales). The contrasting results between South America and Europe alert that broad studies including all biogeographic regions should be conducted to understand wildlife responses to urbanization.

Furthermore, the difference we found in species richness between urban centers and rural areas was larger at lower latitudes (Fig. 3.2), indicating that urbanization had a stronger negative impact on bird richness in tropical than in temperate or arid

Fig. 3.1 Location of the 15 towns along the latitudinal gradient of Argentina. With kind permission from Springer Science + Business Media: Urban Ecosystems, Urbanization altered latitudinal patterns of bird diversity-environment relationships in the southern Neotropics, 18, 2015, 777–791, J. Filloy, S. Grosso, M.I. Bellocq, Figure 1

regions (Filloy et al. 2015). Previous studies showed that bird richness decline from the rural to the core-urban area (e.g., Faeth et al. 2011), a pattern also observed in cities from the Neotropics (Garaffa et al. 2009; Villegas and Garitano-Zavala 2010; Reis et al. 2012). Processes involving a decline in local habitat productivity and changes in species interactions and resource availability with respect to the surroundings may explain the reduced species richness in urban areas (Shochat et al. 2006). However, the latitudinal variation on the degree of impact of urbanization on bird species richness requires consideration of both local and regional primary productivity and vegetation stratification, because the impact differs with the climatic context in which urbanization develops (Filloy et al. 2015). In towns developed in tropical or subtropical climates, impervious areas reduced primary productivity and vegetation stratification compared to the seminatural forest where more bird species are able to coexist. In contrast, in settlements located in arid or semiarid zones, water irrigation and vegetation management increase primary productivity compared to seminatural adjacent areas, partially compensating the reduction of vegetation due to impervious areas. In some arid environments, bird species richness may even reach higher values in town centers than in rural zones (Mills et al. 1989). The observed latitudinal differences in the degree of urbanization impact on species richness are also related to patterns of variation in
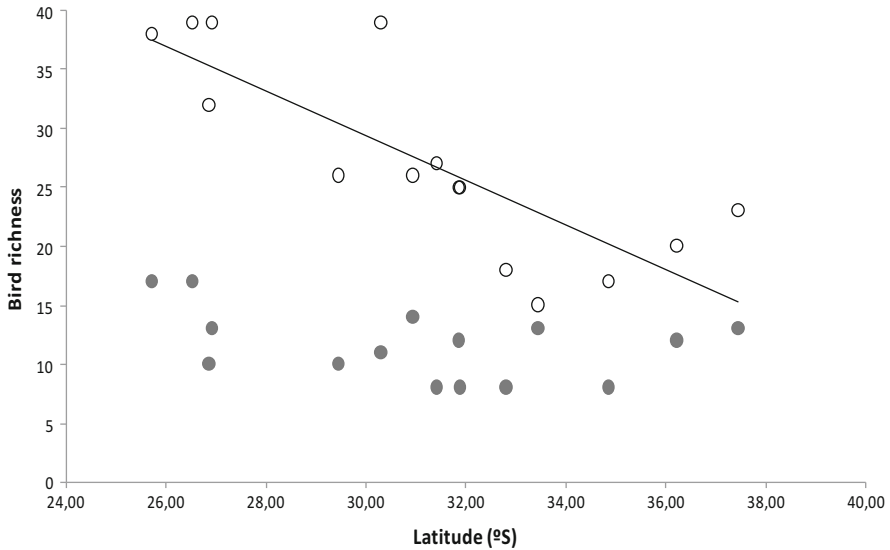
Fig. 3.2 Bird species richness in 15 core-urban areas (*black dots*) and their correspondent rural areas (*white dots*) along a latitudinal gradient from 26° to 38°S in Argentina. *Line* depicts a significant negative linear trend for rural areas, whereas core-urban areas did not show a significant relationship with latitude. With kind permission from Springer Science + Business Media: Urban Ecosystems, Urbanization altered latitudinal patterns of bird diversity-environment relationships in the southern Neotropics, 18, 2015, 777–791, J. Filloy, S. Grosso, M.I. Bellocq, Figure 3

community composition reflecting life history traits. The environmental filter imposed by urbanization results in assemblages composed by a set of species able to exploit or to adapt to urban environments, characterized by broad tolerance to environmental conditions or specific tolerance to built-up environments (McKinney 2006; Kark et al. 2007). Thus, the larger the regional species pool, the larger the impact of urbanization on species richness.

Urbanization worldwide is expected to influence global biota distribution. Physical environmental homogenization due to human activities developed over large extensions of land, such as urbanization, promotes global biotic homogenization (McKinney and Lockwood 1999). Composition of bird communities was more similar between urban centers than between adjacent seminatural areas at any distance along a range of 1400 km in Central Argentina (Fig. 3.3). Similarly, other studies around the world showed that urban bird assemblages had higher similarity in species composition than nonurban assemblages, indicating that urbanization causes biotic homogenization (Clergeau et al. 2006; McKinney 2006; Luck and Smallbone 2011).

Similarity in species composition between communities reflects the spatial turnover in species composition, or beta diversity. Close communities tend to share more species than communities far apart. Similarity in the composition between assemblages declines with increasing geographic distance between them,
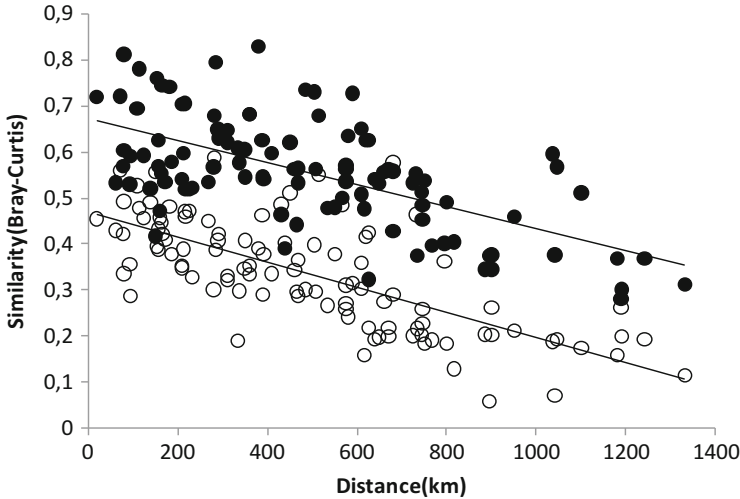
Fig. 3.3 The distance decay in similarity for urban (*black dots*) and rural (*white dots*) bird assemblages along a latitudinal gradient from 26° to 38°S in Argentina. With kind permission from Springer Science + Business Media: Urban Ecosystems, Urbanization altered latitudinal patterns of bird diversity-environment relationships in the southern Neotropics, 18, 2015, 777–791, J. Filloy, S. Grosso, M.I. Bellocq, Figure 5

a pattern referred to in the literature as the distance decay in similarity (Nekola and White 1999). Such pattern occurs as a response to gradual spatial changes in environmental conditions, and it has been documented across a wide range of geographic gradients and organisms (Soininen et al. 2007). Distance decay in bird community similarity was also recorded across regions in the southern Neotropics (Fig. 3.3). Because environmental similarity is expected to be higher between urban than between nonurban environments, similarity in species composition is expected to decay with distance at a lower rate in urban centers than in the surrounding areas, a pattern observed in Australia (Luck and Smallbone 2011) and Europe (Clergeau et al. 2006; Ferenc et al. 2014). In contrast, when comparing the pattern between core-urban and rural areas in southern South America, Filloy et al. (2015) found similar rates of decay indicating that urbanization had no effect on the rate at which bird community composition changes with the geographic distance at the interregional scale (Fig. 3.3). The similar rate in distance decay between urban centers and seminatural areas likely reflects that the composition of urban bird assemblages is highly dependent on the regional species pool along the study gradient in South America.

3.2.2   Bird Community Responses to Urbanization Gradients

The empirical evidence consistently indicates that bird communities respond to urbanization. The influence of town size on the spatial patterns of richness along urban–rural gradients and the variation of functional groups have been much less explored.

3.2.2.1   Bird Responses to Urbanization in Temperate Agrosystems

Spatial variations in bird taxonomic richness along gradients of urbanizations have long being described. The general pattern indicates that richness declines from rural or seminatural areas to the core-urban area (Chace and Walsh 2006; Faeth et al. 2011), although unimodal relationships may also occur (Marzluff 2001).

Spatial patterns of bird species richness were studied along urban–rural gradients in 15 cities ranging 18,000–25,000 inhabitants in the Pampean region of Argentina, where the original grasslands were intensively modified by agriculture. There was consistency in the decline of species richness from the rural zone to the core-urban area (i.e., city of Suipacha, Fig. 3.4a), associated to the increase in impervious areas (Fig. 3.4b).

3.2.2.2   Influence of Town Size on Bird Community Responses

Evidence from temperate agrosystems of the Pampean region indicates that bird community responses to urban–rural gradients depend on town size. To test whether spatial patterns in community attributes along urban–rural gradients change with town size, Garaffa et al. (2009) surveyed birds in nine urban centers ranging 472 to 520,000 inhabitants and 0.9–10.0-km gradient extend at similar latitude (between 34 and 35°S) in the Pampean region of Argentina (Fig. 3.5). Bird species richness responded to urbanization along urban–rural gradients longer than 1.4 km and human population size of the settlement over 7000 inhabitants (Fig. 3.6). That indicates a threshold below which bird richness showed no response to urbanization. The existence of a threshold was also reported for wintering birds in Finland (Jokimäki and Kaisanlahti-Jokimäki 2003) and breeding birds in west–central Mexico (MacGregor-Fors et al. 2011). Values of the threshold, however, differed among study regions indicating that factors beyond town size are influencing responses of bird species richness to urbanization.

There is evidence from the Pampean region that patterns of bird abundance along urban–rural gradients were also affected by town size. Garaffa et al. (2009) plotted bird abundance against the first factor scores obtained from environmental variables in principal component analysis for settlements of varied size (Fig. 3.7). In villages and most small towns, abundance of native species was similar along the gradients (Fig. 3.7a–d); but in settlements over 13,000 inhabitants, abundance of
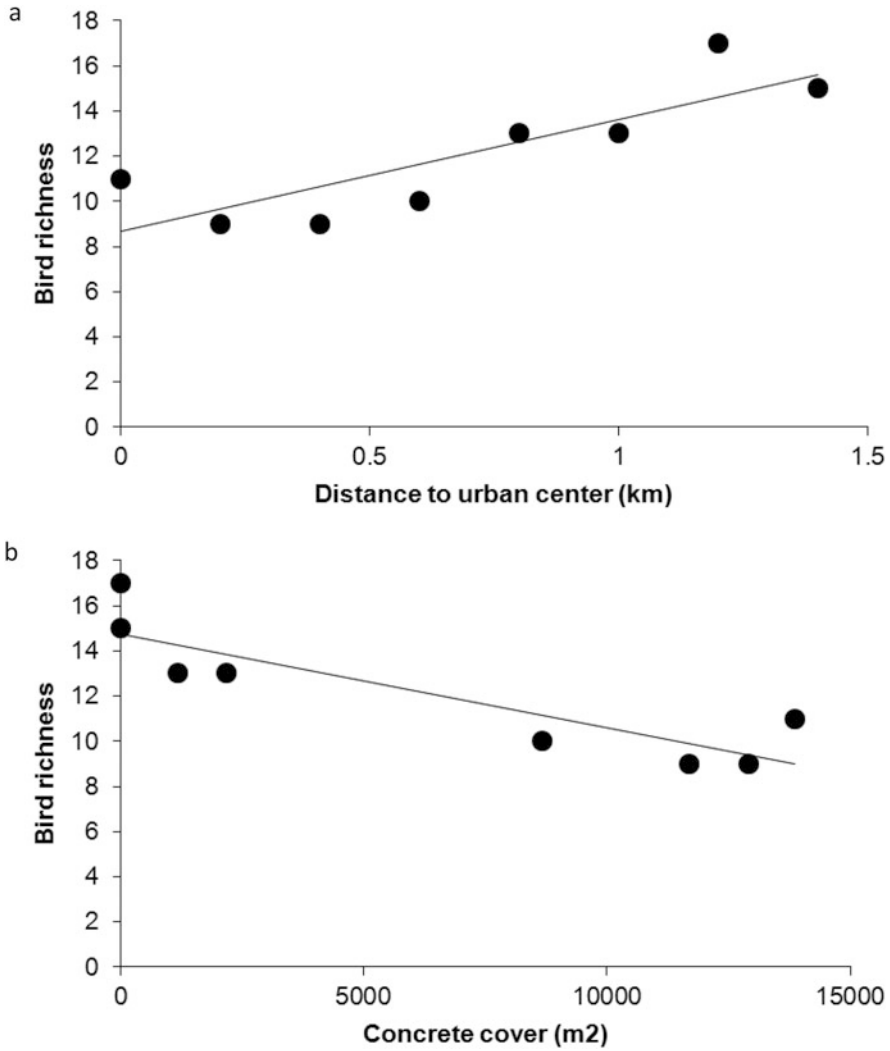
Fig. 3.4 Number of bird species recorded in observation points located at different distances from the core-urban area (**a**) and in relation to cover of impervious areas (**b**) in the city of Suipacha (7149 inhab.), a typical human settlement of the Pampean region, Argentina

native species decreased from the rural zone to the core-urban area (Fig. 3.7e–g and i). When exotic species were included, three different patterns of bird abundance were found: increased (Fig. 3.7a and h), decreased (Fig. 3.7e and g), or remained constant (Fig. 3.7f and i) from the rural zone to the core-urban area. Villages and towns below 13,000 inhabitants showed no response in the abundance of both native and total birds along gradients (Fig. 3.7b–d).
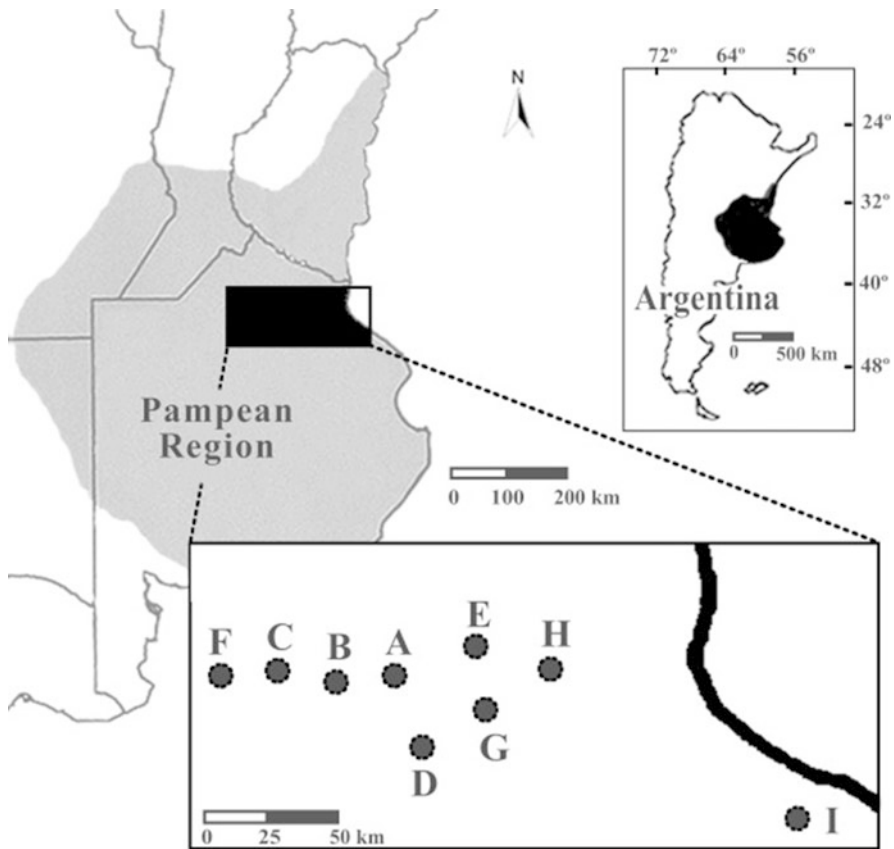
Fig. 3.5 Location of the nine urban–rural gradients in the Pampean region, Argentina. Ascending alphabetic order indicates increasing urbanized area size. (A) Rivas, (B) Castilla, (C) Rawson, (D) Suipacha, (E) SA Giles, (F) Chacabuco, (G) Mercedes, (H) Lujan, (I) La Plata. Reprinted from Landscape and Urban Planning, 90 (1), P. Garaffa, J. Filloy, M.I. Bellocq, Bird community responses along urban–rural gradients: Does the size of the urbanized area matter?, 33–41, Copyright (2009), with permission from Elsevier

3.2.2.3 Variation of Functional Groups Between Urban and Rural Areas

Knowledge of the relationships between bird species traits and urbanization may improve our understanding of which bird species will become part of the urban avifauna in the future (Conole and Kirkpatrick 2011; Ikin et al. 2012). To gain more insights on the effects of urbanization on life history traits of birds, we analyzed data from seven urban centers (ranging 20,000 to 30,000 inhabitants) in the Pampean region (Cañada de Gómez, Firmat, Lincoln, Coronel Suárez, Bolivar, Balcarce, and Miramar). Habitats considered were urban (>50 % cover of impervious areas) and rural (no cover of impervious areas). Bird surveys were conducted

Fig. 3.6 Correlation coefficient between bird species richness and the distance to the core-urban area for nine cities of the Pampean region as a function of the length of the urban–rural gradient
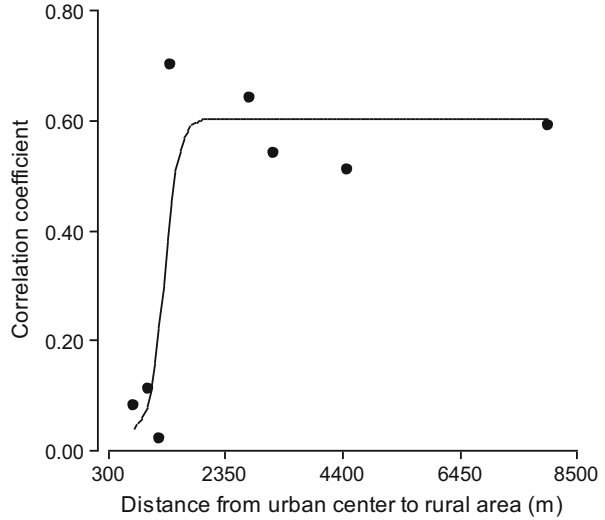
once during the breeding season by either point or transect counts. In Cañada de Gómez, Firmat, Lincoln, Coronel Suárez, and Bolivar City, seven 50-m-radius point counts were conducted in each habitat type, whereas in Balcarce and Miramar, five strip transects (100 × 50 m) were surveyed in each habitat type. Density of each species was calculated for each habitat and city, for a total of 14 sites. Species were classified according to five life history traits (following Narosky and DiGiacomo 1993; De la Peña 2010a, b): (1) nest substrate (ground, trees and shrubs, buildings, or parasite), (2) diet (omnivorous, granivorous, insectivorous, or carnivorous), (3) residency status (migratory or resident), (4) gregarious behavior (solitary or gregarious), and (5) foraging habit (ground, vegetation, or air). Then, we created a matrix of sites ($n = 14$) by density (individuals/hectare) of traits ($n = 11$). Given that traits can be related to each other, exploratory factor analysis was performed to obtain the underlying factors representing functional groups (Leveau 2013). A maximum likelihood factor extraction method was used, and factors were rotated using the varimax normalized method. Site scores of factors were compared between urban and rural sites with a Mann–Whitney test.

Exploratory factor analysis explained 78 % of the variance and produced three factors or functional groups (Table 3.1). Functional group 1 had higher value scores in urban habitats ($U = 4.00$, $P = 0.009$) (Fig. 3.8) and was related to traits that allow success in highly urbanized areas: nesting in buildings, omnivorous diet, resident, and gregarious. Functional group 2 had higher value scores in rural habitats ($U = 7.00$, $P = 0.025$) and was related to nesting on the ground, insectivorous, and carnivorous diets, feeding on the air and vegetation, and a solitary and migrant behavior. Finally, functional group 3 had similar value scores between habitats ($U = 17.00$, $P = 0.338$) and was negatively related to a granivorous diet and nesting on trees.
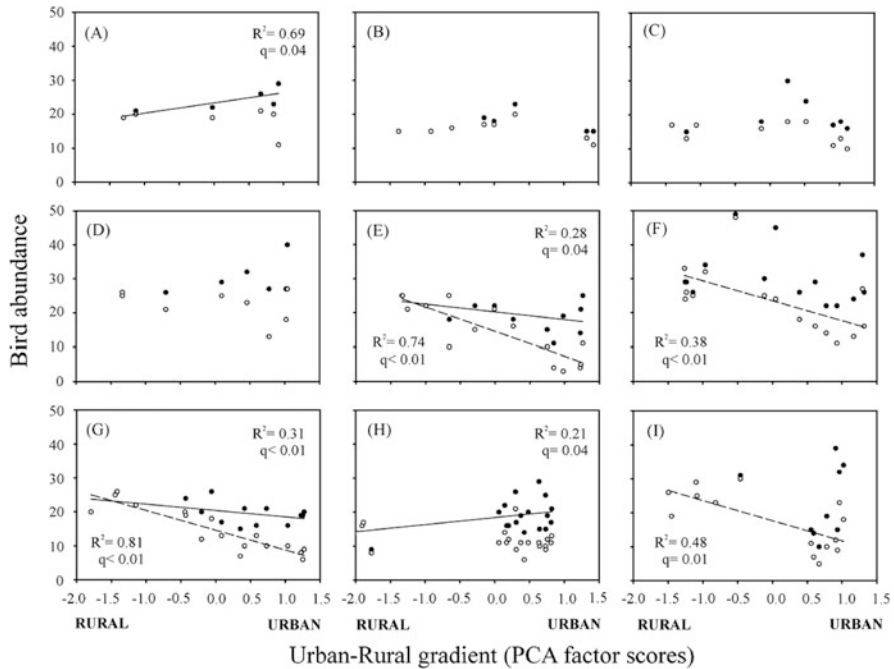
Fig. 3.7 Bird abundance (individuals/point count) arranged across the first factor scores resulted from principal component analysis. Native species: *dashed lines*, *white dots*. Both native and exotic species: *solid lines*, *black dots*. Coefficient of determination and significance are represented for native (*bottom left*) and both native and exotic species (*top right*) in each square figure. Ascending alphabetic order indicates increasing urbanized area size. (**A**) Rivas; (**B**) Castilla; (**C**) Rawson; (**D**) Suipacha; (**E**) SA Giles; (**F**) Chacabuco; (**G**) Mercedes; (**H**) Lujan; (**I**) La Plata. Reprinted from Landscape and Urban Planning, 90 (1), P. Garaffa, J. Filloy, M.I. Bellocq, Bird community responses along urban–rural gradients: Does the size of the urbanized area matter?, 33–41, Copyright (2009), with permission from Elsevier

Results from our analysis in the Pampean region showed that birds nesting on the ground, having insectivorous and carnivorous diet, feeding on vegetation and in air, and having a migratory status were negatively impacted by urbanization, which is consistent with patterns found in other studies (Kark et al. 2007; Blair and Johnson 2008; Croci et al. 2008; MacGregors Fors et al. 2010; Leveau 2013; Jokimäki et al. 2014). However, in our analysis, traits related to nesting in trees and granivorous diet were not affected by urbanization; tree abundance in our urban centers may be higher than that of rural areas because cities are set in a grassland biome (e.g., Leveau 2013). Therefore, trees probably were not a limiting substrate for nesting in urban habitats.

Table 3.1 Loadings of the three factors produced from the trait-site matrix of birds in urban and rural habitats of Central Argentina. Higher trait-factor loadings are highlighted in bold

| Traits	Factor 1	Factor 2	Factor 3
Nest build	**0.90**	−0.38	0.03
Omnivorous	**0.91**	−0.32	−0.06
Resident	**0.85**	0.01	−0.47
Gregarious	**0.87**	−0.25	-0.34
Feed ground	**0.87**	−0.08	−0.44
Nest ground	−0.51	**0.77**	0.05
Insectivorous	−0.38	**0.81**	0.14
Carnivorous	−0.37	**0.75**	0.22
Migrant	−0.09	**0.81**	0.12
Solitarious	−0.45	**0.80**	−0.08
Feed air	−0.06	**0.77**	0.19
Feed veget	−0.51	**0.58**	0.02
Granivorous	0.15	0.00	**−0.91**
Nest tree	0.28	−0.18	**−0.83**
Brood parasite	0.03	0.28	−0.07
Eigenvalues	7.07	2.82	1.57
% Variance	33.2	29.8	14.5
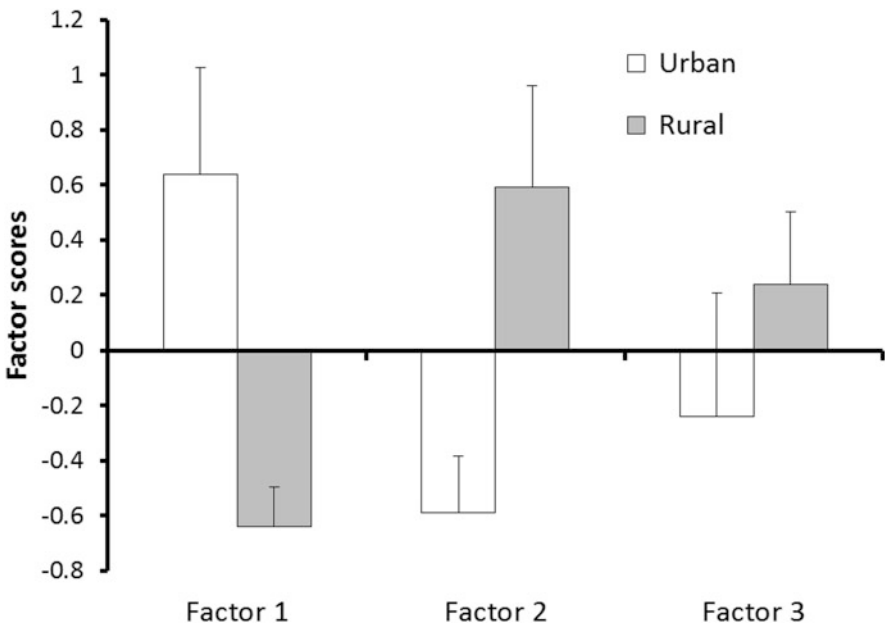
Fig. 3.8 Mean score values and standard errors of factors from the bird traits in urban and rural habitats of seven cities in Central Argentina

3.3 Temporal Variability in Community Attributes

In several cities, urbanization was associated to a dampening of the temporal fluctuation in habitat structure and the availability of food and water (see Shochat et al. 2006). This stabilization of resources may influence the seasonal and interannual bird community dynamics.

3.3.1 Seasonal Variability in Community Attributes

Seasonality, or the predictable change in environmental conditions of a site throughout the year, is expected to determine the proportion of resident and migratory species in a community (Herrera 1978a; Hurlbert and Haskell 2003). Increasing resource availability between the winter and the summer will be associated to an increase in the proportion of migrant species in the community. However, evidence from several studies showed that at least two factors of the urban environment may reduce seasonality of bird communities (see Macías-García et al. 2016). First, seasonal environmental variability may be reduced in urban centers relative to nonurban areas because of vegetation management and water irrigation (White et al. 2002; Shochat et al. 2006; Faeth et al. 2011; Buyantuyev and Wu 2012). Second, migrant birds may be excluded from urban areas due to a lack of tree cover and a lack of herbaceous vegetation and food supply (Blair and Johnson 2008; MacGregors Fors et al. 2010; Leveau 2013).

We compared the seasonal change in bird community attributes in two levels of urbanization in the coastal city of Mar del Plata (38° 00′ S 57° 33′ W, 600,000 inhabitants). Birds were surveyed during three breeding (spring–summer) and nonbreeding (autumn–winter) seasons in 100×50 m strip transects, during 2002–2005. Fifteen transects were located in urban areas ($>50\%$ building cover) and 14 in peri-urban areas (5–20% building cover) at the city fringe. Seasonal change in bird richness and abundance was determined by the coefficient of variation (CV), comparing bird richness and abundance of each strip transect between the nonbreeding and the breeding season. The change in community composition between seasons was calculated with the Jaccard index (for more details in methods, see Leveau and Leveau 2012), comparing bird composition in each strip transect between the nonbreeding and the breeding season.

Seasonal similarity in community composition was higher in the urban (mean = 0.72, SE = 0.05) than in the peri-urban (mean = 0.58, SE = 0.03; Student test, $t = 2.18$, P = 0.038) area. In contrast, the seasonal change of bird richness was similar between urban (mean = 0.20, SE = 0.04) and peri-urban (mean = 0.23, SE = 0.03; $t = 0.55$, P = 0.586) areas. Furthermore, the seasonal change of bird abundance tended to be significantly higher in the peri-urban area (mean = 0.29, SE = 0.04; urban area, mean = 0.18, SE = 0.04; $t = 1.88$, P = 0.070). The literature indicates that seasonal dynamics of bird communities depends on the arrival of

migratory species in Central Argentina (Cueto and Lopez de Casenave 2000; Isacch and Martinez 2001; Isacch et al. 2003; Codesido et al. 2008; Leveau and Leveau 2011; Apellaniz et al. 2012). However, those migrant species are mostly excluded from highly urbanized areas. In our study, the presence of migrant species in the urban area was only occasional, whereas in the peri-urban area, four species were recorded [glittering-bellied emerald (*Chlorostilbon lucidus*), fork-tailed flycatcher (*Tyrannus savana*), tropical kingbird (*Tyrannus melancholicus*), and small-billed elaenia (*Elaenia parvirostris*)]. Those migrant species nest in trees and feed on insects and, in the case of glittering-bellied emerald, on nectar. Therefore, the lack of tree cover and food resources in highly urbanized areas compared to low urbanized areas may be the cause of low numbers of migrant species and the lack of seasonality in bird community composition. Our findings of lower seasonality in bird community composition and richness in highly urbanized areas agree with patterns found in Europe (Clergeau et al. 1998; Caula et al. 2008), North America (Clergeau et al. 1998; La Sorte et al. 2014), Australia (Catterall et al. 1998), and Argentina (Leveau et al. 2015; Cid and Caviedes-Vidal 2014). On the other hand, the lower seasonal variability of bird abundance in the urban area could be related to a constant supply of resources between seasons (Shochat et al. 2006).

3.3.2   Year-to-Year Variability in Community Attributes

Interannual variability in climate, resources, and habitat structure is thought to influence the interannual dynamics of bird communities (Järvinen 1979; Therriault and Kolasa 2000). However, urban environments may have a reduced interannual variability in resource availability and habitat structure relative to the nonurban areas (Shochat et al. 2006). The constant supply of food resources provided by humans may stabilize the temporal dynamics of bird communities in highly urbanized areas (Suhonen and Jokimäki 1988). Moreover, highly urbanized areas generally are dominated by a few cosmopolitan species, such as the house sparrow (*Passer domesticus*) and the rock dove (*Columba livia*), promoting interannual stability of bird communities (Collins 2000; Sasaki and Lauenroth 2011). Highly abundant species are usually more persistent because they have lower extinction risk than rare species (Collins 2000). Conversely, bird communities dominated by less abundant species and having more rare species are expected to show deeper fluctuations among years.

   Recent studies in Mar del Plata City showed little year-to-year variation in community composition in the core-urban area compared to peri-urban (Fig. 3.9) and rural areas that was related to the abundance of the dominant species in the most urbanized areas (Leveau and Leveau 2012; Leveau et al. 2015). In fact, the house sparrow and the rock dove represented each one between 20 and 29 % of the individuals recorded in the most urbanized sites (Leveau and Leveau 2012). Moreover, these species were the two most temporally persistent in that sites,
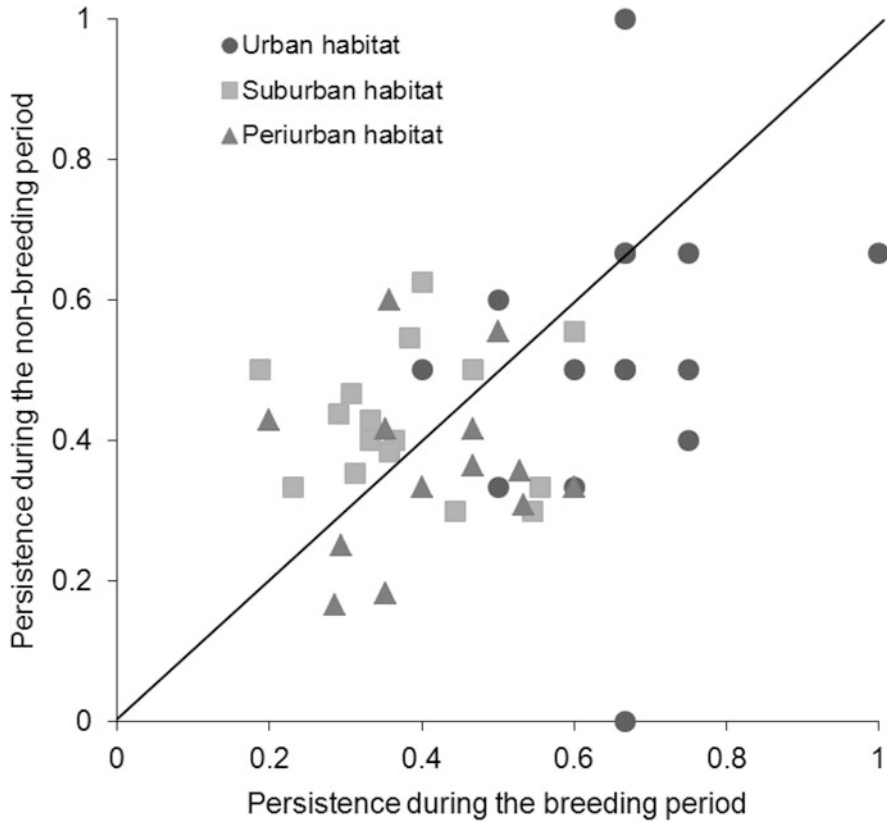
Fig. 3.9 Interannual variability of bird community composition along the urban gradient of Mar del Plata city, showing the values of persistence during the breeding and nonbreeding seasons. Persistence values vary from 0 (no species were recorded in all 3 years) to 1 (all species were recorded all 3 years). The *continuous line* indicates that the level of persistence was the same in both periods. Adapted from Leveau and Leveau (2012)

being recorded every year. On the other hand, the two most persistent species in suburban and peri-urban sites only represented the 11 % of the species recorded. A higher proportion of rare species in these suburban and peri-urban areas may be related to a lower stability of community composition. Furthermore, a constant food supply provided directly or indirectly by humans in the most urbanized sites may contribute to the high abundances and, therefore, higher temporal stability.

Interannual variability in bird community composition in the core-urban area was higher during the breeding than during the nonbreeding season (Fig. 3.9). This pattern is consistent with the hypothesis that bird communities are more stable during the breeding season, because species have stricter habitat affinities at this time (Rice et al. 1983; Tellería and Santos 1997).

Our results obtained in Mar del Plata (Leveau and Leveau 2012; Leveau et al. 2015) of a lower interannual variability in community composition agree

with those found in Finland by Suhonen et al. (2009). However, Barrett et al. (2008) did not find differences in the long-term dynamics of bird assemblages in areas of high and low human population densities. The differences in the temporal and spatial scales used in studies may be related to their contrasting results.

3.4   Future Directions

Studies conducted in the Northern Hemisphere, Australia, and Argentina showed that urbanization altered the seasonal dynamics of bird communities. Given that seasonal variation of climate and, consequently, of bird communities in natural areas increases with latitude (Herrera 1978b; Newton and Dale 1996a, b), we expect that the impact of urbanization on the seasonal dynamics of bird communities also increases toward the poles. Future studies should explore the interaction between latitude and urbanization in affecting the seasonal dynamics of bird communities. On the other hand, results from Finland and Argentina showed that urbanization stabilizes the interannual variation of community composition. Therefore, in a recent article, we proposed that urbanization promotes a temporal homogenization of bird communities, lowering the seasonal and interannual variations of bird composition (Leveau et al. 2015). However, further research is needed to understand to what extent urbanization reduces the temporal dynamics of bird communities.

Most conceptual models on the response of biodiversity to urbanization are based on the experience in developed economies. The evidence from studies conducted in southern South America indicates that latitudinal patterns of bird assemblages in urban areas differed between South America and Europe and that the negative impact of urbanization on species richness is the strongest in highly rich regions such as the tropics. Given the environmental, historical, and socioeconomic scenarios of the different regions of the world, a comparison of bird response to urbanization among biogeographical regions should be conducted to better understand global patterns; certainly, efforts should be made for filling information gaps. Such comparison should use a mechanistic approach to allow explaining the observed patterns and help to develop a unified heuristic framework.

The inclusion of complementary components to the traditional taxonomic local diversity (alpha diversity) is only recently being incorporated in the study of urban biodiversity, and it is virtually unexplored in South America and in most other regions of the world. Future studies should incorporate the turnover of species along urbanization gradients (beta diversity), the functional and phylogenetic facets of biodiversity, and ecosystem processes and functions (i.e., predation, pollination). Birds are good biological models to increase our understanding of the responses of biodiversity to urbanization because they proved to be sensitive to urbanization and are relatively well known and easy to survey worldwide.

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Chapter 4
Bird Diversities and Their Responses to Urbanization in China

Shuihua Chen and Siyu Wang

Abstract China has been experiencing remarkable urban expansion in recent decades. The rapid urbanization progress also drew much attention of researchers on urban birds and the effect of urbanization on birds. We summarized the papers on urban birds in China published from 1962 to 2014. To understand the urban bird diversities in China, we selected 17 cities across different bioregions even biogeographical realms whose bird diversities had been carefully surveyed and chose ten most abundant resident birds representing the urban birds of the cities. We measured the phylogenetic structure and the family diversity of ten species of each city and then examined their variations with the city's population, latitude, and longitude. The results showed that 49 species dwell in the 17 cities as the top 10 abundant birds which cover three orders and 20 families. Crows, starlings, tits, and bulbuls are the most abundant species in the urban areas in China. The cities, on the one hand, close in geography have close bird lists which implied that local fauna has important impacts on urban bird assemblages. On the other hand, some cities far apart also share close bird lists probably due to the process of homogenization of urbanization. The cities with higher latitudes usually support birds more discretely in phylogenetic structure, but with lower family diversity. We also reviewed the urbanization effects on the birds. Evidences showed significant patterns of birds in response to urbanization in China at community, species, and even individual levels.

Keywords Urbanization • Bird • Community • Population • Bird diversity • Human disturbance • Urban habitat • China

4.1 Introduction

China has been experiencing a remarkable urban expansion since its reform and opening up, primarily due to rapid economic development and population growth (Normile 2008; Qiu 2010; Liu et al. 2012). The proportion of the urbanized population in China has increased from 18 % in 1978 to 53.7 % in 2013

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(Fig. 4.1). China has the largest urban population in the world (758 million) and has 6 out of 28 (21.4 %) megacities with populations more than 10 million and 10 of 43 (23.3 %) large cities with populations between 5 and 10 million in 2014 (United Nations 2014). Most cities in China are still rapidly developing. It is expected that some 292 million people will be added to the country's urban population by 2050. However, this widespread urban expansion of China has resulted in an extensive loss of natural habitat (Li et al. 2006; He et al. 2014) and has seriously threatened the country's biodiversity (Wang et al. 2007; Li et al. 2010b).

Birds are common and widespread in urban areas, and as one of the most favorite wildlife of urban citizens, they have long drawn much attentions of biologists. Furthermore, since their diverse groups exhibit a variety of responses to environment (Rodewald 2012), they are also viewed as the valuable indicators for monitoring biodiversity (e.g., Blair 1999; Pereira and Cooper 2006) and understanding the effects of urbanization (e.g., Lepczyk and Warren 2012).

China is located in the eastern part of Asia, with a territory of 9.6 million km^2, quite complex topographies and climates, diverse natural environment as well as rich biodiversity. By now 1371 bird species have been estimated in the country (Zheng 2011). China's early ornithology began with the observations and specimen collections by foreign naturalists and missionaries in late nineteenth century. In the early twentieth century, the ornithology in China speeded up due to the works of Chinese biologists. However, almost all attentions in the early time were primarily
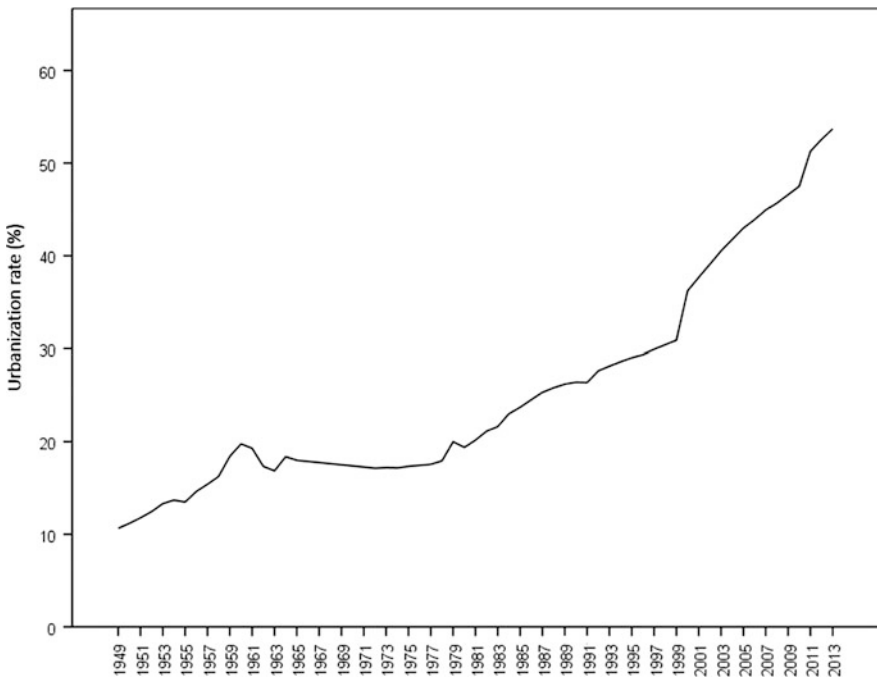

Fig. 4.1 The urbanization rate in China from 1949 to 2013

focused on the avifauna and their distribution in the vast territory, mostly in the wild lands and countryside. The real urban bird research appeared in early 1960s (Zheng 1962) in which wintering birds and their distributions in Beijing were surveyed and analyzed through comparison of different habitats in urban areas and countryside. Since then, especially in the recent decades, China witnessed a fast development in ornithology as well as in urban bird studies. Most of the papers are written in Chinese and widely scattered. So far, they have not been summarized under any term. In this paper, we have attempted to review the literature on urban birds in China, understand the characteristics of bird diversities in China's urban environment, and summarize their responses to urbanizations in China.

4.2 Methods

We searched for published papers on urban birds in China using "urban (城市)" and "bird (鸟类)" as key words at two Chinese journal databases of CNKI and CQVIP, and Google Scholar for Chinese website. Besides, we checked the references of all the collected papers for any potential literatures overlooked. We excluded the reviews and the theoretical articles.

We selected 17 cities with populations ranging from 2.79 to 28.84 million whose bird diversities had been carefully surveyed in their urbanized area. The fauna in China can be categorized into two biogeographic realms (The Oriental realm and the Palaearctic realm) and seven bioregions (Zhang 1999; Zheng 2011). These cities are located in 16 administrative districts (provinces, autonomous regions, or municipalities directly under the central government), across most of the zoogeographic regions in China (Fig. 4.2). We chose ten most abundant resident birds that are represented as the urban birds of these cities, avoiding water birds whose occurrences are closely related with that of wetland habitats. To understand the urban bird assemblages of these cities in different geographic and zoogeographic regions, we conducted a hierarchical cluster analysis for the 17 cities based on the top 10 urban bird lists.

We used mean pairwise distance (MPD) to measure the phylogenetic structure of the ten species of each city (Webb 2000):

$$\text{MPD} = \frac{\sum_{i=1, j=1, j \geq i}^{n} D_{ij}}{C_n^2}$$

where D_{ij} is the phylogenetic distance between species i and j and C_n^2 is the species pair number. The phylogenetic information and branch length were obtained from Sibley and Ahlquist (1995). If some species lacked further phylogenetic information under its genus, we juxtaposed them under the node of the genus.
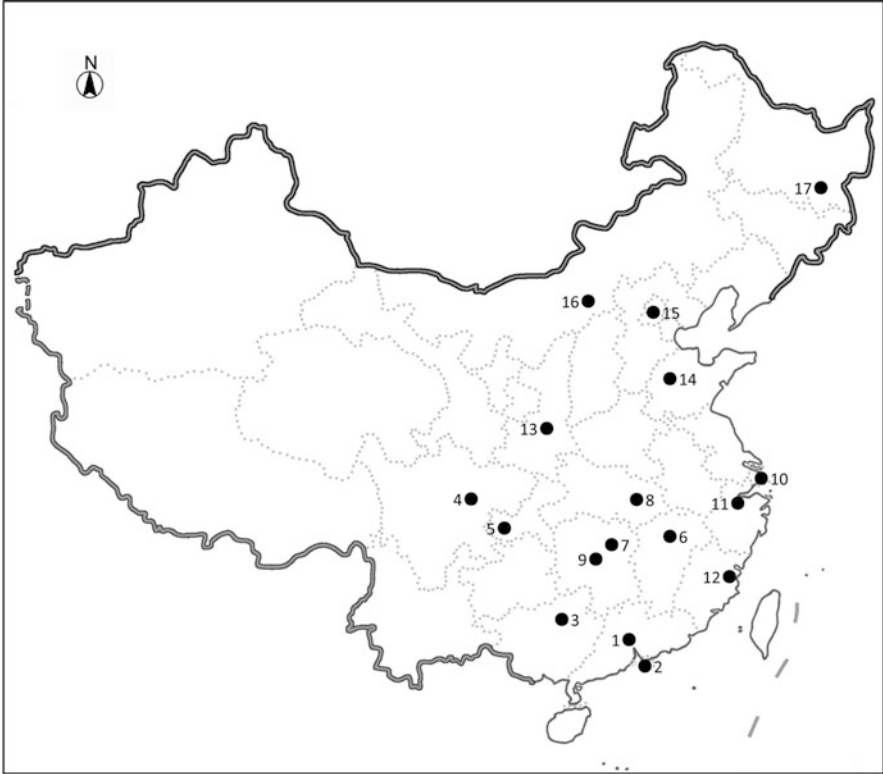
Fig. 4.2 The distribution of 17 selected cities in China. *1* Guangzhou, *2* Hong Kong, *3* Liuzhou, *4* Chengdu, *5* Chongqing, *6* Nanchang, *7* Changsha, *8* Wuhan, *9* Loudi, *10* Shanghai, *11* Hangzhou, *12* Fuzhou, *13* Xian, *14* Jinan, *15* Beijing, *16* Huhehaote, and *17* Mudanjiang

We used Shannon-Wiener diversity to calculate the family diversity of the ten species of each city:

$$H' = -\sum_{i=1}^{s} (p_i \ln p_i)$$

where H' is the family diversity index, $p_i = n_i/N$, n_i the species number of family i, N the total species number, and S the total family number. The bird classification system was referred to Zheng (2011).

We then examined the trends of the family diversity and phylogenetic structure with city's population, latitude, and longitude using curve estimation in regression analysis.

The published papers concerning urbanization effects and birds' responses were summarized at three levels: community, species, and individual.

4.3 Results and Discussions

4.3.1 Urban Bird Studies in China

In total, we collected 125 papers on urban birds in China published from 1962 to 2014 (Fig. 4.3). Among them, only ten papers are in English and the other 115 in Chinese, and 108 (86.4 %) were published after 2000. Based on their contents, these papers were categorized into nine topics: avifauna, bird diversity, community and habitat relationships, community's responses to urbanization, species' responses to urbanization, individual's responses to urbanization, community dynamics, bird and urban planning, and others (Fig. 4.4).

Studies on urban birds in China increased since 2000, and a large volume of reports have been published in the last 10 years. This is in coincidence with the urbanization rate of China, which increased rapidly by 73.8 % during the same period. Before 2000, most papers on urban birds focused on avifauna, bird diversity, and relationship between community and habitat. Though bird diversity and community-habitat relationship are still the major topics, the urbanization-induced ecological problems began to draw attentions since 2000 (Chen et al. 2000a; Zhang et al. 2013). The topics covered urbanization effects on community, species, and even individual level.
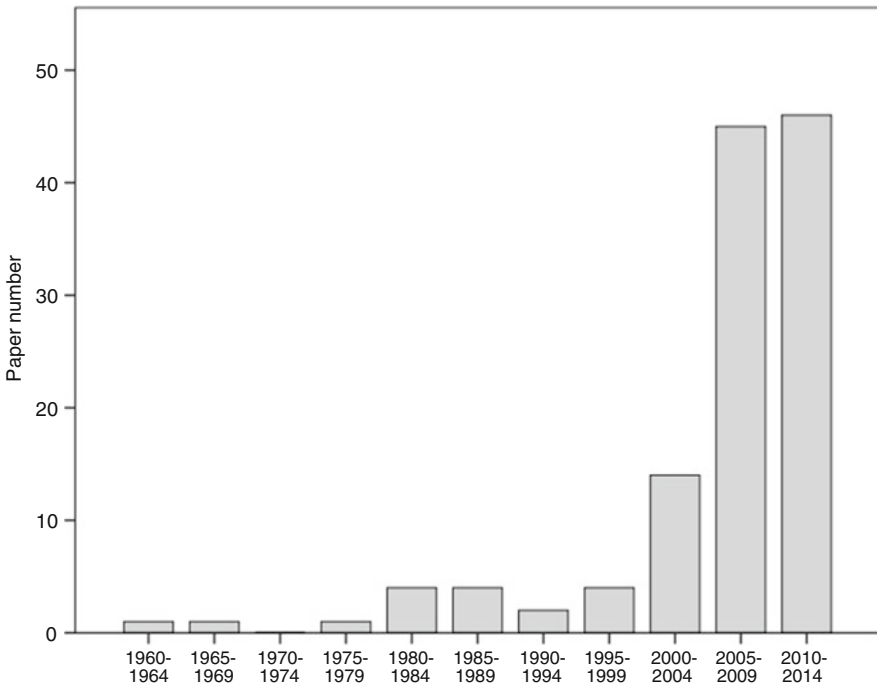

Fig. 4.3 The number of published papers on urban birds in China since 1962
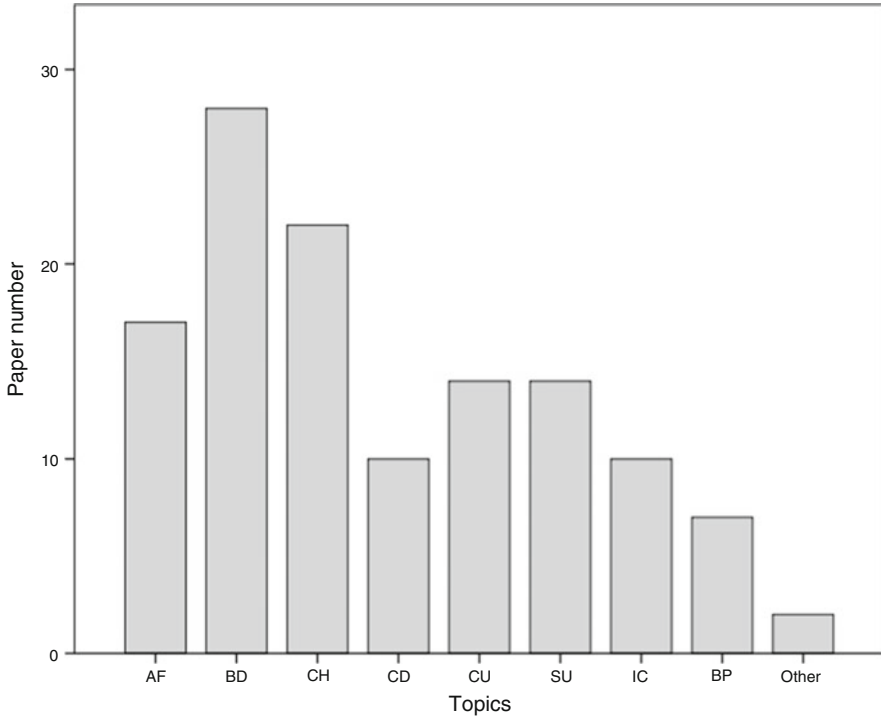
Fig. 4.4 The major topics and the number of papers on urban bird in China. Topics include *AF* avifauna, *BD* bird diversity, *CH* relationships between community and habitat, *CD* community dynamics, *CU* community's responses to urbanization, *SU* species' responses to urbanization, *IU* individual's responses to urbanization, *BP* bird and urban planning, and others

4.3.2 Urban Bird Diversities in China

There are 49 species in the 17 cities as the top 10 abundant birds (Table 4.1). Eurasian tree sparrow (*Passer montanus*) had the highest occurrence frequency which is distributed in all the 17 cities. It was followed by Spotted dove (*Streptopelia chinensis*) as the second wide distributed urban bird occurring in 13 cities. The Chinese bulbul (*Pycnonotus sinensis*) is a typical oriental species in 12 cities covering almost all the cities in south China. The other birds with occurrence frequency more than five included Great tit (*Parus major*), Common blackbird (*Turdus merula*), Crested myna (*Acridotheres cristatellus*), Long-tailed shrike (*Lanius schach*), White wagtail (*Motacilla alba*), Oriental magpie robin (*Copsychus saularis*), Common magpie (*Pica pica*), and Azure-winged magpie (*Cyanopica cyana*). Moreover, 21 species occur only in one city as the top 10 abundant birds.

The 49 species cover 3 orders and 19 families (Zheng 2011). They include four species in Columbidae of Columbiformes, two species in Picidae of Piciformes, and

Table 4.1 The top 10 abundant resident birds in 17 cities of China

	Occurrence Frequency	Guangzhou	Hong Kong	Liuzhou	Chengdu	Chongqing	Nanchang	Changsha	Wuhan	Shanghai	Loudi	Fuzhou	Hangzhou	Xian	Jinan	Beijing	Huhehaote	Mudanjiang
Latitude		23.16	22.20	24.33	30.67	29.59	28.68	28.21	30.52	31.22	27.71	26.08	30.26	34.27	36.65	39.92	40.82	44.60
Longitude		113.23	114.10	109.40	104.06	106.54	115.89	113.00	114.31	121.48	111.96	119.30	120.19	108.95	117.00	116.46	111.65	129.58
Human population (million)		12.70	7.18	3.76	14.05	28.85	5.04	7.04	9.79	23.02	3.79	7.12	8.70	8.47	6.81	19.61	2.87	2.80
Reference		Zheng et al. (2008)	Zhou and Chu (2014)	Tan (2013) and Xiao and Zhou (2001)	Wen et al. (2014) and Yang et al. (2007)	Cao (2013)	Zhang et al. (2009)	Deng et al. (2014)	Zhang et al. (2006)	Lu et al. (2007)	Li et al. (2013)	Tang et al. (2008)	Wang et al. (2005b)	Gao et al. (2008)	Sai (1994)	Guo (2008)	Zhao et al. (2011) and Shi (2005)	Jin et al. (2009)
Mean pairwise distance (MPD)		19.88	25.62	21.57	26.45	26.80	26.40	27.28	27.04	27.28	29.89	26.13	26.66	27.15	26.79	27.19	37.70	32.23
Family diversity index (H')		1.75	2.16	2.03	2.03	2.30	1.97	2.16	2.16	2.30	2.16	2.16	2.30	2.16	1.36	1.36	1.70	1.56
Eurasian tree sparrow *Passer montanus*	17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Spotted dove *Streptopelia chinensis*	13	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0
Chinese bulbul *Pycnonotus sinensis*	12	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Great tit *Parus major*	12	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1	1
Common blackbird *Turdus merula*	9	0	0	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0
Crested myna *Acridotheres cristatellus*	8	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Long-tailed shrike *Lanius schach*	8	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0

Table 4.1 (continued)

	Occurrence Frequency	Guangzhou	Hong Kong	Liuzhou	Chengdu	Chongqing	Nanchang	Changsha	Wuhan	Shanghai	Loudi	Fuzhou	Hangzhou	Xian	Jinan	Beijing	Huhehaote	Mudanjiang
White wagtail *Motacilla alba*	7	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0	0	0
Oriental magpie robin *Copsychus saularis*	7	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0
Common magpie *Pica pica*	6	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1
Azure-winged magpie *Cyanopica cyana*	6	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	1
Japanese white-eye *Zosterops japonicus*	5	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Vinous-throated parrotbill *Paradoxornis webbianus*	4	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Black-throated tit *Aegithalos concinnus*	3	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Oriental turtle dove *Streptopelia orientalis*	3	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Red-whiskered bulbul *Pycnonotus jocosus*	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oriental Greenfinch *Carduelis sinica*	3	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0

Red-billed blue magpie *Urocissa erythrorhyncha*	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
White-cheeked starling *Sturnus cineraceus*	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
White-browed laughingthrush *Garrulax sannio*	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Great spotted woodpecker *Dendrocopos major*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Grey-headed woodpecker *Picus canus*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Large-billed crow *Corvus macrorhynchos*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Daurian magpie *Corvus dauuricus*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
House sparrow *Passer domesticus*	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Black-collared starling *Gracupica nigricollis*	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Common tailorbird *Orthotomus sutorius*	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

Table 4.1 (continued)

	Occurrence Frequency	Guangzhou	Hong Kong	Liuzhou	Chengdu	Chongqing	Nanchang	Changsha	Wuhan	Shanghai	Loudi	Fuzhou	Hangzhou	Xian	Jinan	Beijing	Huhehaote	Mudanjiang
Silky starling *Sturnus sericeus*	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hill pigeon *Columba rupestris*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Eurasian collared dove *Streptopelia decaocto*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hwamei *Garrulax canorus*	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Masked laughingthrush *Garrulax perspicillatus*	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grey-cheeked fulvetta *Alcippe morrisonia*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Large-billed crow *Corvus macrorhynchos*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Collared crow *Corvus pectoralis*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rook *Corvus frugilegus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Brown shrike *Lanius cristatus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fork-tailed sunbird *Aethopyga christinae*	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species																						
Coal tit *Parus ater*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Marsh tit *Parus palustris*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Yellow-bellied tit *Parus venustulus*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sooty-headed bulbul *Pycnonotus aurigaster*	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chestnut bulbul *Hemixos castanonotus*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yellow-bellied prinia *Prinia flaviventris*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plain prinia *Prinia inornata*	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oriental skylark *Alauda gulgula*	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Scaly-breasted munia *Lonchura punctulata*	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
White-rumped munia *Lonchura striata*	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yellow-billed grosbeak *Eophona migratoria*	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

other 43 in Passeriformes: Corvidae (8), Pycnonotidae (4), Sturnidae (4), Paridae (4), Timaliidae (4), Laniidae (2), Fringillidae (2), Turdidae (2), Rhipiduridae (2), Estrildidae (2), Motacillidae (1), Alaudidae (1), Paradoxornithidae (1), Sylviidae (1), Zosteropidae (1), Aegithalidae (1), and Nectariniidae (1). Though urban habitats are regarded to be superior quality to raptors because there they are often free from persecution and have an adequate food supply (Chace and Walsh 2006); no raptor species enter the top 10 urban bird lists for any of the 17 cities, while in most US cities, raptors are the major dwellers (Cade et al. 1996).

There were not two cities that shared the same list of abundant urban birds. The result of hierarchical cluster analysis showed that cities close in geography had close bird list, such as Chengdu and Chongqing, Changsha and Wuhan, Fuzhou and Hangzhou, and Beijing and Huhehaote (Fig. 4.5). This implied that the local fauna has important impacts on urban bird assemblages. Of course, this can also be explained by similar vegetations of the neighboring cities. However, there were also some cities in different zoogeographic regions that shared a close bird list, such as Xian and Fuzhou, Nanchang and Chengdu, and Shanghai and Loudi. This possibly resulted from the process of homogenization of urbanization (McKinney 2006). To meet the needs of human dwellers, cities homogenize the physical
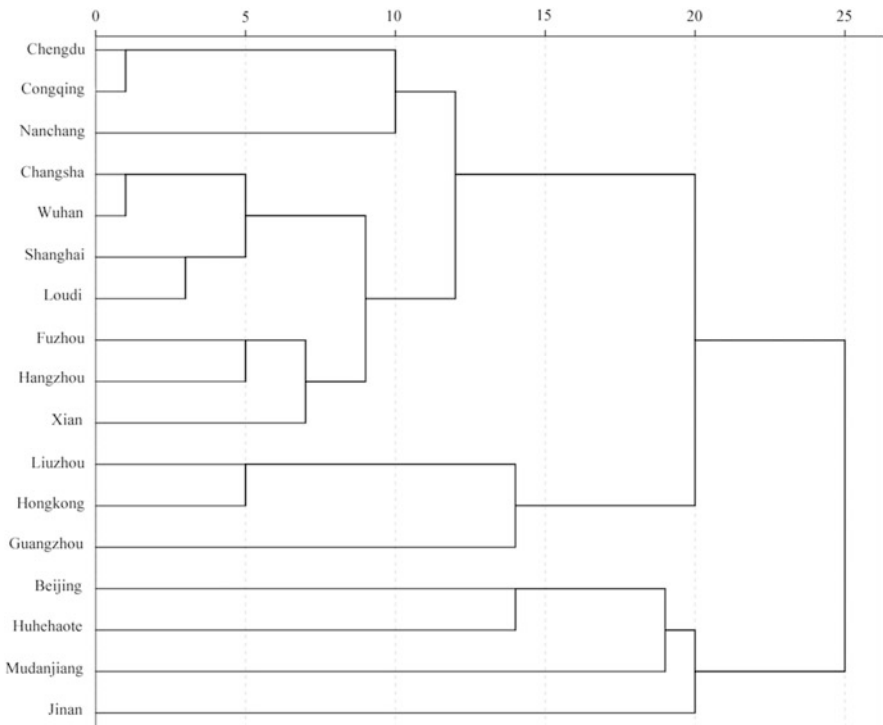
Fig. 4.5 The hierarchical cluster analysis for 17 cities in China based on top 10 abundant resident bird assemblages

environment, create special habitats, and thus support the same or similar "urban-adapter" species worldwide. In general, the cities in the Palearctic realm are dominated by Corvidae, Columbidae, Paridae, and Picidae, while those in the Oriental realm support more Pycnonotidae, Sturnidae, Timaliidae, and Cisticolidae.

The results of the regression analysis showed that there were no significant variations in MPD and family diversity index with the population and longitude of the cities; however, the MPD showed a significant increase with an increase in the latitude of the cities ($p = 0.001$, Fig. 4.6a), and the family diversity significantly decreased with increasing latitude ($p = 0.008$). The best fitted curve model between family diversity and latitude was quadratic function ($p = 0.006$, Fig. 4.6b), which indicated that the cities with moderate latitude have a relatively higher family diversity, which then started to decrease significantly with the increase in the latitude. Our results suggested that the cities in China with higher latitude usually support birds more discretely in phylogenetic structure, but with lower family diversity.

4.3.3   Bird's Responses to Urbanizations in China

4.3.3.1   Community Patterns in Response to Urbanization

Habitat modification or shifting is a primary feature of urbanization. The relationship between bird and habitat in urban environment has drawn much attention. The richness of the avian community in urban woodlots is usually the results of synthesized action of multifactors, such as patch size, habitat diversity, human disturbance, local avifauna, and urban landscape structures (Chen et al. 2002a). Generally, city parks with larger size, higher habitat diversity, and less human disturbance support higher bird diversities (Lu et al. 2007). In most urban green areas, tree species diversity, especially native plant richness, and foliage height diversity have a significant positive relationship with the bird species richness (Chen et al. 2002b; Ge et al. 2005). In a regional scale, heterogeneity among urban habitats is of importance in maintaining the urban bird diversity (Chen et al. 2002b). Most habitats in the urban area are highly fragmented. Chen et al. (2006a) examined the community patterns in response to habitat fragmentation in Hangzhou urban area in Eastern China. They found that: (1) though larger woodlots usually had more bird species, bird richness was higher per unit area in the smaller woodlots than the larger ones, and the overall bird density decreased with the increase in the size of the woodlot; (2) the evenness of species abundance increased with the area of the woodlot, and small woodlots were usually dominated by higher density species and large woodlots by medium density species; (3) most species occurring in small woodlots also occurred in larger woodlots; thus bird communities among urban woodlots showed a nestedness pattern in assemblage. Wang et al. (2013) further found that habitat nestedness was the main driver of species nestedness for all the bird assemblages. Human disturbance played an
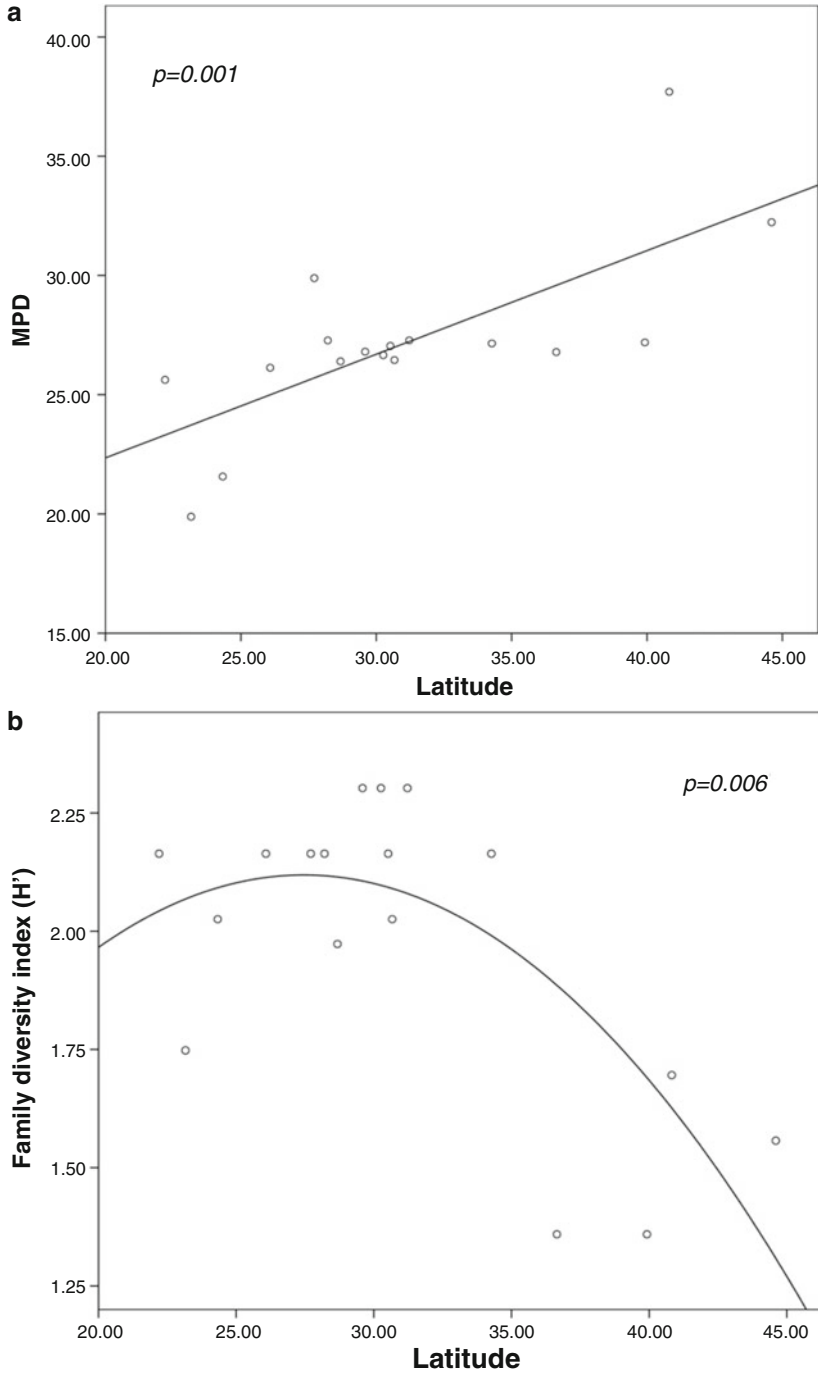
Fig. 4.6 The variations in phylogenetic structure (mean pairwise distance, MPD) and family diversity of the 17 cities in China with their latitudes

important role in the development of species nestedness for breeding birds, but not for winter species. These results suggested that we should protect woodlots with diverse habitats priority and refrain from using breeding birds and wintering species as surrogates for each other in developing conservation planning.

The effects of human disturbance on urban birds showed seasonal variations in the parks of highly populated areas in Hong Kong (Zhou and Chu 2012). Species richness was negatively affected by the visitor rate in the winter season, but the total bird density increased with the visitor rate in the breeding season. Regarding water birds in urban environment, Chen et al. (2000b) found that the habitat characteristics on landscape level (wetland shape, percent of surrounding building, wetland connectivity, and distance from city center) and disturbance (noise and human disturbance) showed strong relationships with species distributions. Diversity of food and human disturbance played significant roles in determining the variety of water bird species throughout the year. Species density and diversity decreased with increasing urbanization. There was no real adapter for water bird. Li et al. (2010a) surveyed the functional diversity of breeding birds in Hangzhou across an urbanization gradient. They found that the functional diversity showed a quadratic relationship with urbanization, i.e., functional diversity declined with increased urbanization only slightly at first but then dropped at an accelerated rate.

4.3.3.2 Different Species in Response to Urbanization

Different species had varied selectivity to urban habitats (Chen et al. 2002b). With increase in urbanization, the numbers of the foraging guild and the species number of the foraging guilds tended to decrease as a whole (Wang et al. 2004b; Huang et al. 2013). Urbanization had different impact patterns for different nesting guilds. The abundance of natural cavity/building nesters increased with urbanization, but that of canopy nesters, shrub nesters, ground nesters, and natural cavity nesters declined with increased urbanization. Among them, shrub nesters and ground nesters were particularly sensitive to urbanization (Li et al. 2009). Compared with new growth area in Hong Kong, there are more granivores, but fewer insectivores and insectivores-frugivores appeared in the developed areas, and introduced species were only recorded in the developed areas (Zhou et al. 2012). Flush distance, i.e., how close one can reach a bird before it flushes, reflects the adaptation of birds to human intrusion. To examine the responses of the birds to human intrusion and its influencing factors, nine dominant and widely distributed species were selected among 42 species surveyed in Hangzhou (Wang et al. 2004a). The results suggested that most species had adapted to human intrusions to some extent and that the birds with larger body, or those occurred in the habitats with higher visibility or closer to the ground, had relatively lower adaptation to human intrusions. Ye et al. (2014) further found that intruders with bright-colored clothes and higher walking speed could cause larger flush distances for the Eurasian tree sparrows in the urban environment.

Street trees are the important habitats for birds in urban area, and some birds choose to nest in street trees. Breeding birds and their nests were surveyed in the street tree strips in Hangzhou (Wang et al. 2003). The results indicated that Common blackbirds, Black-crowned night herons (*Nycticorax nycticorax*), Cattle egrets (*Bubulcus ibis*), Chinese pond herons (*Ardeola bacchus*), and Common magpies (*Pica pica*) tend to build nests on taller trees, White-rumped munias and Spotted doves tend to nest at the street tree strip with higher foliage height diversity, whereas Chinese bulbuls tend to nest at street tree strip with dense canopy cover. Furthermore, most birds nesting on street trees avoided human disturbances and have a higher nest height in an urbanized environment than its countryside counterpart. The characteristics of roost trees for birds had been surveyed in Kunming City, Yunnan Province (Li et al. 2011). The results showed that Brown-breasted bulbul (*Pycnonotus xanthorrhous*) preferred to roost in trees with tall buildings in the West. Black-headed greenfinch (*Carduelis ambigua*) and Eurasian tree sparrow preferred to roost in trees with shorter sunshine hours and high canopy density. Liu and Xu (2014) investigated the bird collisions with glass wall in Harbin urban area during migration season. They found that adjacent high street trees or forest reflecting in large-sized glasses would attract some small migrating birds, such as Dusky warbler (*Phylloscopus fuscatus*) and Arctic warbler (*P. borealis*) toward the glass walls. The Eurasian tree sparrow is regarded as one of the most abundant species in urban area, but evidences showed that highly urbanized areas are not suitable habitats for this species (Zhang et al. 2008; Zhang and Zheng 2010).

4.3.3.3 Individuals in Response to Urbanization

The Eurasian tree sparrows had higher densities in urban areas than that in rural ones. This tendency increased in winter season due to deficiency in food caused by heavy snow in the rural areas (Zheng and Huang 1965). However, The Eurasian tree sparrows in high urbanized area were found having lower body weight, higher proportion of heterophils (H), lower proportion of lymphocytes (L), and, consequently, a larger Nr (H):Nr (L) stress index, than the rural ones. These indices reveal that urbanized environments lead to the Eurasian tree sparrows to show the typical stress syndrome (Zhang and Zheng 2007). Baseline corticosterone concentration (BCC) has been found to increase slightly in some bird species in response to certain environmental challenges, such as decreased food availability (Marra and Holberton 1998; Angelier et al. 2007). Baseline corticosterone levels could, therefore, provide some information on the ability of the individuals to cope with environmental challenges (Kitaysky et al. 1999). Zhang et al. (2011) showed that the BCCs of Tree sparrow populations were strongly and positively correlated with the degree of urbanization of the habitat. Average BCC of Eurasian tree sparrows from high-rise residential areas and a university campus were significantly higher than those from the rural areas, suggesting that Eurasian tree sparrows living in highly urbanized areas have greater environmental challenges than those in the rural areas. The Chinese bulbul is a common species that occurs widely in southern

China. It is abundant and nests even in dense urban areas (Lan et al. 2013). Studies found that this bird not only adjusts its diets and flush distance to urbanization (Wang et al. 2004a; 2005a; Chen et al. 2006b) but also adjusts the composition of their nests in response to urbanization, i.e., the proportion of anthropogenic nesting materials increased significantly with urbanization (Wang et al. 2009). The adaptation behaviors were also documented in other urban adapters. For the Black-billed magpie, it was found that their nest heights from the ground increased significantly with urbanization intensity (Wang et al. 2008; Lu et al. 2008). This adjustment can be attributed to the increase in human disturbance. The Common blackbirds in urban environments were documented frequently using anthropogenic structures such as nesting sites (Wang et al. 2015). These nesting behavior shifts that resulted from the increase in the available anthropogenic nesting sites and decrease in the number of natural nesting sites may aid them to colonize in the urban environments. Human-induced food resources are usually the major causes attracting some birds toward urban habitats (Chace and Walsh 2006). In this context, Wu et al. (2009) found that human feeding in urban areas can cause wintering Black-headed gull (*Larus ridibundus*) to lose their wildness, making them reluctant to go back to their breeding regions during summer, and increasing the risk of infection of avian flu.

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Chapter 5
Why Are Exotic Birds So Successful in Urbanized Environments?

Daniel Sol, Cesar González-Lagos, Oriol Lapiedra, and Mario Díaz

Abstract Many nonindigenous organisms, including birds, are often restricted to human-altered environments within the region of introduction. The classical explanation is that human-related alterations make the environment easier to invade by reducing biotic resistance and offering new niche opportunities. However, the pattern may also reflect that many more species have been introduced in human-altered environments and/or that traits associated with invasion success and the ability to thrive in these environments are related. In this chapter, we argue that if we want to fully understand why exotic organisms are mainly successful in human-altered environments, we need to see the invasion process as a set of stages with different probabilities of being transited. Applied to birds, this framework suggests that there is a high probability that an exotic species ends up associated with human-altered environments if the species: (1) is more abundant (and hence more available for introduction) in urbanized environments; (2) has a higher chance to be successfully transported, as it is already habituated to humans; and (3) has a higher probability to be introduced in an urbanized environment, where most humans live. If these arguments are true, then the exotic species is

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likely to successfully establish itself in the new region because the species should already have the traits needed to persist in the novel environment. Although more supporting evidence is needed, the proposed framework provides a general solution for the paradox that many invaders are more successful in the new environment than most native species.

Keywords Biological invasions • Invasion success • Biotic resistance • Novel niches • Life history • Anthropocene

5.1   Introduction

Ever since Elton (1958), environmental disturbances are deemed essential to understanding invasion success. This is reflected in the higher success of invaders in altered environments than in more pristine ones (Sax and Brown 2000). Birds fit well to this pattern; not only they tend to be more frequent and abundant in such environments, notably urbanized environments, but many seem to be unable to expand to more pristine habitats (Case 1996; Fig. 5.1). Diamond and Veitch (1981) first noted this in New Zealand, where alien birds are highly abundant in human-altered habitats yet virtually absent from unmodified forest.

In the present chapter, we ask why exotic birds often proliferate in urbanized environments. This involves addressing (1) why they are able to succeed in such environments and (2) why they rarely expand to more natural habitats. While these two questions may be seen as the two sides of a same coin, each also has their own singularities. The concept of disturbance is central to resolve the first question. By altering natural environments, humans may be creating new niche opportunities for invaders and reducing biotic resistance, making the new environments more susceptible to be invaded (Case 1996). While this hypothesis alone could explain why exotic birds are common in urbanized environments, two alternative explanations
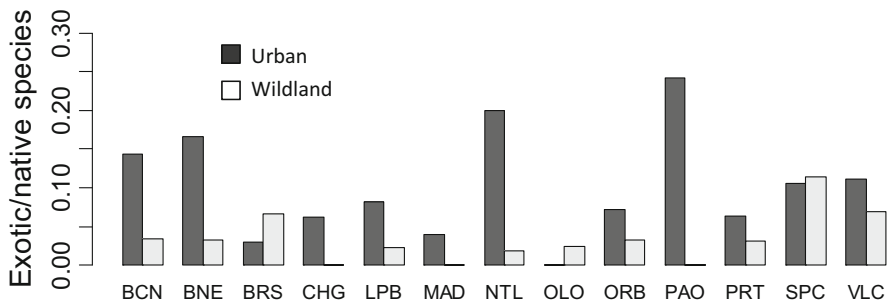
Fig. 5.1 Ratio of exotic-to-native avian species in urban habitats and non-urban surrounding wildland for several regions worldwide. Abbreviations correspond to BCN = Barcelona, BNE = Brisbane, BRS = Bristol, CHG = Cameron Highlands, LPB = La Paz, MAD = Madrid, NTL = Newcastle, OLO = Olongapo, ORB = Orebro, PAO = Palo Alto, PRT = Pretoria, SPC = La Palma, and VLC = Valencia. For references, see Sol et al. (2014)

also need to be considered. On one hand, although human-altered environments may seem highly susceptible to be invaded, this may simply reflect that many more species have been introduced there. On the other hand, an association of exotic birds with urbanized habitats is also expected if traits associated with invasion success and the ability to thrive in close proximity to humans are related (Ehrlich 1989). We argue that these two alternatives also contribute, along with disturbances, to explain the proliferation of exotic birds in human-altered environments.

In contrast, the question of why exotic birds rarely expand to more natural habitats is less clear, although some hypotheses have been advanced. Higher biotic resistance and stronger environmental filtering in more natural communities are obvious explanations (Diamond and Veitch 1981), yet a number of alternatives exist, including insufficient time for the invader to spread or behavioural preferences for human-altered habitats. We discuss these hypotheses and suggest that the study of the few exceptions of exotic birds invading natural environments provide unique opportunities to tease them apart.

5.2 Why Are Exotic Birds Able to Succeed in Human-Altered Environments?

5.2.1 Susceptibility of Urban Environments to Avian Invaders

Human-induced disturbances may facilitate invasions by increasing resource opportunities and reducing biotic resistance (Case 1996). A resource opportunity refers to the availability of resources on which an invader depends (Shea and Chesson 2002) and can arise from the non-random loss of native species in urbanized habitats (Simberloff 1995). This loss results from the drastic environmental alterations associated with urbanization, which includes a replacement of natural vegetation by built structures, a shift from natural to artificial resources and a higher frequency of human disturbances (Marzluff et al. 2001; McKinney 2002). These alterations may act as strong environmental filters by limiting the persistence of those species incapable of tolerating them (Evans et al. 2011; Sol et al. 2014).

Although a reduced species diversity may imply the absence of entire functional groups (Simberloff 1995), human activities offer at the same time a variety of novel resource opportunities to which native species have had little opportunity to adapt (MacLeod et al. 2009). These include food supplies like artificial feeders and garbage and nesting sites such as holes and cavities in buildings. If a species is able to exploit these opportunities while tolerating the human presence, this may facilitate population growth and establishment in the novel region (for a review of the influence of these factors on the establishment of native species in cities, see Tomiałojć 2016).

The combination of low diversity of native species and high levels of novel niche opportunities may make communities less resistant to invaders that are able to exploit these opportunities (Shea and Chesson 2002). First, the number of potential competitors should not only be reduced in urbanized environments but the few that thrive there may have had insufficient time to adapt to efficiently exploit the local resources. Second, the pressure from enemies should also be reduced due to the release from their natural predators and parasites, which usually are not introduced with the exotic species (Shochat et al. 2010). Finally, human-related alterations may generate spatial and temporal environmental heterogeneity through the fragmentation of natural habitats and the creation of artificial environments. A structurally heterogeneous region may provide a greater array of microenvironments, increasing the likelihood that the invader encounters a favourable niche not monopolized by native species.

Although still limited, evidence is accumulating that human-induced environmental alterations facilitate invasions by opening resource opportunities and decreasing biotic resistance from resident native species. For example, Barnagaud et al. (2013) reported that in New Zealand, exotic and native bird species segregate along gradients of anthropogenic disturbance, with exotic species being more common in disturbed environments. Interestingly, native and exotic species overlapped little in functional traits related to habitat selection. Hence, habitat segregation patterns are probably mediated more by environmental filtering processes than by competition at landscape and local scales.

Likewise, in SE Australia, the success of exotic birds in highly urbanized environments does not seem to be associated with their competitive superiority over native birds but with the existence of resource opportunities derived from human activities (Sol et al. 2012a). Thus, the most successful avian invaders were generally smaller and less aggressive than many natives and were excluded from experimental food patches where competition was strong. Instead, the most successful exotic birds were those less afraid of taking advantage of food opportunities provided by humans, consistent with the view that exotic species that opportunistically exploit the abundant food accidentally or deliberately produced by human activities may reach high population densities (Marzluff 2001; Shochat et al. 2010; Møller et al. 2012).

This is not to say that contest competition is irrelevant during the establishment stage. In ring-necked parakeets (*Psittacula krameri*) introduced to southern Spain, detailed observations by Hernández-Brito et al. (2014) suggest that these parakeets are outcompeting native species with similar nest-site requirements. However, there is currently little evidence that traits that provide competitive advantages favour establishment in birds (Duncan et al. 2003). In contrast, as discussed in later sections, evidence is accumulating for a set of traits that may facilitate the adoption of novel niches with no need of aggressive displacements.

5.2.2 Adaptations to Find a Niche in Urbanized Environments

While the physical environment may in some cases have a negligible impact on habitat invasibility (Von Holle and Simberloff 2005), the existence of environmental filtering suggests that most birds do not tolerate well the drastic alterations associated with urbanization (Sol et al. 2014). If so, why are many exotic species so successful in urbanized environments? Do they have adaptations that allow them to be successful urban dwellers? A number of features have been found to predict invasion success in birds, including behavioural plasticity (see Miranda 2016), ecological generalism and particular aspects of their life history (Sol et al. 2012b). Importantly, these same traits have also been associated with tolerance to urbanization (Table 5.1).

A major feature of successful avian invaders appears to be behavioural plasticity. Ever since Mayr (1965), behavioural plasticity has been considered a main feature of successful avian invaders on the grounds that a species that accommodates its behaviour to the demands of the new environment is generally more likely to succeed than a species that persists with the behaviours of its place of origin. Indeed, there is evidence showing that the likelihood of establishment in novel regions increases with the propensity to learn new behaviours and the underlying neural substrates (Sol et al. 2005, 2008; Amiel et al. 2011). Behavioural adjustments (Kark et al. 2007; Lowry et al. 2012; Sol et al. 2013), together with the associated brain structures (Maklakov et al. 2011, but see Sol et al. 2014), are also

Table 5.1 Evidence for common traits facilitating invasion success of exotic birds and tolerance of native birds to urbanization. Abbreviations: NS = non-significant; + = Supporting evidence

Traits and metrics	Evidence for urbanization	Sources	Evidence for invasions	Sources
Behavioural flexibility				
Relative brain size	NS, +, NS, +, NS	a–e	+, +, +, +	f–h, m
Innovation propensity	NS, +, +	a, i, j	+, +, +	f–h
Niche features				
Niche position	+, +	c, e		
Niche breadth	+, +	b, e	+, +, +	k, l, m
Life history				
Brood value	+	e	+	m
Human tolerance				
Mean flight initiation distance (FID)	+, NS, NS	n, b, i	None	o
FID intraspecific variation	+, +	b, p	+	q

References: a = Kark et al. (2007), b = Carrete and Tella (2011), c = Evans et al. (2011), d = Maklakov et al. (2011), e = Sol et al. (2014), f = Sol and Lefebvre (2000), g = Sol et al. (2002), h = Sol et al. (2005), i = Møller (2009), j = Sol et al. (2013), k = McLain et al. (1999), l = Cassey et al. (2004), m = Sol et al. (2012b), n = Møller (2008), o = Sol et al. (2012a), p = Møller (2010), q = Sol et al. (2011)

deemed essential to persist in urban environments. These include the need to develop innovative foraging techniques to exploit novel foods, to habituate to the human presence and to learn how to avoid risks like being run over by cars (Møller 2008, 2009; Liker and Bókony 2009; Sol et al. 2011, 2013; Husby and Husby 2014).

In addition to behavioural plasticity, a broad ecological niche should also increase the likelihood that an invader can find the necessary resources and suitable physical conditions in the novel environment (Ehrlich 1989; McLain et al. 1999; Cassey et al. 2004). In birds, species that are either dietary or habitat generalists are more likely to establish themselves successfully in new regions (McLain et al. 1999; Cassey et al. 2004). Ecological generalism can also increase urbanization tolerance, as evidenced by the fact that urban exploiters have broader environmental tolerances than avoiders, at least in terms of habitat breadth and geographic range size (Bonier et al. 2007; Evans et al. 2011; Sol et al. 2014).

Finally, recent evidence suggests that the life history of birds also affects their invasion success. Specifically, successful avian invaders appear to prioritize future over current reproduction, either by having a long reproductive life or by reproducing more frequently (Sol et al. 2012b). This strategy reduces the costs of a reproductive failure due to bad decisions (e.g. nesting in an inappropriate site) and allows skipping a reproduction when conditions are unfavourable. The possibility to delay reproduction increases the time available for acquiring environmental information and for improving performance in exploiting the resources and avoiding enemies. A life history strategy that prioritizes future returns also seems to characterize urban dwellers, according to a recent global comparative analysis (Sol et al. 2014). This is illustrated by dark-eyed juncos recently established in an urbanized environment in San Diego (California), which lay more clutches per season than those living in their traditional habitats and hence compensate for the lower success of each breeding attempt (Yeh and Price 2004).

5.2.3   Selective Filters Favouring Adaptations to Urbanized Environments

While there is increasing evidence that traits associated with urbanization also favour establishment in human-driven introductions, the question arises of why these features should be present in species selected for introduction. In fact, many introduced species are neither particularly ecologically and/or behaviourally plastic nor have a future returns life history strategy, which in part explains the high rate of failure in avian introductions (Duncan et al. 2003; Sol et al. 2012b). Still, the fact that a substantial fraction of introduced species do have adaptations to persist in urbanized environments warrants explanation. One possibility is that these properties are widespread among birds, so even if the species were selected at random, many should possess them. However, this is unlikely to be the case for all traits. Indeed, the combination of adaptations that make species successful urban dwellers does not seem to be very

common in nature (Sol et al. 2014). Alternatively, the same process of transport and introduction may select for species with the adaptations needed to persist in urbanized environments. In fact, it has been known for some time that introduced birds are a distinctly non-random subset of the world's birds (Blackburn and Duncan 2001; Duncan et al. 2003). Because species with enhanced behavioural plasticity, broad ecological niches and life histories that prioritize future reproduction are more likely to be abundant close to human settlements (Evans et al. 2011; Sol et al. 2014), they should also be more readily available for introduction. Even species that thrive in urban environments thanks to more specialized adaptations can be favoured in introductions if they are more readily available.

Urban species may be easier to obtain not only because they live close to humans but also because they can attain higher densities in these environments due to the release from enemies and the high availability of resources (Shochat et al. 2006; Møller et al. 2012). Because they are easier to obtain, it is even possible that urban birds are introduced in higher numbers than non-urban birds. This is relevant because a large propagule size is known to facilitate establishment by reducing the risk of extinction by demographic stochasticity and Allee effects (Lockwood et al. 2005; Simberloff 2009) as well as by enhancing phenotypic variation (Holt et al. 2005). However, whether urban birds are more likely to be introduced in large numbers than non-urban birds remains to be tested.

Not only are some species more available for introduction than others because of their higher abundance close to human settlements but the subsequent stages in the invasion process can also filter species according to their features. This is because only those birds with appropriate phenotypes negotiate any given stage of the invasion process successfully (Chapple et al. 2012). Such a 'selective filter' may sometimes favour phenotypes better adapted to urbanization (Fig. 5.2). Møller et al. (2015), for example, proposed that the adaptations that enable birds to live in the proximity of humans, like reduced fear to humans, can also better predispose them for coping with capture, transport and introduction. Likewise, animals that are flexible in their behaviours and that have broader diets and environmental tolerances should better cope with captivity as they can adjust to such conditions more readily (Mason et al. 2013). While there is current controversy regarding whether there exist some traits that favour crossing all the stages of the invasion process (Chapple et al. 2012), the existence of traits associated with human-altered environments emerges as one of the few plausible generalizations.

The 'selective filter' can further strengthen the relationship of birds with humans if individuals are kept in captivity for several generations before being released, as this can artificially select for traits that facilitate living and reproducing close to humans (McDougall et al. 2006; Carrete and Tella 2008). Artificial selection for frequent reproduction in their domestic ancestors is thought to allow feral pigeons to increase offspring productivity (Janiga 1991), contributing to compensate for the high mortality rate associated with starvation and car accidents. Nevertheless, if an exotic species has been bred in captivity for long periods of time, artificial selection can have eroded many of its behaviours and other phenotypic traits needed to survive in nature (McDougall et al. 2006; Carrete and Tella 2008; Sol 2008). This
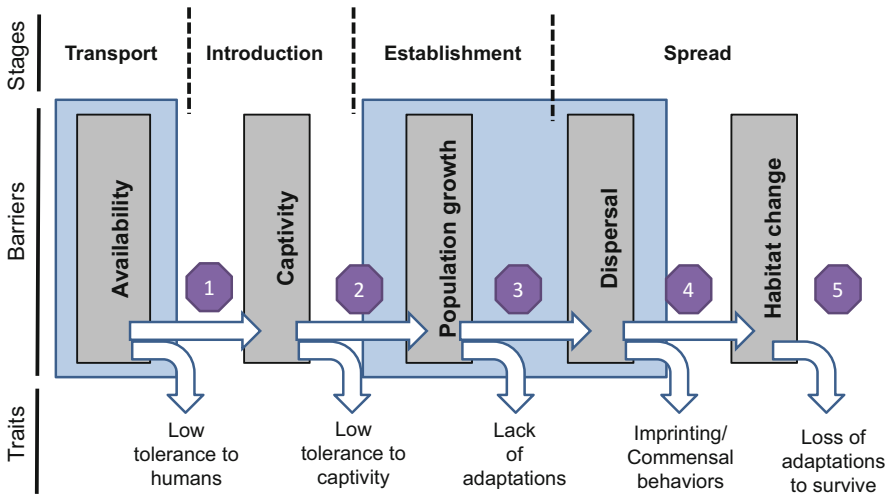
Fig. 5.2 Successful invasion of a new location involves a four-stage process (Blackburn et al. 2011). Each stage selects for different traits, both among and within species, which may in part explain why exotic birds mostly proliferate in urbanized environments. The species must firstly be deliberately or accidentally transported (transport stage) and introduced (introduction stage) to a new location outside their native range; this is more likely if the species exhibits tolerance to humans and human-altered environments (barriers 1 and 2), thereby increasing availability and enhancing survivorship in captivity. Next, the species must establish a self-sustaining population in the novel environment (establishment stage); this further sorts out birds according to traits that enhance the probability of finding an appropriate niche in human-altered environments, such as behavioural plasticity and broad ecological tolerances (barrier 3). Then, the population must subsequently increase in abundance and expand their geographic area (spread stage); spread towards more natural habitats can be limited by behavioural decisions that force individuals to settle in urbanized environments (barrier 4). Finally, the expansion to more natural environments may be further limited by a lack of appropriate adaptations (barrier 5)

is less of a problem in species that rely on resources directly provided by humans. The high invasion success of feral pigeons, for example, is in part related to the exploitation of the large amount of food provided by people (Sol 2008).

Humans could not only unintentionally select species for introduction that are capable of thriving in cities, but may also enhance their establishment success by yet another way, releasing them in urbanised environments. As humans are more likely to accidentally or deliberately introduce organisms close to where they live, this predicts a certain association between exotic species and urbanized environments. In Barcelona, for example, the earliest observations of the currently large population of monk parakeets (*Myiopsitta monachus*) were near the zoological garden, from where they presumably escaped (Batllori and Nos 1985). Likewise, for European settlers in the eighteenth and nineteenth centuries moving to the Americas, Australia, New Zealand and South Africa, introducing birds close to their homes was a common practice in their attempt to recreate their European homeland (Duncan et al. 2003). By accidentally transporting exotic birds from one city to another, humans may have also favoured their spread.

5.3 Why Are Exotic Species Unable to Expand to More Natural Habitats?

Although the reasons why exotic birds do not expand to more natural habitats are largely unknown, for birds limited dispersal capabilities does not seem to be the explanation considering their well-developed flying capabilities. Moreover, cities are often located within mosaics of natural habitats, again suggesting that distance is not limiting spread. Alternative explanations are thus needed.

Following our previous arguments, an obvious explanation for the failure of exotic birds to expand to more natural surrounding habitats is that they cannot persist there. This can occur because of higher biotic resistance of these environments, which is expected if these communities are more diverse and mature. Alternatively, the invader may lack adaptations to persist in such environments (Shochat and Ovadia 2011).

Other explanations need to be considered as well. First, many introduced populations might have had insufficient time to increase in numbers so as to generate enough propagules to expand to new habitats. Time lags between establishment and spread are commonly reported in the literature (Williamson 1996) and have been attributed to factors such as the time required to adapt to the new environment or changes in the way the invader interacts with native species (see Chapple et al. 2012; Hufbauer and Facon 2012). If time lags are the cause of some exotics being restricted to urbanized environments, we expect that the species expand the range of habitats used over time following classical habitat selection models that predict shifts to alternative habitats when the preferred ones become saturated (Křivan et al. 2008). There is indeed some evidence that avian invaders behave as habitat specialists during the earlier stages of the invasion process and subsequently relax their preferences when the preferred habitats become saturated (Sol et al. 1997; Kövér et al. 2015). However, there are also well-documented cases where an exotic bird has remained restricted to human-altered environments despite having had good opportunities to spread to surrounding natural habitats. In the city of Valencia, for example, 35 years after initial settlement of different Psittacidae species, they are still largely confined to the urban area (Murgui 2001; Murgui and Valentín 2003).

Second, exotic species can exhibit a strong preference for urbanized habitats in the new region. The singularity of urbanized environments may for instance favour strong habitat imprinting, making individuals to prefer settling in the habitat type in which they were born (Evans et al. 2009). If this mechanism is important, we would only expect shifts to more natural environments when urbanized environments become saturated and when the bird has enough plasticity to overcome the influence of imprinting. Alternatively, if species have been selected for traits that force them to live in close association with humans during the capture and transport, this can also enhance their preference to settle in urbanized environments once released. This can be particularly important when artificial selection has eroded the behaviours and other phenotypic features needed to survive in nature (McDougall et al. 2006; Carrete and Tella 2008), which may make the population highly

dependent on human assistance. Feral pigeons (*Columba livia*), for example, still preserve some characters engendered through artificial selection during their ancestral period of domesticity, notably a disproportionally longer tarsus; this leg morphology appears to limit the use of food resources other than those directly provided by humans and, as a result, increases mortality when individuals have to search for their own food (Sol 2008).

While many exotic species are restricted to human-altered environments, a few have been able to invade more natural habitats. This is the case of the red-billed leiothrix, *Leiothrix lutea*, which has been able to establish itself in forests from the Western Mediterranean region and Japan. Combining historical information, phylogenetic analyses and field observations and experiments, Vall-llosera et al. (2016) reported that leiothrixes established themselves with relatively little resistance or significant consequences for most native species, reflecting the opportunist-generalist nature of both the invader and the invaded native community. Moreover, some of their key niche requirements were poorly represented in the native community, suggesting that the species is using an infra-utilized niche. While this fits well with the view that the existence of niche opportunities and reduced biotic resistance is crucial for the success of exotic birds, additional studies in other species invading natural habitats are warranted.

5.4 Conclusions

Human-altered environments may be particularly susceptible to invaders, but this alone is insufficient to understand the success of exotic birds in urbanized environments. We argue that if we want to further understand this, we need to see the invasion process as a chain of stages with different probabilities of being transited (Fig. 5.3). The adoption of such a framework highlights that the odds are high that an exotic bird ends up associated with urbanized environments if the species (1) is abundant in urbanized environments and hence more available for introduction; (2) has a higher chance to be successfully transported, as it is already habituated to humans; and (3) has a higher probability to be introduced in an urbanized environment, where most humans live. Given that habitats are altered by humans in similar ways worldwide, birds that do well in human-altered habitats in their native range should also perform well when introduced within similarly human-altered habitats (Ehrlich 1989; Hufbauer and Facon 2012). The existence of such human-mediated environmental matching is supported by two comparative analyses. The first study reported that species that use urban environments in their native regions are more likely to be successfully introduced outside their native ranges (Sol et al. 2002), although subsequent studies with broader samples failed to provide similar evidence (e.g. Sol et al. 2012b). More recently, Møller et al. (2015) tested the hypothesis with a stronger measure of urbanization tolerance based on changes in abundance between urban and rural habitats. They found that the most tolerant species were also more likely to succeed when introduced to Pacific Islands. While
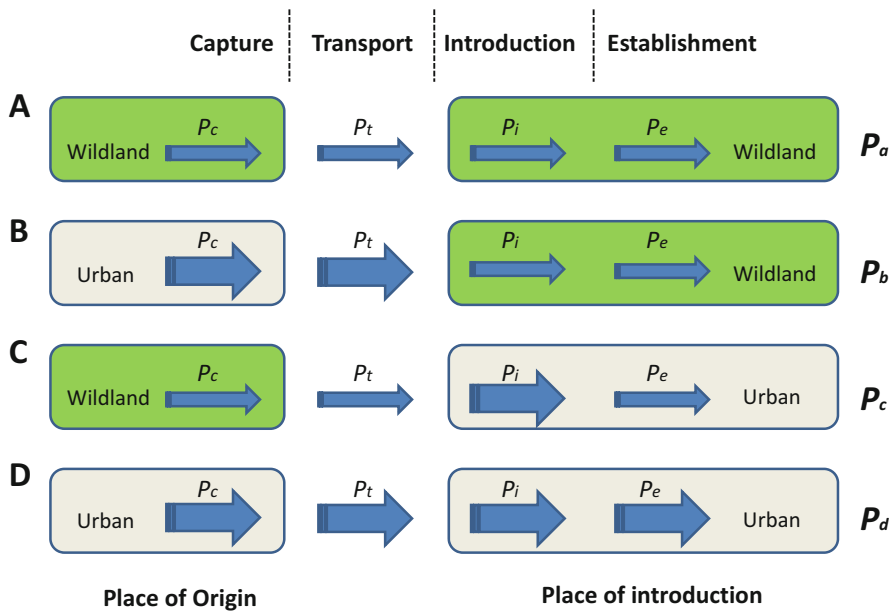
Fig. 5.3 Framework to understand why we expect many exotic species to be successful in urbanized environments. The scheme represents four scenarios defined by the habitats of origin and introduction of the exotic species (from A to D). The size of each arrow represents the probability that a species is captured (P_c), transported (P_t), introduced (P_i) and successfully established (P_e). These probabilities multiply along the pathway to determine the probability of observing an exotic species in the final habitat (P_a to P_d), with $P_a < P_b < P_c < P_d$

this result yields important support for the existence of human-mediated environmental matching, more studies are needed to further support the pattern and unravel the underlying mechanisms.

Understanding why exotic birds are mostly restricted to human-altered environments allows resolving a major paradox in invasions biology, namely, why exotic species that have had little opportunity to adapt to the novel environment are able to proliferate there and even become more abundant than many native species (Simberloff 1995; Case 1996; Sax and Brown 2000). According to the framework we propose in this chapter, the success of many avian invasions is not a paradox. Rather, it may be understood if we consider that (1) successful invaders are occupying infra-utilized or novel ecological niches associated with human activities that most native species are unable to use (Sax and Brown 2000; Sol et al. 2012a), and (2) exotic species possess the necessary adaptations to invade these niches because human activities facilitate environmental matching by determining which, where and how the species are introduced. Although our focus here is on birds, we suspect our conclusions must also apply to other organisms (see Bartomeus et al. 2011 for an example in plants).

5.5 Conservation Implications

The above conclusions have two main implications for conservation. The first is related to biotic homogenization, that is, the increased resemblance of biotas across different regions due to the extinction of native species and the introduction of exotic species. As pointed out by McKinney (2006), urbanization increases biological homogenization because the few species capable to persist in such environments become increasingly widespread and locally abundant across cities. Successful avian invaders that proliferate in urbanized environments not only contribute to the homogenization process in such environments but also scale up the effect to a global level (but see Aronson et al. 2014). This goes against the increasingly perceived role of cities as future reservoirs of biodiversity (Secretariat of the Convention on Biological Diversity 2012).

The second implication for conservation concerns the impact of invaders. If exotic birds are restricted to use altered environments, it follows that their impact over native species should be more reduced. This fits well with evidence that exotic birds have caused few extinctions in the past (Sax and Gaines 2008). Although Case (1996) reported a positive relationship between the numbers of established and recently extinct bird species at locations around the world, this relationship does not arise because introduced birds cause the extinction of native species as most extinctions occurred prior to bird introductions. Rather, this pattern may reflect that human disturbances simultaneously reduce the diversity of native species and create new habitats favourable for the establishment of introduced birds (Case 1996; Duncan et al. 2003). Sax and collaborators (2008) even suggested that established exotic birds could contribute to increase biodiversity at local and regional scales. However, the fact that most exotic birds occur in disturbed environments indicate that they do not simply compensate the loss of native species but that they often play different functional roles in the ecosystem.

In any case, the conclusion that exotic birds do not generally pose risks for native species should be taken with caution. Extinctions can take time, and hence it is possible that some avian introductions are too recent for the impact to be observed. Moreover, the possibility remains that some exotic birds have not yet had time to expand to more natural habitats. Although some of the reasons that link exotic species to urban environments may also explain their limited success in more natural environments, the reasons why they rarely expand to more natural habitats are largely unknown. Given the difficulties to investigate why a species is absent from a particular habitat, the alternative to shift the focus to those few exotic birds that are present in natural habitats is likely to represent an important avenue for future research.

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Chapter 6
Becoming Citizens: Avian Adaptations to Urban Life

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Abstract Although cities have existed for some millennia, it has been only in the last few centuries that they have expanded to become a dominant feature of the landscape. Their growth displaces original habitats and creates new ones, facing birds with the challenge of adjusting their behaviour, physiology and life histories to the novel conditions or be displaced into a shrinking and also increasingly altered rural landscape. Here we identify the salient features—habitat structure, seasonality, interspecific interactions and pollution—in which cities differ from natural environments and to which birds must adjust. Then we describe the several ways in which urban birds have been found to differ from their rural counterparts. Finally, we evaluate whether these differences constitute adaptations to urban conditions or whether they are expressions of pre-existing adaptations to natural conditions, such as behavioural plasticity, which also permit the colonisation of urban habitats.

Keywords Urban birds • Adaptation • Cities vs natural areas • Pollution • Urban habitat structure

6.1 There Was Once a Country Sparrow

Organisms constantly modify the environment, and it has been argued that virtually every trait they exhibit has consequences on other organisms (Bailey 2012). Indeed, our constant physical and chemical interactions with the surroundings, including the biota, influence in several ways the functioning of the ecosystems. While most such influences may be important, their impact on the environment is usually minor, yet some have major, even drastic environmental effects. The history of life on

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Earth provides several examples of massive effects of organisms on the environment, such as the modification from a reductive to an oxidative atmosphere by photosynthetic cyanobacteria. This biotic influence fundamentally changed the way in which living organisms, erstwhile adapted to an anaerobic atmosphere, reorganised their metabolic pathways to create aerobic respiration, thus using toxic oxygen to extract energy from organic compounds (Kasting and Siefert 2002). Such major effects of organisms on the environment constitute selective pressures that may bring about extinction but also can promote adaptations of species to the changing conditions. In this era, which has been dubbed Anthropocene (Zalasiewicz et al. 2010; Monastersky 2015), urbanisation is becoming a major source of change, as cities sprawl over increasingly larger proportions of the land, facing species with novel ecological conditions in which they may thrive or from which they are displaced (Adams 2005; Goddard et al. 2010). The transformation of natural landscapes into urban zones creates areas with similar ecological conditions through the globe, contributing to biotic homogenisation (Blair 1996, 2001).

Although in the long run new conditions may favour ecological novelty, which is often an engine of speciation (cf. the many adaptive radiations that followed the transformation of the atmosphere from reductive to oxidant), it seems clear that in the short term, the main effect of major environmental disturbances is a loss of biodiversity.

This seems to be the typical consequence of urbanisation, in which environmental alterations are often so drastic and rapid that exceed the limits of tolerance of many species including plants, arthropods, amphibians, birds and mammals (Sih 2013). Yet, some species appear not only to be little affected by the urbanisation process but to take advantage of it, which has allowed them to grow in number and expand their range (Sol et al. 2013). Interestingly, these species seem to have some behavioural attributes in common such as behavioural plasticity, which although not a novelty, that may promote the spread and perhaps the diversification of urban biota. Indeed, there are several examples of avian species that seem to be particularly successful at colonising cities and which have consequently been often studied with the aim of determining what enables them to become good city dwellers.

To explore what distinguishes those bird species that are widespread in cities from those restricted to natural sites and to assess whether phenotypic differences could be due to plasticity or to evolutionary change (see also Chap. 7 by Miranda 2016), we first identify the main factors in which cities differ from rural to natural environments and that are likely to influence avian ecology. We then look into some of the species which have inhabited the cities for longer periods of time trying to identify which attributes they share and which ones allow them the successful colonisation of cities. Finally, we discuss whether differences in the attributes between urban and rural/wild populations or species can be safely regarded as adaptations to urban life.

6.2   How Are Cities Different from Natural Areas?

6.2.1   Habitat Structure and Seasonality

Cities represent a local change in habitat structure, climate and productivity, in which the adaptations of local organisms to the pre-existing natural environment may no longer work. Such disturbance alters ecological interactions thus leading to changes in the biological communities (Shochat et al. 2006). Both the identity and the distribution of plant species—sources of food, shelter, nesting places and materials for native birds—are different between the cities and their surroundings (e.g. McDonnell et al. 1997), and bird communities are responsive to those differences (Day 1995; Carbó-Ramírez and Zuria 2011; Becker 2013). Cities are not built to promote biodiversity; thus their plant communities include only a small number of species, often ornamental of exotic origin, which may not cover the needs of the local avifauna (but see Gleditsch 2016). Nevertheless, green islands of vegetation—parks and gardens— which receive regular irrigation, palliate some of the consequences of urbanisation. Urban gardens help to buffer the fluctuations of temperature and humidity due to the dryness and reflection coefficient (albedo) of concrete and asphalt surfaces (Gilbert 1989; Jauregui 1991). Gardens also provide birds with regular food supplies in the form of invertebrates that feed on the irrigated plants and thrive in the thermal conditions provided by the vegetation (Pickett et al. 2001). Finally, gardens offer shelter from the weather and predators to potential nesting places; it is in them that native and exotic avian species alike concentrate (Susca et al. 2011; Lugo et al. 2012). Urban gardens may also be frequented by predators, thus potentially acting as ecological traps (Sorace and Visentin 2007). Because of the constant irrigation, and also from design (as they include many perennial species), these urban green islands can also represent a buffer from seasonality.

Many organisms adaptively time several aspects of their life history to the predictable periodic changes that are caused by geophysical cycles (Lack 1968; Murton and Westwood 1977; Nicholls et al. 1988). In addition to internal rhythms, such tracking of the seasons occurs in response to changes in environmental variables (e.g. temperature, photoperiod, rainfall and food availability; Dawson 2008). In cities, however, seasonality is buffered, and the cues that birds use to track it may be blurred by gardening activities (Haggard 1990; Shochat et al. 2006). Also urbanisation could alter phenology through altered photic conditions due to artificial lights at night. Yet, reduced seasonality does not necessarily need to be bad for birds and may be the key to the success of some urban birds. For instance, bird assemblage composition in parks of Valencia is maintained through the constant arrival of migrant species through the year, arguably favoured by the stability of the conditions, including food availability (Murgui 2007). These circumstances favour resident species that can become dominant by excluding others from their urban park territories and also contribute to the lack of functional response, by which population size responds to fluctuations in food production.

For other species, however, becoming urban residents is not an option, either because they are migrants who need to reach their breeding or wintering grounds on time or because the seasonality of key elements of their ecology (e.g. food or predators) is not influenced by the conditions in the cities. Therefore, it is crucial for them to correctly read the changes in the season in order to not risk local extinction through the timing of food, shelter and other resources (Lugo et al. 2012).

6.2.2 Interspecific Interactions

Urbanisation modifies the structure of animal communities and the way in which organisms interact. Cities do harbour a much reduced diversity of vertebrate predators than natural environments (McKinney 2002). This is somewhat counterbalanced by the very high numbers of those predators that are found in cities, particularly domestic cats (*Felis catus*), whose reported effect on urban birds can range from minor (e.g. Gering and Blair 1999; Gillies and Clout 2003) to severe (e.g. Woods et al. 2003; Loss et al. 2013), often compromising the persistence of urban bird populations (e.g. Baker et al. 2005; Van Heezik et al. 2010). The latter may be particularly true for native bird species in areas where cats are not originally native (Sorace 2002). Predation by cats may influence the composition of the urban bird assemblage, with the least susceptible species becoming dominant (e.g. Noske 1998); it is intense, affecting millions of birds every year, although perhaps not more so than in nonurban environments (Baker et al. 2008), and it appears to afflict birds in low condition (old, diseased, injured), as would be expected elsewhere (Baker et al. 2008).

The responses of avian predators to urbanisation vary between species and as a function of the urbanisation process. Specialist predators, being more sensitive to changes in the prey community, are typically much less frequent in cities than in the surrounding habitats (Blair 2001; Mckinney 2006), which is not the case of more generalist predators (Sorace and Gustin 2009). It has been argued that since predator size is positively correlated with flight distance (from humans), large predators are less likely to colonise urban habitats, thus allowing some relative large prey species to settle there (Møller et al. 2012). This process would not apply to nocturnal predators, as human activity is much reduced at night (Chace and Walsh 2006; Sorace and Gustin 2009).

An impoverished community of large predatory birds (see Møller et al. 2012) appears to contribute to the settlement of large corvids in some cities (e.g. Vuorisalo et al. 2003). Corvids, in turn, are often responsible for high rates of nest predation in cities (Major et al. 1966). Other known nest predators such as snakes and small carnivores (i.e. viverrids or procyonids) are also scarce in most cities, which instead harbour unnaturally high concentrations of cats.

Th evidence of how urbanisation affects the interaction between birds and predators is not uniform, probably due to the fact that the planning of urban landscapes varies across cities, thus affecting the assemblage and functioning of

urban biological communities. Some authors report that predation decreases with urbanisation (e.g. Møller 2010), which is consistent with the fact that the density of breeding birds is higher in urban areas than in their surroundings (although the diversity of breeding species follows the opposite trend; Lancaster and Rees 1979; Beissinger and Osborne 1982; Shochat 2004). However, other works report that in the cities, there is a higher risk of predation, particularly on nests (Haskell et al. 2001; Sorace 2002; Jokimäki et al. 2005; Chace and Walsh 2006), which constitutes a crucial limiting factor for avian populations (Martin 1993; Conway and Martin 2000). Again, cats frequently prey on fledglings, and it has been argued that they have a major negative impact on breeding success of urban birds (Sorace 2002; Woods et al. 2003; Baker et al. 2008).

Because urbanisation brings about major changes in the composition of biological communities, it is reasonable to expect that it has an effect on parasite-/pathogen-host interactions. In the case of birds, this possible link has not been very extensively investigated (c.f. Delgado and French 2012), but available information suggests that the effect of urbanisation on the prevalence of avian parasitic infections is a function of the parasites' life cycle. On the one hand, both helminth parasite richness and prevalence (Aponte et al. 2014; Calegaro-Marques and Amato 2014) and diversity of blood parasites have been found to decrease with urbanisation, arguably due to loss of intermediate hosts (Fokidis et al. 2008; Geue and Partecke 2008). Conversely, viral infection (*Avipoxvirus*) and the severity of coccidial (*Eimeria* spp.) infection are positively associated with the degree of urbanisation in the house finch (*Haemorhous* [= *Carpodacus*] *mexicanus*; Giraudeau et al. 2014). These two pathogens are directly transmitted, and their prevalence may be linked to the high density of finches in the cities and possibly also to the abundance of bird feeders that promote contagion. This latter effect is worrying, since high densities of parasitised urban birds may spill infection to the wild bird living in the neighbourhood of cities (see Bradley and Altizer 2007).

It is unclear why intermediate hosts (mainly ectoparasites) should be less abundant in the cities than in rural areas, given that a large proportion of avian ectoparasites complete their life cycles in the bird nests (López-Rull and Macías García 2015) or on their plumage, while small water deposits that act as breeding sites for *Diptera* (mainly mosquitoes) are normally abundant in urban areas. As indicated above, most studies suggest that the effect of urbanisation on avian parasite biology depends on the life cycle of the parasites, yet other factors such as pollution may mediate this link. For instance, Bichet et al. (2013) found that lead pollution, which is high in cities, is linked with prevalence of *P. relictum*. This protozoan is responsible for one type of avian malaria, and since it requires an intermediate (arthropod) host, it would not have been expected to be too prevalent in cities.

6.2.3   Pollution

Pollution by chemicals, light and sound is a defining attribute of cities that can negatively affect the physiology and disrupt the communication of birds. Organisms inhabiting anthropogenic environments are exposed to both inorganic and organic pollutants (see Kekkonen 2016) that often get into the tissues of birds (e.g. lead accumulation in the kidneys of pigeons (*Columba livia*); Johnson et al. 1982). This has prompted the use of urban birds to monitor pollution (e.g. house sparrows [*Passer domesticus*] used to track heavy metals in cities; Swaileh and Sansur 2006). At high concentrations, heavy metals can promote hatchling mortality (Scheuhammer 1987), but even sublethal concentrations can compromise bird condition (e.g. reducing both song repertoire and song output in great tits [*Parus major*]; Gorissen et al. 2005) or increase susceptibility to disease (Bichet et al. 2013). The progressive abandonment of leaded fuel has stalled the accumulation of lead in the cities, although it persists in the soil and finds its way into birds via earthworms and possibly other food (Scheifler et al. 2006). Currently the risk of heavy metal intoxication is probably greatest in areas where metals are extracted (see, for instance, Eeva and Lehikoinen 1996) than in cities, thus adaptations to contend with metal pollution—if they do exist—may not be particular to urban birds.

City birds are exposed to organic pollutants such as insecticides and rodenticides which are toxic to birds. These are often endocrine disruptors and as such can have a variety of effects in birds (Giesy et al. 2003), from interfering with sex determination to promoting the expression of sexually selected attributes, as in some British populations of common starlings (*Sturnus vulgaris*; Markman et al. 2008). Insecticides were first implicated in raising the mortality of urban birds by Carson (1962) in his inspirational *Silent Spring* and were famously recognised as the main cause of peregrine falcon (*Falco peregrinus*) decline in eastern USA (Peakall 1970; Cade et al. 1971). This rose concern about the ecological consequences of organochlorine insecticides (DDT in particular) and was partly responsible for the drive to develop less persistent organophosphorous insecticides. As with heavy metals, bird exposure to insecticides is not greater in cities than in rural areas, and thus any adaptation that may arise to contend with them would not be particular to the cities. Similarly, rodenticides are widely used in agriculture to control voles and other rodents, but also in cities, where they are ingested and damage several species of both rural and urban birds (see Godfrey 1986).

Plastics and other materials discarded by humans also constitute a form of pollution that can affect birds, particularly when used as nest materials. Thus crows and probably many other birds bring plastic debris to their nests. This often leads to entanglement and entangled chicks fail to fledge (Townsend and Barker 2014). Interestingly, the probability of entanglement for nestling crows is a function of the length of the plastic stripe/thread, which is larger in rural habitats where plastic mesh and wiring are widely used in agriculture-related activities (Townsend and Barker 2014).

Light pollution is present within and outside the cities, yet while it only affects a small proportion of rural birds, virtually every bird in the cities has to contend with it. Human sources of light are unlikely to match the quantity of light that birds are exposed to during the daylight hours, but can generate light that is qualitatively different to sunlight, and, more importantly, extend the period during which birds are exposed to light (see Dominoni 2016). Conventional low-frequency fluorescent tubes emit light that flickers at a rate below 100–120 Hz. When the rate is too low, the flicker can be perceived by and be stressful for some birds, particularly of fast flying species (as they need to update the visual scene frequently; Evans et al. 2012). This effect may be of concern for captive birds maintained under artificial light, yet although urban birds may be exposed to low-frequency fluorescent light, this would only occur by night and may have negligible effect on them.

Artificial light in cities and roads extends the perceived day length. This has several physiological effects on urban birds which are covered by Dominoni (2016, and see also references therein). Briefly, urban light can affect the circadian rhythms, reduce the age at maturity, advance the laying date and interact with other anthropogenic pollutants such as noise and chemicals. It can compromise the foraging efficiency and limit the foraging time of nocturnal birds dependent on light-sensitive prey (but see Weaving and Cooke 2010).

The effect of sound pollution—from traffic and other forms of anthropogenic noise—on organisms other than humans has been intensively studied, particularly since the seminal paper by Slabbekoorn and Peet (2003). In contrast to natural environments, the impervious surfaces of cities scatter sound waves and create multiple reverberations that can cancel and distort acoustic communication (Slabbekoorn et al. 2007). We now know that sound pollution causes major disruptions in the communication of many taxa (insects (Schmidt and Balakrishnan 2014), fish (Popper and Hastings 2009), amphibians (Hanna et al. 2014), mammals (Richardson et al. 1995; Schaub et al. 2008) including birds (see a recent review by Gil and Brumm 2013). Noise masking has led to shifts in the composition of local avian fauna (Francis et al. 2012) and has a major effect on the onset of the dawn chorus (Gil et al. 2015).

6.3   Which Avian Species Thrive in Cities?

Because of the challenges that birds face in urban environments, not all species seem to be able to thrive in cities, but of those that do, some seem to perform even better in urban areas than in the wild. Bird communities in the cities tend to include a large proportion of omnivores, granivores and aerial/ground insectivores, and often the resident species dominate over noninvasive immigrants (Allen and O'Connor 2000; Kluza et al. 2000; Poague et al. 2000; also see Lepczyk et al. 2016; Chen and Wang 2016). Invasive species such as the house sparrow, on the other hand, often outcompete ecologically similar native species such as the North American House finch (*Carpodacus mexicanus*; Bennett 1990), and they can

breed explosively and become noxious pests, such as the common pigeon, which transmits disease and is harmful to buildings (but note that in some areas, notably in western Europe, house sparrow populations seem to be collapsing; see Summers-Smith 2003). Such preponderance of a few species also hints at different processes structuring avian—and possibly biological—communities in cities and in the wild.

The distributions of birds such as the house sparrow (*Passer domesticus*) and the pigeon (*Columba livia*; Driscoll et al. 2009) have become global as they moved from the relatively few ancient Eurasian cities to virtually all the cities that sprawled around the globe in the last 2000 years or so (Cocker and Tipling 2013). In part because of this ubiquity, they have been thought to possess particular attributes that favour life amongst humans. Yet even if they do have some traits that facilitate their living in urban environments, the subsequent colonisation of non-Eurasian cities by local fauna—which constitute most of the biodiversity in those cities (Aronson et al. 2014)—suggests that whatever attributes facilitate city dwelling, they are not exclusive of the few original urban species.

6.4   Recognising Adaptations

Since in this chapter we are exploring possible avian adaptations to urban life, it is crucial to distinguish between attributes that evolved in nature but allow birds to thrive in cities (e.g. noise and avian song; Brumm and Naguib 2009), from those that may have evolved in response to the selective forces acting in the cities. Normally, an adaptation is defined as the consequence of natural selection promoting the reproduction of organisms with particular heritable attributes which then become better represented in the next generation. Of the ten methods to detect natural selection listed by Endler (1986), only two (or three; see below) have been used to evaluate whether attributes in which urban bird differs from their rural counterparts amount to adaptations to life in the cities. Such differences are systematically referred to as adaptations (see Diamond 1986), yet in most cases, alternative explanations have not been ruled out. Demonstrating that natural selection has been involved is not the only way to determine whether an attribute is an adaptation. When phenotype and environment (e.g. urban/rural) are correlated, common-garden experiments provide the method of choice to infer that the differences are the consequence of adaptation, and not of phenotypic plasticity, trans-generational epigenetic effects or constitute preadaptations that evolved in natural contexts where the selective agents are similar to those found on sites. For instance, the surroundings of large waterfalls, which can be as noisy as the streets of a city, have an influence on bird song that is comparable to that of anthropogenic noise (see Brumm and Slater 2006).

Regardless of the underlying mechanism, ecological differences between birds living in cities and those living natural sites are notable and ubiquitous. This suggests that species exploiting urban environments typically adjust their phenotype to face the new challenges imposed by urbanisation. In the next section, we

will review some examples of phenotype changes following urbanisation and the nature of them.

6.5 Adapting to Life in the Cities

6.5.1 Habitat Structure and Seasonality

Responsiveness to attributes that indicate seasonality varies amongst and between species and depends on phenotypic plasticity, which allows colonisation of different environments (Lambrechts et al. 1996). As we saw above, cities buffer the seasonal changes in the weather and in food availability. Cities also blur some of the cues that can be used by birds to adjust their physiology/behaviour to changes of the season. These changes should have led urban birds to become less seasonal. One demonstration that this is the case comes from studies showing increased sedentariness in urban blackbirds (*Turdus merula*; Partecke and Gwinner 2007). The authors looked at the pattern of nocturnal activity and fat deposition, two variables tightly linked to predisposition to migrate, of hand-reared birds from urban to nonurban localities and found that the former had a significantly reduced tendency to migrate. An earlier common-garden experiment by the same group (Partecke et al. 2004) demonstrated that, although the timing of reproduction was not different between birds from urban to nonurban areas, the former initiated earlier (both sexes) and finished also earlier (females) their reproductive hormonal activity, implicating a genetic difference in their physiological response to environmental cues (see also Partecke et al. 2005). As the authors recognise (Partecke and Gwinner 2007), these experiments do not quite preclude the possible influence of early developmental (e.g. maternal) effects, yet taken together they constitute one of the most convincing cases so far of adaptation by birds to urban life. As indicated above, light pollution is associated with the adaptive shift in the timing of breeding and sedentariness of urban blackbirds (Dominoni and Partecke 2015), yet other ecological variables are associated with life-history differences between city and field blackbirds in Spanish populations (Ibáñez-Álamo and Soler 2010). Since membership to different lineages suggests that blackbirds have invaded European cities several times independently (Evans et al. 2009), it is conceivable that different processes have led to subtly different adaptations to urban life in different cities, although to date only the case of the Munich population (Partecke et al. 2004; Partecke and Gwinner 2007) constitutes a demonstration of life-history adaptation of blackbirds to life in the cities.

Other environmental variables may also drive changes in seasonality or migratory patterns of urban birds. For instance, regular food availability promotes earlier breeding in urban than rural populations of Florida scrub jays (*Aphelocoma coerulescens*; Schoech and Bowman 2001), possibly because it reduces the production of corticosterone, a hormone with negative effects on reproduction. The

fact that supplementing food to wild jays advanced their breeding time (Schoech and Bowman 2001) shows that this is a plastic attribute, and thus there is no indication of adaptation of breeding time in urban Florida scrub jays.

Adaptation may be implicated in changes of migratory habits. In particular, the famous example of central European populations of the blackcap (*Sylvia atricapilla*) migrating to Britain and Ireland to overwinter there instead than in the traditional Mediterranean wintering grounds (Berthold and Terrill 1988) may represent an adaptation to urban life. Blackcaps overwintering in Britain make extensive use of feeding stations (bird tables and bird feeder) which are much more abundant in the cities of the British Isles than in those around the Mediterranean. Recent evidence has demonstrated that migratory direction is heritable and controlled by only a few genes (Helbig et al. 1994) and can diverge rapidly due to substantial additive genetic variance (Berthold and Pulido 1994). Populations overwintering in Britain and Ireland arrive earlier at their breeding ground and thus are temporally segregated from those migrating southwards (Rolshausen et al. 2009). The two groups have diverged genetically (as assessed using neutral markers) and phenotypically, westward-migrating birds having rounder wings, slenderer bills (presumably linked to generalist-feeding habits at bird tables) and a darker back colour than those that migrate to the south (Rolshausen et al. 2009). Based on data from Fiedler (2003), Rolshausen et al. (2009) suggest that similar processes may be taking place in as many as 50 bird species. If, as seems the case in the blackcap history, exploitation of urban resources is a causal factor, then shifts in avian migratory behaviour may be the most frequent avian adaptation to urban conditions.

6.5.2   Food Availability

Food availability has also been implicated in the marked phenotypic-dependent mortality of urban pigeons. Haag-Wackernagel et al. (2006) found that, in comparison with wild populations, the proportion of urban pigeons with a colour pattern known as checker decreased, whereas that of pigeons with bronze colour pattern augmented. Although the causal link between juvenile colour and survival is unclear, other authors have suggested that by remaining continuously in breeding condition, dark-morph feral pigeons cannot accumulate fat reserves between breeding periods and are therefore more vulnerable to food shortage than lighter morphs (e.g. Murton 1970). It is unclear, nevertheless, whether this differential mortality of urban pigeons leads to adaptation to city life.

The distribution of food resources differs markedly between cities and rural/wild environments. Food of various types is abundant in urban environments, yet apart from the case of the westward-migrating European blackcaps (which appear to have evolved a beak morphology to suit the exploitation of a variety of seeds offered in British and Irish bird tables; see above), there seems to be no examples of adaptation of birds to human-provided food. Food processed for humans contains various

toxicants and has generally a low ratio of nutritional to energetic content. This might have promoted adaptations in generalist urban birds to avoid less nutritious/ more toxic food as well as physiological adaptations in food-supplied urban birds (such as hummingbirds which are commonly attracted to feeders) to cope with a diet rich in refined sugars.

Reports abound of birds starting to exploit anthropogenic food sources, from the opening of milk bottles by tits in Britain to the cracking of nuts using cars by Japanese crows (*Corvus macrorhynchos*; Nihei and Higuchi 2001). Blue (*Cyanistes caeruleus*) and great tits (*Parus major*) were originally found in 1921 to open milk bottles to consume the cream accumulating under the lid. At the time fresh milk was customarily delivered at the doorstep in glass bottles fitted with a flexible metal lid (tin and more recently aluminium). As bottles remained some time before being taken indoors, this provided opportunity for birds to approach, inspect and exploit this source of fat. The spread of this behaviour was mapped and quantified by Fisher and Hinde (1949; Britain) and Hinde and Fisher (1951; Europe). This enabled Lefebvre (1995) to evaluate the spread rate with models used in the study of human cultural transmission (Cavalli-Sforza and Feldman 1981). That bottle opening by Paridae was culturally transmitted which was not certain, particularly since Sherry and Galef (1984, 1990) demonstrated that American parids (*Parus* [= *Poecile*] *atricapillus*) are very likely to spontaneously open a bottle and that the probability that this happened was not influenced by the presence of an experienced tutor. Lefebvre (1995) found that accelerating (e.g. exponential) functions best described the spread of bottle opening by tits in Britain and in Belfast. This is consistent with the cultural transmission assumption of an autocatalytic increase in the rate of spread over time. The idea that cultural transmission is involved was further supported by the fact that data only poorly fitted the linear wave-of-advance model which would describe the spread of the behaviour as a function of a constant rate of untutored learning.

We devoted some time to this phenomenon as it is a textbook example of how birds adjust their behaviour to exploit anthropogenic food sources. The controversy regarding the mechanism of spread of milk bottle opening could be framed in the wider discussion of whether such examples are genuinely novel traits that reflect adaptation to cities or whether they represent exaptations (the expression in a novel context of a pre-existing adaptation to deal with similar conditions; in this case the adaptive behaviour of tits to uncover food items under lichens and bark). As seems to be the case, this exemplifies two different exaptations: a tendency to seek food under lichens and bark and a predisposition for cultural transmission. Also it illustrates the transient nature of cities and the challenges and opportunities they pose to colonising birds (and other organisms). The capability of learning—whether socially or otherwise—and thus adjusting the behaviour to novel conditions may be a key factor enabling some species to colonise urban environments (although we note that cognitive abilities such as problem-solving need not necessarily be better in urban than in rural populations; Papp et al. 2015). Maklakov et al. (2011) demonstrated that brain size was positively associated with the probability that members of passerine bird families, as well as individual species, bred in European

city centres. These comparative analyses were prompted by the idea that cities present birds with new challenges, and the previous demonstrations that big brains facilitate the colonisation of novel environments, and that this effect is due to the cognitive consequences of having a big brain (Sol et al. 2005). In their work, Sol et al. (2005) used, as proxy of cognitive ability, the number of foraging novelties reported for the species included in their study. This is a widely used index, yet it is not exempt of problems, for it relies on perfect knowledge of foraging strategies. For instance, the finding that *Parus* (= *Poecile*) *atricapillus* spontaneously opens bottles suggests that this is likely to be an exaptation rather than a genuine urban novelty. Still, employing behaviours evolved in one environment to exploit resources encountered in a novel, one may require a degree of behavioural plasticity. Since both technological and cultural changes ensure that the conditions confronted by urban birds change constantly, it is likely that some degree of behavioural plasticity is required to remain a successful urban coloniser. However, even if behavioural plasticity requires large brains, the reported link between brain size and urbanism (Maklakov et al. 2011) is as likely to be a consequence of differential colonisation of cities by large-brained species as it is of being the result of adaptation to urban life.

6.5.3   Interspecific Interactions

Nest predation influences both nesting strategy (cavity, open, etc.) and patterns of nest attendance (e.g. Conway and Martin 2000) and determines the nature of urban bird assemblages (Jokimati and Huhta 2000). But is there evidence that birds adapt to the particular predation regimes found in cities?

A first line of defence against predation is avoiding encounters with predators. Birds may achieve this by selecting safe/secluded perching, roosting and nesting places (see Marzluff 2001). We are not aware of adaptive differences in those behaviours between wild and urban bird populations; birds in forests and cities alike take readily to breeding in nest boxes, and birds nesting in building crevices are probably even safer than their rural, cliff-nesting counterparts.

Encounters with predators can also be avoided by preventing detection, for instance, through cryptic colouration. There is no suggestion, however, that the reported cases of difference in colour between urban and rural birds (e.g. Haag-Wackernagel et al. 2006; see above) are the consequence of difference in predation regimes. Also, although adaptation is suspected in the case of rapid evolution of geographic colour races of *P. domesticus* in North America, as it parallels the pattern of geographic variation of other species it is now sympatric with (Johnston and Selander 1964), there is no evidence that this is a response to predation, nor that it constitutes an adaptation to urban life.

Early detection of predators in the neighbourhood may allow the birds to either avoid the place altogether (e.g. Amo et al. 2015) or to monitor its behaviour and take evasive action as necessary. In birds, evasive action means to fly, and the

distance at which a bird decides to fly is a function of both its fleeing tendency and of the cost of leaving the place (Blumstein 2006). When low-risk encounters are too frequent, tolerance would be advantageous, as it may allow birds to exploit feeding resources efficiently. Accordingly, Møller (2008) found that urban birds have a reduced flight distance than their rural conspecifics. Further, Møller (2009) found that rural populations of bird species that have successfully become city dwellers have shorter flight distances than sympatric populations of nonurban species. This suggests that short flight distance may preadapt species to life in the city, although the possibility that flight distance in rural populations has been influenced by gene flow from urban populations cannot be ruled out. Mutually supporting evidence strongly suggests that this is useful for city birds to have a short flight distances and that a short flight distances enable colonisation of urban habitats. Yet there is no evidence so far demonstrating that flight distance of a particular species has been reduced following colonisation of cities and that such modification is genetically based, i.e. short flight distance appears to be and exaptation, not an adaptation to life in the cities.

Urbanisation also affects the interaction between parasites and their hosts. One intriguing possibility is that cities provide some effective means for birds to deal with ectoparasites. Indeed, urban birds have been reported to collect discarded cigarette butts, rip them open and use the tar-loaded filter fibres as lining material for their nest, thus bringing about a reduction in the number of ectoparasites recovered from the nests (Suárez-Rodríguez et al. 2013). Since a similar effect is achieved by wild birds using green material from plants with known repellent activity (Dubiec et al. 2013), such behaviour may not be an adaptation to life in cities but a modification of the materials used for antiparasitic defence. This assumes that similar cues at the nest trigger the use of green aromatic plants and discarded cigarette butts and that similar cues are also used to find and gather both materials. On the other hand, the effectiveness of both aromatic plants and discarded cigarette butts as ectoparasites repellent has not been compared. It may be that the high concentration of substances in the smoked-through filters makes them more effective at repelling ectoparasites (and also toxic; Suárez-Rodríguez and Macías Garcia 2014), thus further promoting their use. The impact of urban nest materials on ectoparasites abundance and diversity, and hence on the prevalence of the pathogens they transmit, remains hypothetical.

6.5.4   Pollution

Pollution may, in principle, select for advantageous physiological traits to detoxify (chemical), adjust response thresholds (light) or modify the emission of signals to avoid masking (noise). Although chemical pollution has diverse impacts on bird populations, both within and outside the cities, we found no reports of novel adaptations to contend with it, but there is one possible case of an exaptation (Chatelain et al. 2015). The capture of zinc (and other heavy metals) by feather

melanin makes advantageous for birds to be dark in areas polluted with heavy metals. Urban pigeons have been found to be darker than their suburban counterparts (Chatelain et al. 2015), and this seems to represent an example of directional selection in cities of an attribute evolved earlier in the lineage of vertebrates. Work in this area is likely to become more common as avian genomic tools become more abundant (see Zhang et al. 2014), which will allow the characterisation of urban-rural differences, if any, on the expression of genes involved in detoxification.

Birds undoubtedly adapt to prolonged exposure to light in the cities, as they sleep through the night (albeit less than in wild conditions; see above). Yet this is likely sensory adaptation and is unlikely to be different from that undergone through the year by birds living at high latitudes. But this sensory adaptation is not complete, and as we saw above, hormonal activity, circadian rhythms, length of breeding season and onset of maturity are all affected by urban light patterns in a way that suggest that no evolutionary adaptation to light pollution is taking place.

Sound pollution in cities evokes a variety of responses from birds. When exposed to noise that may mask their vocalisations, birds can modify the song output (Díaz et al. 2011), increase the duration of their songs (Ríos-Chelén et al. 2013) or otherwise modify their structure (Francis et al. 2011), and they may be uttered at different times (Fuller et al. 2007) and/or have some frequency components altered (see reviews in Slabbekoorn 2013; Gil and Brumm 2013). A small but growing number of papers also report that some bird species can adjust in real time their songs in response to sudden bursts of noise (Bermúdez-Cuamatzin et al. 2009, 2010; Gross et al. 2010; Verzijden et al. 2010), whereas only a handful involve species which lack (or appear to lack) the capability to vary their songs (Francis et al. 2011; Ríos-Chelén et al. 2013). These later cases may be examples of adaptation to urban conditions by non-learning songbirds, although some degree of vocal plasticity in suboscine birds cannot be ruled out (e.g. Ríos-Chelén et al. 2005, 2012), and other mechanisms such as differential habitat use (discussed in both Francis et al. 2011 and Ríos-Chelén et al. 2013) could explain the difference in song attributes between urban and rural populations of non-learning bird species.

Halfwerk et al. (2011) provide perhaps the best case for the adaptive value of song adjustment to overcome masking of vocalisations by urban noise. They showed experimentally that although low-frequency songs are preferred by females and linked to female fecundity, exposure to urban noise impairs their effectiveness and favours higher-pitched songs. Yet, this convincing evidence of the fitness value of adjusting the frequency of song to prevent masking does not demonstrate adaptation to cities, because male great tits can adjust the frequency of their songs in real time (i.e. this is an adaptive plastic response, presumably evolved elsewhere, that is also useful in cities).

6.6   Conclusion

We have seen that most differences between rural and urban birds can be explained as being consequence of either phenotypic plasticity or of differential colonisation by individuals or species with sufficient behavioural plasticity to move into novel environments. These two patterns raise the question of whether cities in fact represent novel, more complex environments than birds would have experienced in their evolutionary past. It is possible, instead, that cities are as challenging as any novel environment that may confront birds, and the relative paucity of globally successful urban species is the result of the rapid overtaking of other environments by the cities. Still, it may be that the very speed at which urban landscapes spread at the expense of natural ones poses a particular novel challenge to would-be urban birds. We also saw that biodiversity within the cities, although lower than in their surroundings, is dominated by local species.

We argue that, in terms of complexity, cities cannot compare with forest ecosystems, particularly with those in the tropics. Cities do not have the vast numbers of species (and hence of potential interactions) of tropical forests, and their physical complexity is also probably lower. Seasonality is buffered in the cities, and many links to parasite transmission are therein disrupted. It is also unlikely that cities expose birds to physical or biological conditions that are genuinely novel, in the sense of not having being experienced by birds over their evolutionary past. Yet in one attribute, these environments pose a fundamentally different challenge, cities keep changing. The urban conditions that house sparrows confronted in the cities of the Fertile Crescent some 10,000 years ago are much more similar to current rural conditions than to anything the same species confronts in the midst of contemporary cities. Yet this urban species persists, suggesting that it has kept pace with urban change (but see below). Whether being possessed of a large brain has been the key to such behavioural plasticity is an open question. Another open question is whether the current urban species will persist, and the answer to this question seems to be negative in the case of one of the earliest city dwelling birds, the house sparrow currently declining in Europe (Summers-Smith 2003). Even as birds adapt—or adjust—to living in cities, the cities continue changing; waste management modifies every few human generations the distribution and availability of food, while environmental awareness means that measures are taken to promote both the number and the diversity of species in our cities (e.g. green roofs and walls, Baumann 2006; Chiquet et al. 2013). As successful city dwellers become enormously numerous compared with their rural conspecifics, the rural environment shrinks. This may lead to a constant flow of inadequate phenotypes or maladaptive genes from the city to wild, which arguably may drive to extinction the rural populations and seal the destiny of such species that have colonised them, to that of the cities.

Finally, in spite of an already large and rapidly increasing number of works centred on potential bird adaptations to urban life, there is a dire need of studies that use in the cities the same tools traditionally used for detecting adaptation in nature,

the direct measure of fitness in relation to the putative urban-adapted traits, together with measures of its genetic underpinning.

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Chapter 7
Mechanisms of Behavioural Change in Urban Animals: The Role of Microevolution and Phenotypic Plasticity

Ana Catarina Miranda

Abstract A key question in evolutionary behavioural ecology is how species cope with changes in their environments. In the last centuries, humans have caused dramatic changes in our planet that have affected the way many animals behave. In order to live in cities, most animals are forced to adjust their behaviour and life histories to the new urban habitat. While growing evidence reports behavioural differences between rural and urban conspecifics as common and cross-taxonomical, the mechanisms underlying such differences in behaviour remain largely unknown. Recent research using animals with limited experience of their natural urban or rural environments points to the existence of intrinsic differences in behaviour between rural and urban conspecifics. This suggests that phenotypic plasticity might not be the only mechanism explaining behavioural differences between rural and urban individuals and that differences in individually consistent behavioural traits could also be the result of microevolution in the urban environment.

Knowing that urbanization is and will continue to be a major environmental challenge to most living organisms, it is urgent to understand the mechanisms allowing animals to cope with our urbanizing world. In this chapter, I focus on the existence of different behavioural phenotypes between rural and urban animals and on the possible mechanisms leading to such behavioural differences.

Keywords Animal personalities • Anthropogenic environmental change • Behavioural syndromes • Colonization • Microevolution • Phenotypic plasticity • Urbanization

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7.1   Introduction

According to the United Nations (2014), two and a half billion people inhabited our planet in 1950. Remarkably, in 2011, little more than 60 years later, that number had almost tripled to seven billion people, and an impressive increase to over nine billion inhabitants is expected by 2050. Along with the world's extreme human population growth, the last few decades have witnessed an unprecedented increase in the number and size of cities. While in the 1950s 30 % of the human population lived in urban areas, that number suffered a drastic growth to 54 % in 2014 and is estimated to further increase to 66 % by 2050 (United Nations 2014).

In the last decades, the significant development of urban ecology as a scientific discipline reflects the now widely accepted fact that the phenomenon of urbanization has a profound impact on ecological systems, being a major threat to many species (Shochat et al. 2006; Gaston 2010).

In their natural habitats, animals are continuously facing environmental challenges, as coping with disturbances, adjusting to shifts in food availability and distribution and interacting and competing with other animals. The manner in which an individual animal responds to such challenges can greatly affect its future chances of survival and reproduction. Over the last centuries, urbanization arose as a new major environmental challenge that may favour individuals consistently behaving in different ways. The colonization of an urban habitat often requires organisms to adapt, among other factors, to increased disturbance levels, shifts in food resources, new species composition, a different microclimate and increased chemical, light and noise pollution (Klausnitzer 1989; Partecke et al. 2006; Brearley et al. 2012; Lowry et al. 2013; Dominoni 2016; Kekkonen 2016). Typically, the changes caused by urbanization occur in a quick and dramatic manner, being thus expectable that many organisms should be unable to cope with these changes, causing their potential exclusion from urban environments (Hendry et al. 2008; Sih et al. 2011). Accordingly, it is well documented that urbanization leads to a drastic loss in species diversity (Shochat et al. 2010; Daniels and Kirkpatrick 2016). On the other hand, it has been argued that urban environments may offer important benefits for certain species, such as warmer temperatures (Arnfield 2003), nocturnally illuminated foraging areas (Lourenço et al. 2008; Santos et al. 2010) and anthropogenic food (Bateman and Fleming 2012; Gleditsch 2016). Supporting this idea, numerous species seem to prosper in urban environments (Case 1996), being therefore crucial to understand how animals cope with urbanization and which are the consequences of living in the new urban habitats. Evidence suggests that, in many species, urban populations differ in several aspects, including timing of reproduction (see Chamberlain et al. 2009 for a literature review), daily activity patterns (Dominoni et al. 2013), stress physiology (Partecke et al. 2006; Fokidis et al. 2009) and even rates of cellular ageing.

Remarkably, urban animals also frequently change the way they behave, and this is the focus of this chapter. In the next sections, I will begin by reviewing the studies documenting shifts in behaviour between rural and urban conspecifics. Next, I will

focus on the possible ultimate causes that might lead to such behavioural differences between rural and urban animals, namely, phenotypic plasticity or microevolution in the urban environment. I include some considerations about physiology as a possible proximate cause of shifts in behaviour in urban species. Finally, I will discuss some possible impacts of the observed shifts in behaviour in urban species.

7.2   Urbanization-Driven Shifts in Behavioural Traits: The Nature of Urban Behaviour

An individual's behavioural phenotype is a set of elements that is crucial for coping with environmental challenges such as urbanization and that might be related with major life history decisions, as whether to colonize new habitats or not and their consequences. Urbanization is a relatively new and strong selection pressure challenging organismal adaptation capabilities. The environmental challenges driven by urbanization can result in various phenotypic shifts, including shifts in behaviour (Sol et al. 2013; Partecke 2013). Indeed, an increasing body of evidence shows that rural and urban conspecifics commonly differ in many behavioural traits (but see literature review in Table 7.1). In specific, a study has assessed how common are shifts in animal behaviour related to the urbanization phenomenon, by reviewing empirical studies comparing rural and urban conspecifics in different behaviours towards stimuli (Miranda et al. 2013). Here, over 2 years later, using the methodology in the aforementioned study (Miranda et al. 2013), I conducted an identical literature search with the objective of finding studies comparing rural and urban populations in the following behaviours: aggression (attacks or other aggressive interactions or displays), alarm (alarm calls in response to disturbing stimuli), escape (retreat behaviours when facing disturbing or threatening stimuli), exploration (exploration of new environments), innovation (ability to solve problems, usually associated with a food reward), neophilia (attraction to novelty), neophobia (novelty avoidance) and risk-taking (exposure to risk). The literature search was performed in ISI Web of Knowledge (http://www.isiknowledge.com) in April 2015, with the following exact search terms: Topic = (Aggression OR Alarm OR Anti-predator OR Behavioural-syndrome OR Bold OR Defense OR Escape OR Exploration OR Fear OR Flight-initiation-distance OR Flush OR Innovation OR Neophilia OR Neophobia OR Novel OR Personality OR Risk-taking OR Shy OR Temperament) AND Topic = (Urbani* OR (Urban NEAR/1 Rural) a OR "Exposure to Humans") AND Topic = (Behaviour) AND Topic = (Animal OR Species). From the retrieved results, I selected all relevant articles in English from appropriate research areas, as well as articles resulting from backward or forward searches of the original search. Statistically significant differences ($P < 0.05$) were classified into 'rural > urban' or 'rural < urban' depending on the direction of the trend. In articles focusing on multiple species or related behaviours, I considered significant differences when these were shown in at least one species and behaviour in the

Table 7.1 Summary of empirical studies comparing rural and urban conspecific populations in behaviours towards different stimuli

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
Aggression							
	15 bird species	R < U	Wild	Wild	NA	NA	Møller and Ibáñez-Álamo (2012)
	American crow (*Corvus brachyrhynchos*)	NS	Wild	Wild	NA	NA	Knight et al. (1987)
	Noisy miner (*Manorina melanocephala*)	R < U	Wild	Wild	NA	NA	Lowry et al. (2011)
	Mute swan (*Cygnus olor*)	R < U	Wild	Wild	NA	NA	Józkowicz and Górska-Kłęk (1996)
	Song sparrow (*Melospiza melodia*)	R < U	Wild	Wild	NA	Yes	Evans et al. (2010)
	Song sparrow (*Melospiza melodia*)	R < U	Wild	Wild	Yes	Yes	Scales et al. (2011)
Alarm							
	15 bird species	R > U	Wild	Wild	NA	NA	Møller and Ibáñez-Álamo (2012)
	American crow (*Corvus brachyrhynchos*)	R > U (from a distance) R < U (close distance)	Wild	Wild	NA	NA	Knight et al. (1987)
	Black-tailed prairie dog (*Cynomys ludovicianus*)	R > U	Wild	Wild	NA	NA	Adams et al. (1987)

Species	Measure					Reference
Black-tailed prairie dog (*Cynomys ludovicianus*)	NS	Wild	Wild	NA	NA	Magle et al. (2005)
Eastern grey squirrel (*Sciurus carolinensis*)	R < U	Wild	Wild	NA	NA	Partan et al. (2010)
Escape						
5 bird species	R > U	Wild	Wild	NA	NA	Clucas and Marzluff (2012)
10 bird species	R > U (3 species NS)	Wild	Wild	NA	NA	Cooke (1980)
42 bird species	R > U	Wild	Wild	NA	NA	Carrete and Tella (2011)
44 bird species	R > U	Wild	Wild	NA	NA	Møller (2008)
62 bird species	R > U	Wild	Wild	NA	NA	Møller and Tryjanowski (2014)
American crow (*Corvus brachyrhynchos*)	R > U	Wild	Wild	NA	NA	Knight et al. (1987)
Black-tailed prairie dog (*Cynomys ludovicianus*)	R > U	Wild	Wild	NA	NA	Adams et al. (1987)
Black-tailed prairie dog (*Cynomys ludovicianus*)	R > U	Wild	Wild	NA	NA	Magle et al. (2005)
Black-billed magpies (*Pica pica*)	R > U	Wild	Wild	NA	NA	Kenney and Knight (1992)
Burrowing owl (*Athene cunicularia*)	R > U	Wild	Wild	Yes	NA	Carrete and Tella (2013)
Cane toad (*Rhinella marina*)	NS (Novel Prey Exp.) R < U (Novel Object)	Lab	Wild	NA	Yes	Candler and Bernal (2015)

(continued)

Table 7.1 (continued)

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
	Cape ground squirrel (*Xerus inauris*)	R > U	Wild	Wild	NA	NA	Chapman et al. (2012)
	Common mynas (*Acridotheres tristis*)	R > U	Wild	Wild	NA	Yes	Ashlee McGiffin (2013)
	Dark-eyed junco (*Junco hyemalis*)	R > U	Wild	Wild	NA	NA	Atwell et al. (2012)
	Eastern grey squirrel (*Sciurus carolinensis*)	R > U	Wild	Wild	NA	No	Engelhardt and Weladji (2011)
	Fox squirrel (*Sciurus niger*)	R > U (adults[a])	Wild	Wild	NA	NA	Mccleery (2009)
	Garden skink (*Lampropholis guichenoti*)	R < U	Wild	Wild	NA	NA	Prosser et al. (2006)
	House finch (*Carpodacus mexicanus*)	R < U	Wild	Wild	NA	Yes	Valcarcel and Fernandez-Juricic (2009)
	Magpie-lark (*Grallina cyanoleuca*)	R > U	Wild	Wild	NA	NA	Kitchen et al. (2010)
	Noisy miner (*Manorina melanocephala*)	R > U	Wild	Wild	NA	NA	Lowry et al. (2011)
	Song sparrow (*Melospiza melodia*)	R > U	Wild	Wild	Yes	Yes	Evans et al. (2010)
	Song sparrow (*Melospiza melodia*)	R > U	Wild	Wild	Yes	Yes	Scales et al. (2011)

	Species						Reference
	Two-banded plover (*Charadrius falklandicus*)	R > U	Wild	NA	NA	NA	St Clair et al. (2010)
	White-fronted plover (*Charadrius marginatus*)	R > U	Wild	NA	NA	NA	Baudains and Lloyd (2007)
	Woodchuck (*Marmota monax*)	NS	Wild	Wild	NA	Yes	Lehrer et al. (2012)
	Woodlouse (*Porcellio laevis*)	R > U	Lab	Wild	NA	NA	Houghtaling and Kight (2006)
Exploration							
	Dark-eyed junco (*Junco hyemalis*)	R < U	Lab	Lab since juveniles	NA	NA	Atwell et al. (2012)
Innovation							
	House sparrow (*Passer domesticus*)	R < U	Lab	Wild	NA	No	Liker and Bókony (2009)
	House sparrow (*Passer domesticus*)	NS (3tests) $U_{large} > U_{Small} + R_{Small}$ (1 test)	Lab	Wild	Yes (Rural = Urban)	NA	Papp et al. (2014)
Neophilia							
	Blackbird (*Turdus merula*)	R > U	Lab	Brought as nestlings to the lab	Yes	Yes	Miranda et al. (2013)
Neophobia							
	Blackbird (*Turdus merula*)	R < U	Lab	Brought as nestlings to the lab	Yes	Yes	Miranda et al. (2013)
	Cane toad (*Rhinella marina*)	NS (Novel Prey and Novel Food)	Lab	Wild	NA	NA	Candler and Bernal (2015)

Table 7.1 (continued)

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
	Eastern grey squirrel (*Sciurus carolinensis*)	R > U	Wild	Wild	NA	NA	Bowers and Breland (1996)
	House sparrow (*Passer domesticus*)	NS	Lab	Wild	NA	No	Liker and Bókony (2009)
	House sparrow (*Passer domesticus*)	NS	Lab	Wild	NA	Yes	Bókony et al. (2012)
Risk-taking	American crow (*Corvus brachyrhynchos*)	R < U	Wild	Wild	NA	NA	Knight et al. (1987)
	Black-tailed prairie dog (*Cynomys ludovicianus*)	R < U	Wild	Wild	NA	NA	Adams et al. (1987)
	Cane toad (*Rhinella marina*)	R > U (Novel prey and Novel object)	Lab	Wild	NA	NA	Candler and Bernal (2015)
	Cape ground squirrel (*Xerus inauris*)	R < U	Wild	Wild	NA	NA	Chapman et al. (2012)
	Eastern grey squirrel (*Sciurus carolinensis*)	NS	Wild	Wild	NA	No	Engelhardt and Weladji (2011)
	Garden skink (*Lampropholis guichenoti*)	R < U	Wild	Wild	NA	NA	Prosser et al. (2006)
	House sparrow (*Passer domesticus*)	R < U (juveniles) R > U (adults)	Lab	Wild	NA	NA	Seress et al. (2011)
	House sparrow (*Passer domesticus*)	NS	Lab	Wild	NA	Yes	Bókony et al. (2012)

House sparrow (*Passer domesticus*)	NS	Lab	Wild	Yes	Yes	Vincze et al. (2014)
White-fronted plover (*Charadrius marginatus*)	R < U	Wild	Wild	NA	NA	Baudains and Lloyd (2007)
Woodchuck (*Marmota monax*)	NS	Wild	Wild	NA	Yes	Lehrer et al. (2012)

The column 'trend' reports differences in average trait values between rural (R) and urban (U) individuals, where the reported trends are significant ($P < 0.05$), and the non-significant results are reported as 'NS'. For details on the methodology, see Miranda et al. (2013). The literature review was conducted in April 2015

[a]Juveniles possibly with no difference

same category. For clarity, only studies that focused both on rural and urban populations of the same species, excluding studies focusing on gradients of urbanization, or disturbance in only rural or urban environments. Nonetheless, the concept of rural and urban certainly differs in many of the retrieved studies regarding characteristics of the habitat and degree of anthropogenic disturbance.

The literature review reinforces the idea that only individuals able to behaviourally cope with the new urban selection pressures can be successful in urban habitats. However, with the few number of studies available for each species, we can only speculate about the specific behavioural traits that could benefit a specific city dweller. Most likely, there are various ways for an animal to be successful in an urban habitat, and the optimal behavioural strategies might also vary according to different stages of colonization (for a review on the theme, see Sol et al. 2013) or to the characteristics of each urban habitat. It should be noted that not all urban species are urban colonizers in the true sense of the word; instead, for many populations, their natural habitats are 'colonized' by urban settings. Birds seem to be an ideal taxa to study the urbanization-related shifts in behavioural traits, with two thirds of the studies from our literature review focusing on this group (Fig. 7.1).
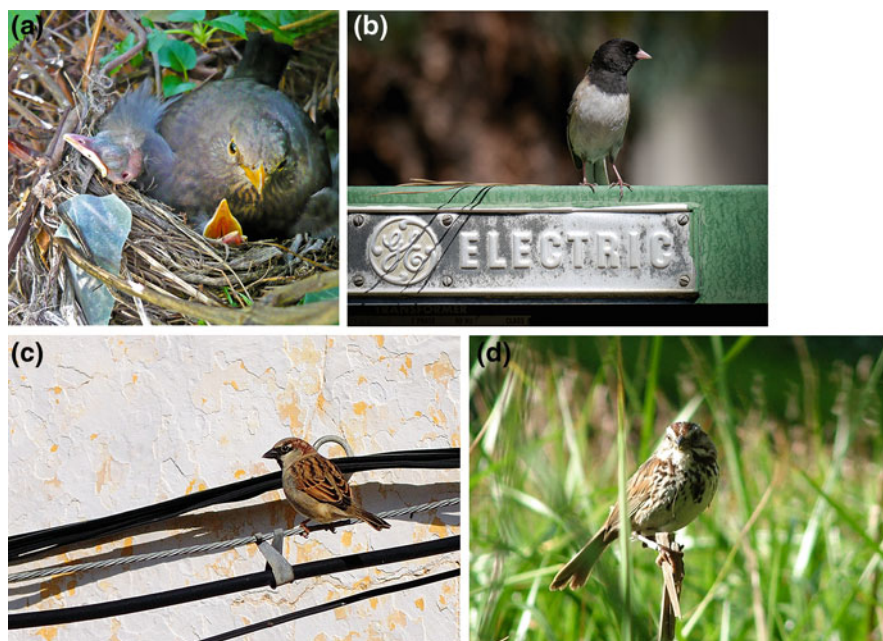
Fig. 7.1 Some of the main bird species used in studies assessing behavioural shifts related with the urbanization process (**a**) European blackbird *Turdus merula* (female and nestlings at an urban nest, picture taken by A.C. Miranda); (**b**) dark-eyed junco *Junco hyemalis thurberi* (picture taken by Jonathan Atwell/www.juncoproject.org); (**c**) house sparrow *Passer domesticus* (picture taken by P.R. Monteiro); (**d**) *Melospiza melodia* (picture taken by C.D. Santos)

The literature review retrieved 36 empirical studies comparing rural and urban conspecifics in aggressive, alarm, escape, neophilic, neophobic, innovative and risk-taking behaviours towards different types of stimuli (Table 7.1). Most of the studies were made in the wild, with only nine studies made under controlled laboratory conditions and only two of these studies using individuals with limited experience of their natural rural or urban environment (Atwell et al. (2012) made a common garden experiment using birds caught as juveniles; Miranda et al. (2013) made a common garden experiment using birds caught as nestlings). Of the 36 studies, 33 showed significant differences between rural and urban populations for at least one of the behaviours and species analysed. Urban populations seemed to be more aggressive (5 of 6 studies in the wild) and showed reduced escape behaviour (24 of 26 studies), having mixed results regarding risk-taking behaviour (6 of 11 studies found that urban populations incurred in higher risk-taking behaviours). For the other considered behaviours, 9 of 12 studies showed differences between rural and urban conspecific populations. Repeatability was only assessed in five studies, in which four found the behaviours under study to be repeatable. Eleven studies assessed correlations between different behaviours, finding that most of the behaviours were correlated.

Although it is now unquestionable that the conquest of urban habitats by animals is linked to intraspecific behavioural shifts, the underlying mechanisms of this changes remain unclear. Are behavioural changes in urban animals due to phenotypic plasticity or to microevolution? Although behavioural plasticity is likely to play an important role in helping animals to cope with the urban environment, recent studies suggest that behavioural differences between rural and urban individuals might be intrinsic, potentially resulting from divergent selection pressures on rural and urban populations (Atwell et al. 2012; Carrete and Tella 2013; Miranda et al. 2013). Next, I will focus on the two possible responsible mechanisms for behavioural shifts in urban animals, behavioural plasticity and microevolution of behavioural traits.

It should be noted that, while throughout this chapter I portray behavioural plasticity and microevolution of behavioural traits separately for the sake of simplicity, I believe that in most cases both mechanisms contribute in some extent to the behaviour observed in urban animals.

7.3   Behavioural Plasticity in Urban Environments

Phenotypic plasticity is a common phenomenon in nature that can be defined as the capacity of an individual with a particular genotype to alter its phenotype under certain environmental conditions (Thibert-Plante and Hendry 2011). Phenotypic plasticity is the primary mechanism enabling individual organisms to adjust their morphology OR physiology OR behavior OR phenology to better suit changes in their environmental conditions, thereby potentially increasing fitness (Thibert-Plante and Hendry 2011; Van Buskirk 2012).

Behaviour, which consists of a motoric response to a sensorial input, is an essential function for animals to interact with their surrounding environment. Being able to adjust behaviour in response to environmental changes can have important life history consequences for an organism. It is generally assumed that behavioural plasticity plays a critical role for the success of city dwellers, as it enables organisms to more efficiently and rapidly deal with the different challenges of the novel urban environment, as finding new resources and effectively using them and coping with unfamiliar and potentially dangerous animals, objects or situations (Sol et al. 2013; Lowry et al. 2013). Under rapid environmental changes as urbanization, behavioural plasticity can be advantageous over evolutionary changes because it can emerge immediately in response to a new environment. It has been suggested that organisms lacking phenotypic plasticity might be naturally excluded from altered environments (Badyaev 2005).

Although having flexibility in behaviour might be advantageous in specific circumstances, it involves an investment of time and energy, implying important costs that might ultimately have a negative effect on reproduction and survival (Sol et al. 2013). Another potentially negative side effect is that behavioural plasticity, by uncoupling the genotype from the phenotype, might decrease the efficacy of evolutionary responses to selection (Van Buskirk 2012). It is important to note, however, that behavioural plasticity is not independent of the mechanisms involving evolution and adaptation: plasticity can evolve in response to changes in the environment if selection acts on reaction norms or if the trait means are correlated with plasticity (Van Buskirk 2012).

7.4 Microevolution of Behaviour in Urban Environments

In many species, certain individuals exhibit behavioural traits that might make them inherently well suited to occupy urban environments. Behaviours that are consistent across time and contexts for one individual (personality traits) might indeed provide important advantages for invading new environments. Animal personalities are taxonomically widespread, being documented in over 100 species (Wolf et al. 2008). In the last years, a number of studies revealed the variation in (van Oers et al. 2004; Schielzeth et al. 2011).

Despite the generalized evidence showing behavioural differences between urban and rural conspecifics, the vast majority of studies so far were not able to disentangle microevolution from behavioural plasticity (Table 7.1). Nevertheless, two recent common garden experiments conducted with urban and rural conspecific bird populations indicate that consistent behavioural traits differ intrinsically between rural and urban individuals (Atwell et al. 2012; Miranda et al. 2013). These differences are likely the result of microevolutionary changes, although the experimental setups could not fully exclude early developmental influences.

The idea of a genetic basis for behavioural shifts in urban individuals is further supported by a recent comparative study that assessed candidate genes for

behavioural traits on several rural and urban blackbird populations across Europe (Mueller et al. 2013). In the above-mentioned study, a candidate gene for harm avoidance behaviour (the SERT gene) exhibited a significant association with habitat type.

Two different evolutionary processes could be responsible for heritable differences in personality traits between rural and urban conspecifics (Miranda et al. 2013): (1) microevolution in personality traits as an adaptation to new urban selective pressures that shift the behavioural optima (post-colonization adaptation) or (2) microevolution of personality traits via non-random gene flow, through a personality-dependent colonization of the urban habitat (pre-colonization adaptation, Edelaar and Bolnick 2012). The two processes might occur concurrently and potentially under distinct selection pressures indifferent stages of colonization (Martin and Fitzgerald 2005).

7.5 Differences in Physiology as Potential Precursors of Differences in Urban Behaviour

The endocrine system is an essential causal mechanism behind animal behaviour. To understand how hormones might shape behaviours under different selection pressures, it is essential to investigate the covariation between hormonal and phenotypic traits and how those could relate to fitness. It has been suggested that differences in suites of behaviours might be influenced by modifications of the two main endocrine axes, the hypothalamic-pituitary-adrenal axis (HPA axis, related with the production of corticosteroid hormones) and the hypothalamic-pituitary-gonadal axis (HPG axis, related with the production of estrogens or androgens) (van Oers et al. 2011). Understanding if and how the endocrine system relates to differences in behaviours between rural and urban conspecifics should be a crucial focus of research in behavioural urban ecology.

In recent years, several studies have focused on differences between rural and urban conspecifics on hormones associated with the hypothalamic-pituitary-adrenal axis (HPA), such as corticosterone, which might improve the chances of survival under adverse environmental conditions. Studies with captive bird populations suggest the existence of an intrinsically reduced acute corticosterone stress response in urban animals (Partecke et al. 2006; Atwell et al. 2012). However, field studies on the subject provided less clear results (Schoech et al. 2004; French et al. 2008; Fokidis et al. 2009). One recent common garden experiment with rural and urban dark-eyed juncos (*Junco hyemalis*) simultaneously assessed differences in behavioural traits and in HPA responsiveness in rural and urban conspecific, concluding that intrinsic differences in exploratory behaviour might be correlated to differences in the corticosterone stress response (Atwell et al. 2012).

The lack of knowledge is even greater when considering hormones associated with the hypothalamic-pituitary-gonadal axis (HPG), such as estrogens or

androgens (Buchanan and Partecke 2012). An existing study suggests that, in the wild, male rural blackbirds have higher levels of plasma testosterone and luteinizing hormone than urban males (Partecke et al. 2005). However, virtually no study assesses simultaneously differences in behavioural traits and in HPG responsiveness in rural and urban conspecifics.

Although the existence of correlations between baseline or maximum hormone levels and individual consistent behavioural traits have been suggested, they have rarely been found (Johnsen 1998; McGlothlin et al. 2007; but see Atwell et al. 2012). It is possible that correlations between behavioural and hormonal traits are not stable during the annual cycle but rather transient (reviewed in Adkins-Regan 2005). Moreover, while some studies found differences in hormone concentration between rural and urban animals, there is a lack of comparisons of other factors involved in the HPA and HPG axis. In fact, many of the reported differences in behaviour between rural and urban conspecifics could be related to aspects of the HPA and HPG axis, not only hormone concentration but also to differences in transport proteins, differences in the number or sensitivity of hormone receptors or cofactors or hard-wired (neural) differences that are not under hormonal control. All these aspects should be addressed in future studies.

7.6 Synthesis and Directions for Future Research

In this chapter, I revised the literature showing that urban animals across many taxa exhibit differences in behaviour when compared to their rural counterparts. I further focused on how behavioural shifts in urban animals can arise from plasticity or from microevolutionary changes and on the possible relations between differences in physiology and in behaviour in urban animals.

On one hand, species in which individuals show high plasticity in behaviour have an inherent capacity to quickly adjust to altered conditions and, in consequence, might be particularly predisposed to occupy urban environments. On the other hand, microevolution of individually consistent behavioural traits (personality traits) as an adaptation to the urban environment could also explain the observed shifts in behavioural traits in urban animals. By allowing populations to flexibly adjust their behaviours to environmental changes, behavioural plasticity can potentially decrease the need for selection to act on behavioural traits (Price et al. 2003). Conversely, it is also possible that the selection of individuals presenting only specific behavioural traits that are beneficial under urban environmental conditions might be associated with a reduction in behavioural plasticity (Martin and Fitzgerald 2005).

Variation in behaviour, either plastic or intrinsic, is an essential aspect that allows species to respond to environmental challenges as urbanization. Individuals from species with a large variation in their behavioural phenotypes are thought to better cope with urbanization when compared to species with narrower ranges of behavioural phenotypes (Sih et al. 2010). To understand the role of evolution versus

plasticity in shaping behavioural traits, we would ideally need to separate the genetic and environmental components of the behaviour and to assess its fitness value in urban and rural habitats. Although these data might be difficult to obtain, studies with repeated measures of behavioural elements in which family effects can be estimated could be the foundation for revealing the basis of variation in behaviour. In the future, behavioural ecologists working with urbanization should more thoroughly address behavioural variation within individuals (plasticity), between individuals (personality), within populations and between populations (Araya-Ajoy and Dingemanse 2013; Dingemanse and Dochtermann 2013). By gaining knowledge about the variation in behaviour and the environmental correlates, we will be able to better understand which are the species that will be excluded from urban habitats and which will be the ones successfully colonizing them, maybe even being able to foresee the shifts in behaviour in our ever changing world.

If microevolution acts in the urban environment through selection pressures favouring specific personality traits, the decrease in between-individual variation (or lower heritability) could lead to the reduction in genetic diversity that is commonly observed in anthropogenically impacted animal populations and usually attributed to genetic drift (Carere and Maestripieri 2013). To date, few publications have focused on assessing the effects of urbanization on shaping the strength and direction of behavioural syndromes, but it has been suggested that urbanization might act on behavioural syndromes by changing the correlations between behaviours via correlational selection (Bell and Sih 2007) or directly by disrupting certain behavioural traits (Scales et al. 2011; Bókony et al. 2012; Royauté et al. 2013). Variation in syndrome structures between different populations may reflect adaptation to local environmental conditions (Bell 2005; Dingemanse et al. 2007). However, selection can also act on independent behavioural traits. In either case, proving that these traits are adaptive would require the evaluation of selection gradients, such as estimating the survival of each behavioural type in natural conditions (Bell and Sih 2007; Sweeney et al. 2013).

It is also particularly important to assess the individual consistency of the behavioural phenotypes. In theory, selection should only act on traits where the intra-individual variation is larger than the between-individual variation (Boake 1989). Repeatability of a behavioural trait is the proportion of the variance of the trait that is explained by differences among individuals, and in most cases the repeatability of a behavioural trait sets the upper limit for heritability (Falconer and Mackay 1996). Thus, in general, genetically determined traits on which selection is able to act are repeatable.

The majority of studies in urbanization has been done on temperate northern regions, where the process of urbanization is older and more widespread (Sol et al. 2013). But research is also needed on regions where the urbanization process is still at an early stage.

Currently, we only have rudimentary knowledge about the mechanisms that allow some species to cope with anthropogenic environmental change. Developing a realistic interpretation of the mechanisms behind differences in behaviour in urban animals requires an integrative approach, of behaviour, physiology, ecology,

genetics and evolution of urban populations. The answers are likely to be complex, but we will hopefully be able to contribute to unravelling the evolutionary ecological consequences of urbanization.

Although understanding organismic behavioural adaptations to urbanization is a topic of major importance, the most crucial achievement should be changing human behaviour itself. The consequences of human environmental change are so devastating that none of our research efforts will be relevant if humans keep destroying natural habitats and depleting natural resources at the current pace.

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Part III
Spatio-temporal Scale and Methodological
Approaches

Chapter 8
The Role of Landscape-Scale Factors in Shaping Urban Bird Communities

Jennifer Litteral and Eyal Shochat

Abstract The composition of urban bird communities is clearly affected by local habitat factors. These factors often determine whether individuals choose to occupy urban habitats and how they behave and reproduce once they are there. However, landscape-scale factors also play a major role in the shaping of urban bird communities. Most commonly, these are elements of the landscape for which heterogeneity can be meaningfully measured at scales of 500–2500 m. The influence of landscape-scale factors is studied using two approaches—the island biogeography approach and the urbanization gradient approach. Commonly influential factors include the remnant habitat patch size, degree of urbanization, road density, amount of tree or paved area cover and land use (a proxy for human disturbance). While there are no consistent patterns governing the responses of overall species diversity and community composition to landscape-scale factors, when species are grouped by life history guilds, consistent patterns emerge. When considered in conjunction with local habitat factors, research about the effects of landscape-scale factors provides valuable implications for the conservation of avian biodiversity in urban environments, especially when specific species and guilds are the targets of conservation efforts.

Keywords Community biodiversity • Landscape-scale • Urban ornithology • Urbanization gradient

8.1 Introduction

It is well established that individuals of avian species make choices about where they will roost, forage and raise young, based upon a variety of habitat characteristics that include elements of the physical environment and vegetative composition

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and structure. There are also demographic and trophic pressures that emerge in fragmented, urban habitats. Ultimately, these choices and processes, taken as a whole, determine the species diversity and density that define avian communities that we observe in a given metropolitan area. Often, the determining factors are highly local. Birds need appropriate microclimates, water availability, nesting sites and cover in a specific area for successful breeding. At times, however, factors on broader scale, a landscape scale, can have a significant effect. Urban environments provide an especially apt natural laboratory for studying the impact of landscape-scale factors on avian communities because the patches of land-use and land-cover type are highly diverse and edges between them tend to be highly contrasting and well defined (Luck and Wu 2002).

8.2 Local Habitat-Scale Factors

One can view cities as large, built patches in a core of more or less natural habitats. The urban islands "sample" species from a regional pool. In that manner, however, species are sampled from the regional pool nonrandomly. Urban environments attract certain insectivores, granivores, and omnivores and favor resident species over migrants (Chace and Walsh 2006). The urban species composition strongly corresponds with habitat structure. The groups and guilds mentioned are those that find the urban environment suitable enough in terms of structures. Species like swifts, swallows, and martins can find walls for building their nests and lawns as open green spaces where they can feed.

8.2.1 Commonly Important Habitat-Scale Factors

City parks are normally structured as lawns and tall trees, offering perches and bare floor for ground-feeding birds. As many areas are being sprayed with pesticides (Raupp et al. 2010) and most bird feeders contain seeds and grains, urban bird communities are rich with granivorous species: pigeons, doves, sparrows, and finches. Not surprisingly, when habitats are compared within the urban core, species richness peaks at rural areas close to wildlands (Chace and Walsh 2006), where various microhabitats are available and invasive, aggressive bird species are less abundant (e.g., Vallejo et al. 2009).

Synanthropic species, such as the domestic pigeon, prefer highly built areas where they can find nest sites with good access to human-related food sources (Przybylska et al. 2012). Parakeets, a common invasive species throughout the world, prefer urban parks with big trees as nest sites. The distribution of the monk parakeet in Barcelona is best explained by the presence of large trees, but also by the density of humans over 65 years old, apparently because retired people often tend to feed parakeets and other birds (Rodriguez-Pastor et al. 2012). This example

indicates the importance of the human factor in determining bird habitat selection in urban settings.

In contrast, thick vegetation corridors are most important features maintaining high native species diversity in urban settings. Riparian corridors and cattle-grazed lands support high diversity and also affect species diversity in nearby areas, owing to the presence of tall trees and thick vegetation (Dominguez-Lopez and Ortega-Alvarez 2014). For a native species to exist in the city, some crucial elements are essential. When utilizing the urban environment, native species seek structures familiar from wildlands. For example, Cooper's hawks prefer urban territories with large native trees and tracts of native vegetation, where prey is apparently more common than in nonnative vegetation (Boggie and Mannan 2014). Yet as the urban habitat is more productive than adjacent wildlands, the urban territories are small, and Cooper's hawk density is high, compared with wildlands. Syrian Woodpecker abundance in the city of Krakow was best explained by the number of trees, total vegetation cover, proportion of built area, and air pollution (Ciach and Frohlich 2013). In this case, air pollution serves as indicator for food in highly polluted areas, where trees are stressed and bark insects are widespread. The importance of food resources is also evident in Rhode Island, USA, where great egrets gathered to forage at higher density in urban than in rural marine habitat, as fish abundance was higher in the urban habitat. The egrets were more successful in hunting, and their energy intake was higher in the urban habitat (McKinney and Raposa 2013).

8.2.2 Habitat Effects on Individuals (Behavior, Physiology, and Reproduction)

Once the habitat is suitable, in terms of structure and food, species may or may not occur in cities, depending on their tolerance to humans and domestic predators. Synanthropic species, that favor human presence, flourish in urban settings (Chase and Walsh 2004). Some native species show high flexibility in their tolerance to humans and may behave differently in urban environments than in wildlands. Other native species show low tolerance to humans but manage to exist and even flourish in highly urbanized areas (e.g., Fernández-Juricic 2000a). Probably, a fairly high proportion of species not found in cities may not tolerate high human population densities. Tolerance to humans may take time, and common native species in urban parks are those that have long history of coexisting with humans, such as doves, crows, American robins, or European blackbirds (as surrogate species in North America and Europe, respectively). In the case of the latter, several behavioral and physiological differences between urban and rural/wildland have been documented, as adaptations to the urban environment (Partecke et al. 2006; Miranda 2016; Tomiałojć 2016). Urban European blackbirds had a lower stress response than their forest conspecifics,

and this difference was genetically determined (Partecke et al. 2006). Similarly, differences in stress-induced plasma hormones between desert and urban curve-billed thrashers suggest that urban thrashers may better cope with stress (Fokidis et al. 2009; Fokidis and Deviche 2011).

Habitat preference is normally correlated with energy intake or reproductive output, as in the Cooper's hawk and great egret, but complex, opposite relationships, known as "ecological traps," may also occur in urban settings. For example, the spotted towhee prefers forest edges near residential areas and birds selecting this habitat fledge more nestlings in this habitat than in forest interior (Shipley et al. 2013). However, nestling mortality is lower in the forest interior, owing to high predation by cats and owls in the edge. Similarly, Syrian woodpeckers prefer polluted areas rich with bark insects but may be directly, negatively affected by the pollution (Ciach and Frohlich 2013). These examples demonstrate how, while birds enjoy high food abundance in urban settings, other factors such as pollution and high predation pressure may reduce their inclusive fitness in urban settings.

8.3 Defining Landscape-Scale Factors

Whereas habitat structure is clearly a critical factor determining whether a species may be present or absent from the urban landscape, the presence of a suitable habitat does not guarantee the occurrence of particular species. Landscape-scale factors also play a role (for a different view, see Daniels and Kirkpatrick 2016). To have a clear discussion about the influence of landscape-scale factors, there first must be a definition of what spatial scales qualify as landscape scale for birds to differentiate them from those considered local scale. Typically, these are elements of the landscape for which heterogeneity can meaningfully be measured at spatial scales of 0.5 km or more. Some studies have found scales of up to 85 km^2 to be predictive of avian species presence or absence. The scales most commonly found to be most significant are 500 m to 2500 m.

8.3.1 The Effect of Body Size on the Scale of Habitat Choice

Birds of different body sizes have been found to respond to landscape heterogeneity hierarchically and at different scales. Hostetler and Holling (2000) quantified the percentage of canopy cover in areas around bird survey points measuring 0.2, 1.5, 25 km^2, and 85 km^2 in seven cities in North America. They also grouped the patches of trees comprising this cover into size categories. Generally, the percentage of tree cover at larger scales and the presence or absence of larger tree patches were more predictive of the presence or absence of species with medium to large body sizes (16.6 g to 576.0 g), while tree cover at smaller scales and the presence or absence of smaller tree patches were more predictive of the presence or absence of species with

smaller body sizes (3.2 g–16.5 g). However, there were several exceptions, and the effect was much stronger in the spring than in the summer, when birds of all sizes responded to canopy cover at the smaller scales. This is attributed to the difficulty of trying to use human measures to model factors perceived by birds during the habitat selection process (Hostetler 1999; Hostetler and Holling 2000).

8.3.2 The Distinction Between Landscape and Local Scales

With the exception of a well-developed body of work on urban corvids (e.g., Evans et al. 2009; Gregory and Marchant 1996; Konstantinov 1996; Marzluff et al. 2001; Marzluff and Neatherlin 2006; Withey and Marzluff 2005), most urban avian diversity studies that incorporate landscape-scale factors have focused on species within the smaller range of body size. One such study, Melles et al. (2003), drew a clear line between local and landscape variables and compared the predictive influence of each group of variables. They measured local variables in 50 m by 50 m plots around point count sites and landscape variables in circles with 500 m and 1000 m radii around those same sites. Pennington and Blair (2011) draw the line between "small" and "large" scales at 500 m. Stratford and Robinson (2005) used circular buffers to quantify the character of the landscape around point count sites. In their study, they included buffers with radii of 100, 200, and 1000 m. While the same land-cover variables were quantified within each scale, the researchers identify the 1000 m scale as the landscape scale. Also setting it apart is that, in this study, it is the only scale of the three for which measures of configuration, not only quantity, of land-cover types is calculated and included in the analysis. Land use/land cover has been quantified and found to be a significant predictor of avian community composition at radii as large as 5000 m from avian survey points in Dunford and Freemark (2005). They also suggest that their results support the idea that the most effective scale at which to measure surrounding land use/land cover may differ by type (urban, agricultural, park, etc.). Generally, the consensus in the recent literature appears to be that biophysical factors measured at scales of 500 m or larger can be considered landscape-scale factors, so that is the definition we will use in this chapter.

8.4 Landscape-Scale Studies

8.4.1 The Value of Multiple-Scale Studies

While landscape-scale factors measured at a specific range of scales, 1000–2500 m, have been consistently found to have significant effects on urban avian diversity, there is also substantial evidence of the benefits of multiple-scale studies. When the

scale of measurement or observational scale is either much larger or much smaller than the intrinsic scale of the ecological process or pattern that the study is attempting to describe, scale mismatch occurs, and the phenomenon may be missed entirely (Wu and Li 2006). Since the intrinsic scale of ecological processes is often unknown, multiple-scale studies that employ a range of observational scales likely to approximate the intrinsic scale are a logical and common approach to discerning the intrinsic scale of the target phenomenon. In the case of urban avian ecology, these phenomena are the core drivers of biodiversity and community composition including habitat choice, mate availability, interspecific competition, resource availability, and predation. Additionally, the results of several multiple-scale studies have shown that the most predictive models of avian diversity are those that include variables measured at multiple scales (Stratford and Robinson; Melles et al. 2003; Dunford and Freemark 2005; Pennington and Blair 2011; Litteral and Wu 2012; Meffert 2016). This is unsurprising since most bird species choose habitats hierarchically and at multiple spatial scales—habitats within landscapes, territories within habitats, nesting and foraging patches within territories, and so on. The ranges of spatial scales that these hierarchies occupy may differ by guild, species, or individual (Hostetler and Holling 2000; Bentley and Catterall 1997; Garden et al. 2006).

8.4.2 The Urban Gradient Approach and the Island Biogeography Approach

Most studies investigating the influence of landscape-scale factors on urban avian diversity fall into two categories. In the first, diversity is measured within the urban matrix, generally across a gradient of degree of urbanization (the urban gradient approach). In the second, diversity is measured in known habitat patches (remnant natural habitat patches, green spaces, parks, gardens) and characteristics of the habitat patches, themselves (e.g., size, shape, isolation) are the landscape-scale factors (the island biogeography approach) (MacArthur and Wilson 1963, 1967). In more recent decades, the nature of surrounding matrix has also often been included as a landscape-scale factor in studies based on the island biogeography model (Dunford and Freemark 2005; Litteral and Wu 2012; Martin et al. 2006). When it was introduced, the urbanization gradient was typically measured by the distance from the urban center (McDonnell and Pickett 1990); however, further work on patterns of urbanization has revealed that many, if not most, modern metropolitan areas are polycentric, meaning that distance from one urban center may not meaningfully capture the degree of urbanization affecting ecological communities in any given location. Now, the urbanization gradient is more often measured by landscape metrics that characterize the landscape within certain distance from where biological variables, such as avian community diversity, are being measured (Alberti et al. 2001). These metries include measures of landscape composition

(area or percent land cover of defined land-use/land-cover types) and heterogeneity (patch density, diversity indices, dominance) and configuration (contagion, interspersion, fractal dimension).

Stratford and Robinson (2005) provide a case study in this approach. They used data on neotropical migrants from 13 established Breeding Bird Survey (BBS) routes across an urban to rural gradient in Columbus, Georgia, USA. They categorized the landscape patches with different degrees of urbanization and quantified the amount of cover in each type in 100, 200, and 1000 m buffers around each point count site along the BBS routes. To quantify type of land cover, they categorized the landscape into urban, barren, water, pine plantations, open parks and pastures, natural woodlands, and early successional forests and calculated the percent cover of each of these categories, within each buffer size (Fig. 8.1). For the largest buffer size, they also calculated Simpson's diversity index to quantify patch diversity and patch density, edge density and contrast-weighted edge density to quantify configuration. They found that no single scale or variable best predicted species occurrence, but large-scale composition variables had the most influence, specifically urban cover and early successional forest cover at the 1000 m scale. They also found that for their target group, neotropical migrants, the effect of urban cover on species richness was negative and monotypic. Configuration variables were not shown to be particularly influential in this study.

In a similar study conducted in Burnaby, British Columbia, Canada, the scales investigated were 50 m, 500 m and 1000 m. They defined variables measured at the 50 m scale, as local variables, and those measured at the 500 m and 1000 m scales, as landscape variables. They also found that the most successful predictive models included variables with multiple scales (Melles et al. 2003). In this gradient study, the percentage of impervious surface was particularly influential, and, again, configuration variables did not play a major predictive role.

Litteral and Wu (2012) provide a case study in the island biogeography approach from an arid ecosystem. The passerine community was surveyed in 15 habitat reserves (mostly city parks with natural, desert vegetation) in Phoenix, Arizona, USA, and then analyzed as a whole and in groups defined by migratory, feeding, and nesting habits. Measures of species diversity and community composition were compared to characteristics of the reserves, which serve as the "islands." Characteristics of the reserves such as area, D_i (an index that measures edge-to-area ratio), isolation from other "islands" or habitat fragments, and isolation from the "mainland" or outlying desert surrounding the city, were measured. The urban matrix surrounding the reserves was categorized, and the proportion of each land-use/land-cover type was measured within buffers at multiple spatial scales—200 m, 1000 m, and 2500 m (Fig. 8.2). Further, while area was part of almost all competitive models that predicted the community as a whole and individual life history groups, D_i and isolation were not nearly as influential. They found land-use/land-cover variables did not predict overall species diversity well, but some models that included both reserve area and land-use/land-cover types at different scales were predictive of the diversity of certain groups, defined by life history traits.
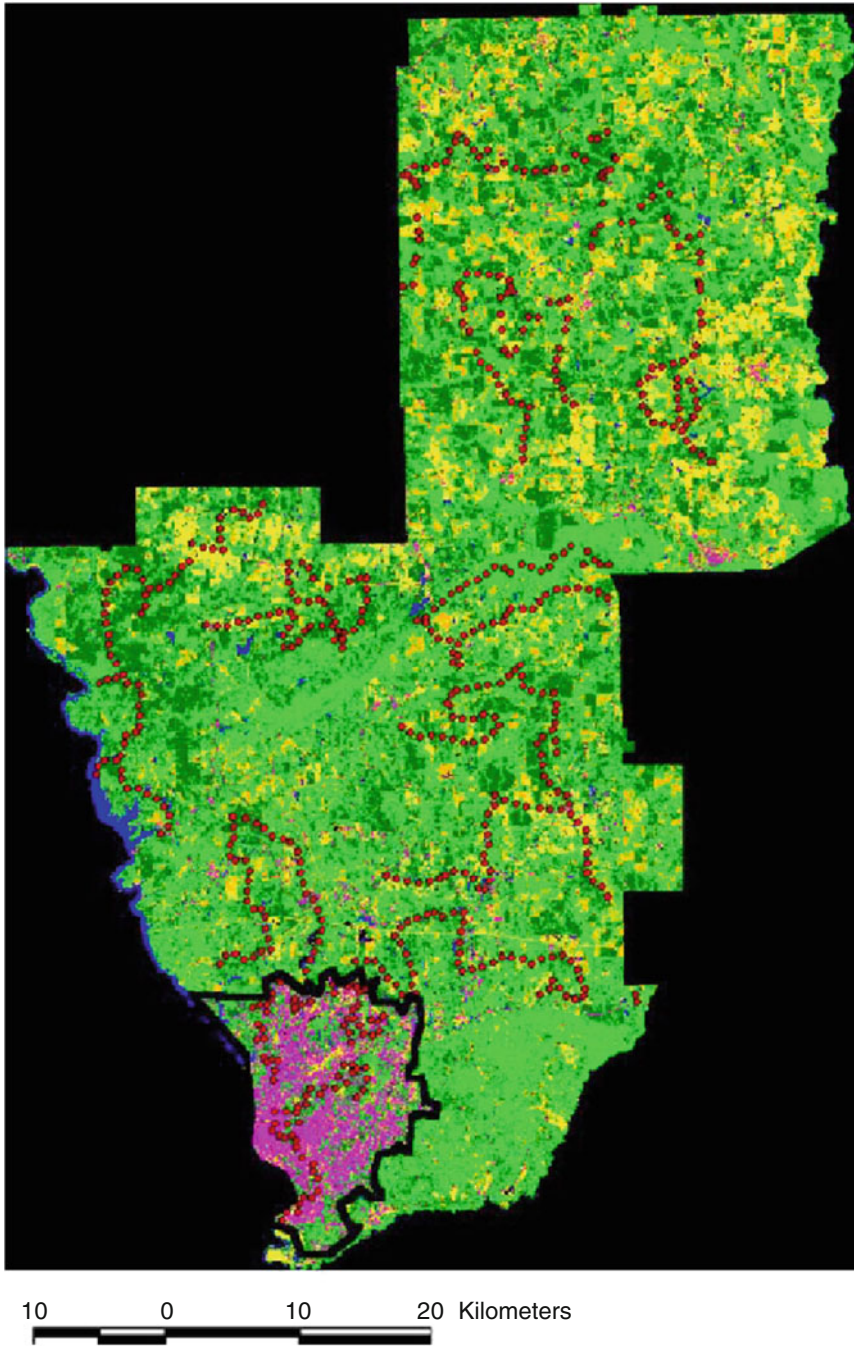
Fig. 8.1 The map of Stratford and Robinson's (2005) study in the Columbus, Georgia, USA area illustrates an urbanization gradient approach (direct urbanization paradigm) study design. The LandSat image broadly shows areas with different degrees of urbanization, with the main urban

A similar study in Stockholm, Sweden, a forested area, was consistent with the results of the arid land study in that, for the five species studied, habitat fragment area was critical, as was urbanization intensity within 1000 m of the forest habitat fragments, even when fragment area was taken into account. Three of the five species studied only occurred in fragments 200 ha in size or larger. Notably, isolation from other fragments was very influential in this study, overwhelmingly so for species dependent upon deciduous forest (Mortberg 2001).

Riparian corridors are an unique and interesting type of island analog. They are particularly interesting in urban studies as many urban areas, regardless of ecoregion or geography, contain riparian corridors which may be more similar to riparian areas in other cities than they are to the urban matrix of the city in which they are situated. The width and quality of the riparian forest is almost always one of the most influential variables affecting species richness and abundance, but the character of the surrounding landscape can also have an impact (Hennings and Edge 2003; Luther et al. 2008; Martin et al. 2006; Saab 1999). Saab (1999) studied riparian parcels along 100 km of the South Fork of the Snake River. Microhabitat characteristics were only the most strongly associated with the presence or absence about one-third of the species studied. The surrounding land-use type within 1 km of the riparian parcels was most strongly associated with the other two-thirds of species. Some land-use types were natural, such as juniper woodland, but others were the result of human development such as agriculture and exurban residential development.

8.5   Community Diversity and Composition Responses to Landscape-Scale Factors

Urban avian community composition is an emergent property determined by the accumulated habitat decisions of individuals and demographic dynamics of species. Species density, richness, and diversity are typically used as measures of different aspects of community composition that can be related to landscape-scale factors. Several studies have also parsed out the community into groups based on life history traits such as migratory habits, nesting substrate, diet, brooding strategy, and synanthropy for separate analyses or analyzed the relationship of individual species presence and abundance to landscape-scale factors.

Fig. 8.1 (continued) center located at the southern end of the study area and several smaller centers in the northeast quadrant of the study area. The *dots* represent bird survey points
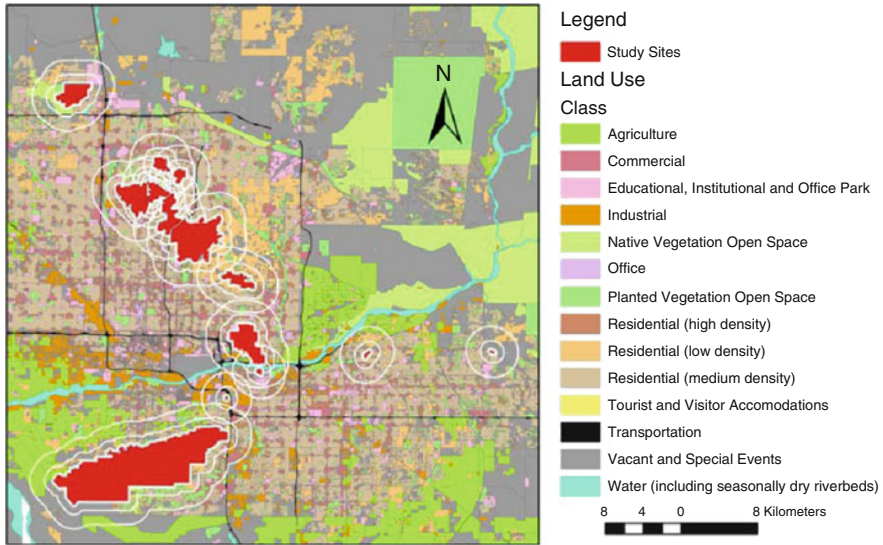
Fig. 8.2 The map of Litteral and Wu's (2012) study illustrates an example of an island biogeography approach (urban context paradigm) study design. The land-use/land-cover categorical map (MAG 2000) shows different types of urban land-use/land-cover types. The study sites are protected natural desert habitat fragments. Avian communities within the habitat fragments were compared to percent cover of each urban land-use/land-cover type within the multiple scale buffers surrounding the fragments

8.5.1 The Effect of Urbanization on Avian Diversity and Community Composition

The most obvious and commonly studied landscape-scale factor related to measures of community composition in urban bird studies is the degree of urbanization. In many urbanization studies, the peak of species richness is generally somewhere in the middle of the urbanization gradient (Blair 1996; Hennings and Edge 2003; Marzluff 2005; Suarez-Rubio and Thomlinson 2009), but there are a few notable exceptions where the relationship between species richness and degree of urbanization was found to be monotypic and negative (Clergeau et al. 1998; Zhou et al. 2012). Density, on the other hand, tends to show a positive relationship with urbanization (Chace and Walsh 2006; Vignoli et al. 2013; Zhou et al. 2012).

This monotypic relationship is fairly intuitive and can be explained by a variety of factors, most obviously through vegetation loss and a correlated increase in paved area. These two measures are oft used as proxies for degree of urbanization overall in an area (Donnelly and Marzluff 2004; Mills et al. 1989; Trollope et al. 2009). Increased auditory disturbance, interspecific competition with introduced species and changes in the predator community may also play roles in the decreased diversity in more urbanized areas.

Some studies, however, have found that species diversity peaks at intermediate levels of urbanization within the landscape. Two main hypotheses have been put forward to explain this phenomenon. The first is the intermediate disturbance hypothesis—moderate levels of disturbance increase habitat heterogeneity on a landscape scale and an increase in species diversity follows (e.g., Blair 2004; Böhning-Gaese 1997; Clergeau et al. 1998; Marzluff 2005). Related to this hypothesis is the idea that there are different characteristic communities in highly urbanized versus natural areas. Usually endemic and otherwise sensitive species inhabit natural areas at one end of the urbanization gradient, while synanthropic and introduced species inhabit the urban core. In areas of moderate urbanization, portions of both communities may persist, creating the diversity peak. The second hypothesis is that suburban landscapes provide significant subsidies to productivity including increased water and fertilizer, which supports more robust populations of more species (Cook and Faeth 2006; Litteral and Wu 2012; Przybylska et al. 2012; Rodriguez-Pastor et al. 2012). Clearly, these hypotheses are not mutually exclusive, and teasing apart the effects of each can be quite difficult. The effects of this process are easier to pinpoint through an analysis of community composition. Even a recent study conducted in the Research Triangle Area of North Carolina, USA, which found no difference in species richness along the urbanization gradient, found significant differences in community assemblage driven by urbanization. This general pattern was consistent across many studies where degree of urbanization, at the landscape scale, was measured in different ways (Minor and Urban 2010).

Some studies directly quantified areas covered or dominated by buildings using LandSat TM imagery and aerial photography (Marzluff 2005; Stratford and Robinson 2005; Suarez-Rubio et al. 2013). While there are limitations to using this technology, including the need for additional ground-truthing to capture features smaller than the grain of the imagery (Gottschalk et al. 2005), it has made widespread study of landscape-scale factors financially and temporally feasible. Other studies have used land-use/land-cover data derived from satellite imagery that have been processed into categories by local governments and other entities (Hennings and Edge 2003; Hostetler and Knowles-Yanez 2003; Litteral and Wu 2012). Stratford and Robinson (2005) used LandSat imagery to quantify percent urban cover defined by impervious surfaces (roads, buildings) and found it to be highly influential at multiple spatial scales on neotropical migrant diversity in Columbus, Georgia, USA. Similarly, surrounding housing density was found to explain the most variation in species richness among nonnative species and native indicator species in a study in Tucson, Arizona, USA (Germaine et al. 1998). Minor and Urban (2010) and Trollope et al. (2009) opted to measure degree of urbanization in the landscape using road density, and, while Minor and Urban (2010) did not find significant differences in overall species diversity between urban and rural areas, they found urbanization to be the most important factor in structuring the community assemblage. Notably, the effect was the same, regardless of the size or traffic on the roads in question.

A cover type that is characterized by human development, but that is not strictly urban, has also been found to be important (see Daniels and Kirkpatrick 2016).

Several studies have looked specifically at the effect of low-density, exurban residential development. It has been hypothesized that landscape-scale factors may have a particularly pronounced effect on structuring bird communities in areas of exurban development because the effects of such development are more diffuse as the intensity is spread out across broader spatial scales (Hansen et al. 2005; Miller et al. 2001). Other landscape-scale factors that have been found to be important in determining avian community composition and diversity include percent paved area, number of buildings, and golf courses (Blair 1996; Chace and Walsh 2006; Hostetler and Knowles-Yanez 2003; Merola-Zwartjes and DeLong 2005). Dunford and Freemark (2005) found that resident species diversity responded most strongly to both low- and high-intensity agriculture in buffers of 1600 m to 5000 m around bird survey points in Ottawa, Canada. Golf courses have been shown to serve as surrogate riparian habitat in arid ecosystems (Merola-Zwartjes and DeLong 2005). Conversely, canopy cover and forest patch size have been found to be important in many studies, especially those using the island biogeography approach (Donnelly and Marzluff 2004; Mortberg 2001).

8.5.2 Species Diversity by Life History Traits (Guilds)

Different bird species have different requirements for survival and reproduction depending on their nesting, feeding, and migratory habits, so it stands to reason that they would dwindle or thrive based on different habitat elements at any scale, including landscape scales. Several studies have incorporated guild-specific diversity analyses with interesting results (Fig. 8.3). These studies also have useful implications for targeted conservation management.

8.5.2.1 Migratory Guilds

Neotropical and other long-distance migrants are well established as a group that is particularly sensitive to landscape-scale urbanization (Friesen et al. 1995; Hennings and Edge 2003; Stratford and Robinson 2005; DeGraaf and Wentworth 1986). Dunford and Freemark (2005) found that neotropical migrant richness decreased in response to urbanization at two distinct ranges of scales, a broad range (1600 m and 2200–5000 m) and a narrow range (200–1800 m); however, abundance of this group only decreased at the narrow range. Resident species richness, in their study, increased with urbanization (and intensive agricultural use) at both of these scales and only decreased with low-intensity agriculture. Hennings and Edge (2003) found that neotropical migrants using riparian habitat patches in their study area (Portland, Oregon, USA) were particularly sensitive to road density in the surrounding landscape, a result not found for short-distance migrants in their study. However, most of the significant relationships they found were at smaller spatial scales. Suarez-Rubio and Thomlinson (2009) also found evidence, from a tropical
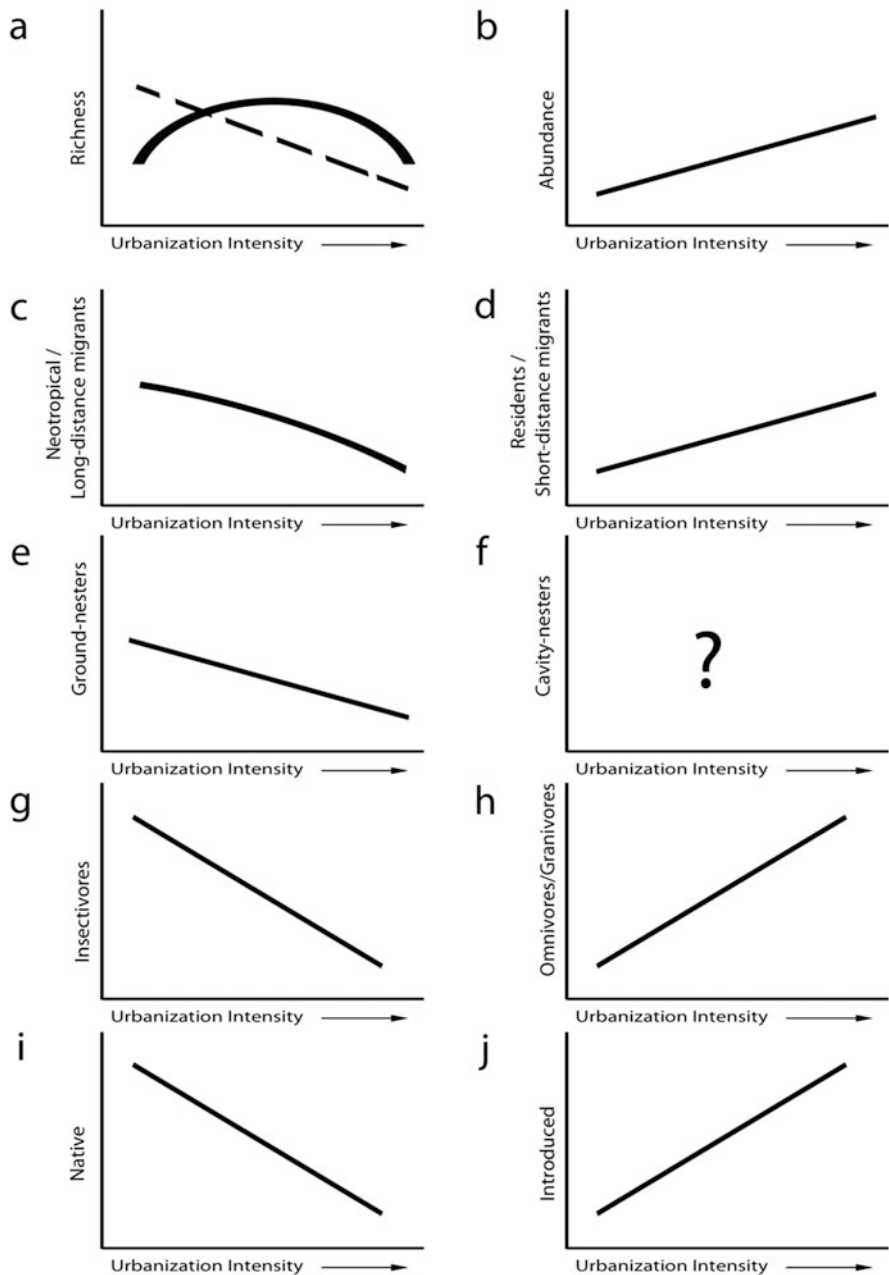
Fig. 8.3 The present review of recent literature shows some general, conceptual patterns of species' responses to urbanization at landscape scales. Overall species richness tends to either decrease with urbanization or peak at some intermediate intensity (**a**). Abundance, on the other hand, shows consistent increases with urbanization intensity (**b**). Species richness within guilds, or subsets of the community defined by functional groups, shows distinct responses. Neotropical and other long-distance migrants are particularly sensitive to urbanization (**c**), but residents show slight increases in species richness (**d**). Ground nesters decrease with urbanization (**e**), while no

ecosystem, that migrants respond most strongly to habitat characteristic at smaller spatial scales. Long-distance migrants have also found to be sensitive to human disturbance in the eastern hemisphere. Park and Lee (2000) found that migratory species were more area sensitive than residents in an island biogeographical study in Seoul, Korea.

Short-distance migrants and resident species seem to be less sensitive to human development activities (Dunford and Freemark 2005; Peris and Montelongo 2014; Park and Lee 2000; Hennings and Edge 2003). Zhou et al. (2012) studied parks within two different types of urban matrix—within the old, long-established part of Hong Kong and a newer area that had only been developed for the last 40 years and found that habitat fragments (parks) within both types of matrix were more dominated by resident species than the surrounding, nonurban environment.

Tryjanowski et al. (2013) provide one potential mechanistic explanation for the disproportionate effect of urbanization on long-distance migrants. They studied mean first arrival date for 18 migratory species in cities and nearby rural areas in western Poland from 1983 to 2010. While they found that, despite well-documented urban heat island effect, species tended to arrive in rural areas earlier than in urban areas, they found that urban birds were rapidly closing the gap, advancing their mean first arrival dates to earlier in the spring at a much faster rate than rural birds. This may lead to broad-scale mis-synchronization of the arrival of individuals with the peak of seasonal resources, especially for insectivores, another sensitive guild.

8.5.2.2 Nesting Guilds

In urban gradient studies, there is generally a decrease in the richness and/or abundance of ground nesters from the periphery to the urban center (Fernández-Juricic 2000a; Vignoli et al. 2013). More generally, Germaine et al. (1998) found an inverse relationship between the degree of the urbanization in the landscape and average nest height of a species. Shrub and tree nesters have been examined less often but also show sensitivity to fragment area in island biogeography approach studies (Donnelly and Marzluff 2004; Suarez-Rubio and Thomlinson 2009; Park and Lee 2000) and sensitivity to degree of urbanization in gradient studies (Lim and Sodhi 2004; Fernández-Juricic 2000a).

Cavity nesters have been broadly studied, but consistent patterns describing how they respond to landscape-scale factors have not emerged. Park and Lee (2000) found that the abundance of cavity nesters was much higher in natural areas than in urbanized areas in Seoul, Korea. Vignoli et al. (2013) documented the opposite pattern, finding that cavity nesters exploited artificial cavities in urban areas which increased their abundance with degree of urbanization in the landscape. Litteral and

Fig. 8.3 (continued) consistent pattern has emerged for cavity nesters (**f**). Insectivores (**g**) and native species (**i**) consistently show declines. Conversely, omnivores and granivores (**h**) and introduced species (**j**) show increases

Wu (2012) found no consistent relationship between landscape-level factors and cavity nesters in Phoenix, Arizona, USA. While not conducted in an urban area, Warren et al.'s (2005) study may shed some light on this lack of any consistent pattern. They specifically studied the habitat preferences of cavity nesters in a managed forest at three scales—100, 300, and 1000 m. At the landscape scale, they measured characteristics such as dominant tree species and stand age; at local scale, they measured several variables including tree species, amount of woody debris, and number of stumps. When the effects of local variables were accounted for, none of the relationships of cavity-nesting species with landscape-level variables remained significant. Cavity nesters appear to make habitat decisions at local scales.

8.5.2.3 Feeding Guilds

Of the most commonly studied feeding guilds, insectivores, show the most consistent declines with urbanization and other development in gradient studies (DeGraaf and Wentworth 1986; Lim and Sodhi 2004: Trollope et al. 2009). In island biogeography studies, insectivores are often the least tolerant of small habitat fragments (Zhou et al. 2012) and of high urbanization intensity surrounding habitat islands (Litteral and Wu 2012). This is presumably due to a lack of sufficient food resources since arthropod communities are also affected by urbanization (Cook and Faeth 2006). The road density within 1000 m of survey points was found to be the most influential factor in predicting the presence or absence of several insectivore species in Melbourne, Australia (Trollope et al. 2009). Surprisingly the negative effect of road density was far more influential than the positive effect of river density at the same scale. Trollope et al. (2009) suggest that demographic factors may also be at play. Several insectivore species in their study display different dispersal abilities and area sensitivity based on sex. This leads to a population that is not successful at reproduction in smaller and more isolated habitat fragments.

Omnivores, unsurprisingly, seem to be the most adaptable to urbanization (Vignoli et al. 2013; Chace and Walsh 2006). Granivores also show high richness and abundance in small fragments and more urbanized areas, possibly due to anthropogenic food supplementation (Peris and Montelongo 2014; Lim and Sodhi 2004; Zhou et al. 2012; Vignoli et al. 2013). Frugivores have not been often studied as a group, but Lim and Sodhi (2004) found that, in Singapore, frugivore diversity increased with the amount of low-density, single family housing within 500 m diameter buffers around bird survey points.

8.5.2.4 Native and Introduced Species

Predictably, nonnative species generally respond positively to urbanization in the landscape (see Sol et al. 2016). In Hong Kong, Zhou et al. (2012) found that most

measures of the avian community as a whole and of groups within it, responded to land-use/land-cover type within 400 m of parks where the avian community was surveyed, endemic and introduced species responded more strongly to urban land-use/land-cover types within 1000 m of focal parks. There were no introduced species present within parks studied in the more recently (40 years) developed portion of the city, only within parks in the old city. In tropical San Juan, Puerto Rico, USA, forest patch size was found to be the most influential factor for both native and introduced species diversity, but the relationship existed in opposite directions with introduced species showing higher diversity in small patches, which native species diversity rose in larger patches (Suarez-Rubio and Thomlinson 2009). Native species richness was also increased by a lower degree of urbanization in the surrounding landscape and, conversely, introduced species richness increased with a higher degree of urbanization in the surrounding landscape. In their study of a desert city, Tucson, Arizona, USA, Germaine et al. (1998) found that introduced species were more responsive to local patterns, while native species are often more responsive to landscape-scale patterns. They found that landscape-scale factors were only included in the most predictive model for native species. Distance to nearest undisturbed wash, which varied from 0 to 5040 m, was included in the model with a negative coefficient. Only variables from their set of variables measured at a 100 m scale were included in the most predictive model for nonnative species.

These broadly varied responses of different guilds (Fig. 8.3) likely account for many of the varied and conflicting results that have been found for the responses of avian diversity and richness to landscape-scale factors. The overall response of a community in a given metropolitan area is likely to be heavily influenced by the proportion of the community that is made up of different guilds in a given metropolitan area.

8.6   Composition vs. Configuration

While the absolute amount or relative proportion of specific types of land use/land cover appear to have significant effects on community composition and diversity, surprisingly, configuration variables have rarely been found to be important (Trzcinski et al. 1999; Fahrig 2001; Murgui 2009). Many urban gradient studies only include landscape composition and do not consider configuration variables; however, most of those that do have found that they have little effect on community composition. Stratford and Robinson (2005) used Simpson's diversity index, patch density, edge density, contrast-weighted edge density, and fragmentation index to measure configuration within their multiple-scale buffers. Only one of these variables, contrast-weighted edge density, made it into the top ten most predictive models for either year included in their study.

On the other hand, studies based on the island biogeography approach almost always incorporate some measures of landscape configuration. Usually these

studies are conducted with parks, riparian areas, or other natural habitat fragments acting as the "islands." Patch size and isolation from other patches or from source populations is almost always calculated and analyzed. In a pattern parallel to that found in urban gradient studies, in most cases patch size, or riparian forest width, both measures of habitat amount, is influential, but isolation, a measure of configuration, is less so. This pattern has been found across a wide range of ecosystems of the Americas (Litteral and Wu 2012; Peris and Montelongo 2014; Stratford and Robinson 2005) Europe (Clergeau et al. 2001; Fernández-Juricic 2000b) and Australia (Platt and Lill 2006). Litteral and Wu (2012) found that, surprisingly, while distance to other fragments was significant for some guilds, distance to the outlying desert, in this case the "mainland," was not.

8.7 Local Habitat-Scale vs. Landscape-Scale Factors

Clearly, both local habitat-scale factors and landscape-scale factors have significant effects on avian community composition in urban environments. Most studies that have attempted to explicitly parse out the influence of local and landscape-scale factors and compare the relative importance of the two have found that local habitat factors are more influential but that landscape factors still play a role. This role usually remains significant even when the role of local factors is statistically accounted for and removed (Fernández-Juricic 2004; Godinho et al. 2010; Hennings and Edge 2003; Jokimäki 1999; Luther et al. 2008; Melles et al. 2003). What is even more interesting and more useful for guiding the conservation of biodiversity is the interaction between the two.

Testing the effects of both landscape- and habitat-scale factors in Vancouver, Melles et al. (2003) concluded that both are important for predicting urban bird diversity. Of the local variables, large coniferous trees, berry-producing shrubs, and the presence of freshwater streams were particularly important. This may suggest a combined effect of resources such as water, food, and nest sites at the local scale. At the landscape scale, park size and the proportion of forest cover were important drivers of diversity.

Habitat configuration, interactions with local habitat factors, or competitive interactions may be more influential in different cities in different types of ecosystems. The importance of landscape-scale variables was well demonstrated in *Parus* spp. in Stockholm (Mortberg 2001). Large patches of suitable forest (200–400 ha) were essential in the landscape for the presence of all species, whereas small patches of suitable habitat were (20–40 ha) not occupied. High proportions of built, open, or flooded areas in the landscape were negatively correlated with most species occurrence, suggesting that these species lacked stepping-stones for dispersal. However, in another city, Valencia, Spain, *Parus major* bred in much smaller and heterogeneous patches (including wooded streets) suggesting other factors may be more important determinants of species presence/absence (Murgui 2007, 2014).

For several species, mostly native, non-synanthropic species, configuration of green spaces and the lack of riparian corridors may directly prevent or slow immigration into urban parks. Landscape factors may also affect species distribution indirectly. In Manila, areas with low proportion of built-up areas and high proportion of wooded areas showed high species richness, diversity, and evenness (Vallejo et al. 2009). Blocks in the city with opposite characteristics had lower diversity and evenness. Whereas these differences may simply be the result of development, it has been recently suggested that uneven communities may indicate loss of diversity as a result of local extinctions due to competitive interactions (Shochat et al. 2010). In this process, increasing habitat productivity and decreasing predation pressure act simultaneously for the benefit of invasive species. Such species that are kept "suppressed" in harsh, native environments, flourish under the new conditions, become dominant, and, being more efficient foragers, may exclude several native, subordinate species from the urban ecosystem. This local competitive process can compound the effects of landscape-scale fragmentation. Since most invasive species are overabundant, their control will be best done locally, after identifying the exact type of interaction, rather than applying "big solutions" such as eradication of invasive species that are expensive and are not likely to work (Shochat et al. 2010)

Patch area may be a good predictor for the number of species, suggesting that landscape variables may be good predictors of species richness. Yet, whereas area explained 96 % of the variation in bird species richness in Manila (Vallejo et al. 2009), it only accounted for 40 % of the breeding bird species richness in Hong Kong (Zhou and Chu 2012). This may suggest that, although park size was the best model accounting for species diversity in Hong Kong, other, not measured factors, have an important role in the variation of community composition. Furthermore, the species-area relationship does not address whether the increase in species richness is based on ecological processes or is simply the result of sampling artifacts. Variation in diversity indices (as found in both Manila and Hong Kong) may hint of biological processes, such as habitat diversity, or source-sink populations, but understanding these processes requires data on species interaction, reproduction, and population dynamics, variables rarely measured in the context of landscape ecology in urban settings.

8.8 Implications for Conservation

Understanding landscape-scale patterns of avian diversity can be applied to the conservation of neotropical migrants, woodland-dependent species, and other groups of native species that may be threatened by urbanization and thus considered conservation targets. This can be implemented through urban planning or through more localized, fine-scale efforts. For conservation of diverse communities in urban environments, the most important thing is to conserve large green spaces (parks) that may serve as proper habitat and/or stepping-stones for native species (Jokimäki

1999; Fernández-Juricic 2000b). These green spaces are particularly important when they remain undeveloped and are remnant patches of native habitat. Large green areas mean higher habitat and microhabitat diversity but also higher chances of survival for larger species that require large spaces per se. Large green urban spaces may function as healthy ecosystems, but many ecological processes may be slowed or arrested with further fragmentation. Therefore, large parks can offer proper ecological conditions for a higher number of species, as well as refuge for subordinate species that may fail to establish in small parks owing to negative interactions with invasive, aggressive species (Shochat et al. 2010).

The area available to be retained as habitat fragments (native habitat, improved urban green spaces, and vegetatively complex streetscapes) is often limited by social, cultural, and economic constraints. Theory suggests that the richness of woodland-dependent species drops off dramatically at 10–30 % natural land cover across the landscape (Andren 1994). In a systematic study of 24 landscapes ranging from 2 to 60 % natural land cover, threshold responses (dramatically reduced species richness) were observed at around 10 % remaining natural land cover. If natural land cover in an urbanizing landscape cannot be kept well above threshold levels, healthy populations of many species are not likely to be maintained (Radford et al. 2005).

It is unclear whether healthy breeding populations can be maintained within the city at all or whether regular immigration from the peri-urban or natural area surrounding the city is necessary. Snep et al. 2006 provide a mechanistic model to explain how this phenomenon may work using butterflies, a similarly mobile group of species as a case study. The literature on metapopulations that include source and sink populations across habitat networks is well developed (see Poiani et al. 2000); however, attempts to address this question statistically have had mixed results. Litteral and Wu (2012) found that a habitat patch's degree of isolation from other patches had a negative effect on species richness, but isolation from outlying natural areas had no significant impact, suggesting that immigration from the peri-urban areas was not important. Hedblom and Söderström (2010) took a more nuanced approach. They found that the effect of the amount of peri-urban woodland on avian diversity in urban areas differed based on focal species, landscape context (farmland or woodland), and the amount of urban woodland present. It is clear that urban planning can be used to try to reach target amounts of remnant habitat within cities and that those areas can be managed in specific ways to promote vegetative complexity, but the role of remnant habitat configuration and in the importance of corridors will require further, more mechanistic, studies.

To improve urban parks as bird habitat, it is important to maintain the missing foliage levels, so that urban parks mimic real forests and woodlands in terms of habitat structure. Urban parks are normally designed as lawns and tall trees. In most cases, they miss shrubs and bushes, or when they exist, they are hedges shaped by trimming. This missing vegetation level is probably the cause for the lack of several bush nesting species for urban settings. These lessons about vegetative complexity can also be applied to the design of urban and suburban neighborhoods. Ikin et al. (2013) found that having a higher proportion of native street trees allowed

native urban adapter species richness to increase and make up a greater proportion of total species richness relative to exotic urban adapters, but increased complexity in vegetative structure was required for richness of native urban avoiders to increase. Lim and Sodhi (2004) hypothesize this effect is largely due to the lack of adequate nesting sites for native species in areas with simplistic vegetative structure. When neighborhoods with complex vegetative structure surround remnant habitats, they may increase the functional size of the habitat patch (Dunford and Freemark 2005; Martin et al. 2006; Litteral and Wu 2012).

Riparian habitat is one of the most important natural habitats in urban settings (Hennings and Edge 2003; Pennington and Blair 2011). In terms of habitat structure and resources, it offers many levels and profiles of thick, green vegetation, water, and food for various bird species that urban park vegetation may fail to mimic. In a systematic landscape study, Bennett et al. (2014) found that, as natural land cover decreases in a landscape, riparian areas shelter a disproportionate amount of avian species richness. Additionally, at the landscape level, riparian habitats are important as they cross large urban areas as corridors may support source populations and therefore bring in many native species. Such species can spread from the corridors into urban, artificial green spaces (Gillies and St. Clair 2008). The preservation of riparian habitats is likely to preserve more species per unit area than other land-cover types and should be considered high value in urban avian conservation planning across many ecosystem types.

Once habitat structure is suitable for a given species, it may still fail to establish in the urban environment if it suffers from competition with dominant, aggressive species. In some cases, it is possible to recognize specifically how invasive species affect native species and apply creative, local solutions. For example, "smart feeders" can turn the disadvantages of subordinate species into advantages. Smaller size normally indicates low ability to compete with larger species, as well as higher chances of becoming prey than larger species. The role of smart feeders is to provide foraging opportunities for small bird species, by blocking access to food for heavier species (e.g., birds vs. squirrels) or by changing the position of the perch, forcing birds to bend (finches vs. sparrows). In environments with a strong human control on biodiversity, where most of the food, especially for seed eaters, is supplied from feeders, such manipulations are essential for increasing local biodiversity in urban settings (Shochat et al. 2010).

8.9   Future Research Needs

While the amount and variety of landscape-scale research in urban areas has grown significantly in the last two decades, specific gaps in understanding remain. Geographic variety has long been a problem in the field. It is critical to understand the scales at which ecological phenomena operate in different ecosystems. The literature on North America, Europe, and Australia is well developed, and studies from Southeast Asia have become more abundant in recent years. However, published

work (in the English language literature) is still lacking from ecosystems in South America and Africa. There are also very few studies that include mechanistic components. While including these in landscape-scale studies is certainly challenging, a handful of well-designed studies could shed substantial light on how demographic, competitive, and dispersal processes operate over large scales.

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Chapter 9
Trends in Long-Term Urban Bird Research

Mason Fidino and Seth B. Magle

Abstract The vast majority of urban bird research is conducted over relatively short time frames (1–2 years), thereby limiting our ability to understand how temporal processes influence urban bird populations and communities. To further evaluate the importance of and contributions provided by long-term (≥ 5 years) ecological studies of urban avifauna, we reviewed the published literature for such studies to (1) explore and characterize the focus of long-term urban bird research, (2) identify gaps in our knowledge base, and (3) make suggestions for future research. We identified 85 papers published between 1952 and 2014 for this review. While long-term studies ranged from 5 to 175 years, most were ≤ 30 years in length. Community-level studies predominately quantified how urbanization affects species richness and composition through time, while population-level studies were primarily on single species of larger body size (≥ 80 g). Almost every study we reviewed was conducted in North America and Europe, a result that is generally unsurprising as temperate zones and wealthier countries are overrepresented in the literature. Overall, long-term studies provide unique insights into how slow and subtle processes, land-use legacies, time-lagged responses, and complex phenomena influence urban birds. To better encourage the inclusion of long-term studies in urban avian ecology, we suggest that ecologists should (1) keep long-term phenomena in mind when constructing short-term studies, (2) make published datasets accessible, and (3) provide adequate metadata regarding how data was collected.

Keywords Conservation • Literature review • Long-term studies • Urban birds • Urban ecology

9.1 Introduction

Ecological systems are largely controlled by two interrelated but fundamental factors, space and time, which influence patterns and processes at multiple scales. When considered individually, many theories (e.g., island biogeography) and

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concepts (e.g., connectivity, edge effects, and spatial autocorrelation) from spatial ecology have greatly influenced the way we shape and address ecological questions (Wolkovich et al. 2014). In the same vein, a multitude of ecological properties that influence species inherently include temporal components (e.g., resource availability, Rey 1995; predator-prey dynamics, Benoit-Bird and Au 2003; and colonization and extinction, Levin 1974). However, space and time must be considered together as they are inherently linked. For example, spatial patterns can change through time, and patterns observed today may be a function of time-lagged responses (Kuussaari et al. 2009; Krauss et al. 2010) or land-use legacies (Foster et al. 2002). Indeed, space and time are two axes of dynamism that influence the landscape in complex and interrelated ways (Delcourt et al. 1982; Wiens 1989; Dunning et al. 1992; Ramalho and Hobbs 2012). Thus, space, time, and their interaction must be accounted for to better understand the myriad ways in which individuals, populations, and communities interact with their environment.

Both spatially and temporally, the human modification of landscapes through processes such as urbanization has significantly altered ecological processes (Booth and Jackson 1997; Vitousek et al. 1997; Baker et al. 2001; Imhoff et al. 2004; Halpern et al. 2008) and the distribution and abundance of wildlife (Marzluff et al. 2001a; McKinney 2002, 2006; Aronson et al. 2014). In the last decade, humanity has transitioned from primarily living in rural to urban areas, and 66 % of the world's population is expected to live in urban environments by 2050 (United Nations 2014). In response, the rate of urbanization continues to accelerate worldwide (Forman 2008; Dearborn and Kark 2010), which has negatively influenced many species (Czech and Krausman 1997; Czech et al. 2000). At least partially as a result, there has been increased interest in the study of urban ecosystems and wildlife (Mcdonald et al. 2008; Mayer 2010), and publication rates of urban wildlife literature continue to rise (Magle et al. 2012).

Birds are by far one of the most studied taxa in urban areas (Magle et al. 2012), and literature focused on their ecology and conservation in cities is growing rapidly (Bird et al. 1996; Marzluff et al. 2001a; Lepczyk and Warren 2012). Because birds are appreciated by people (Turner et al. 2004), are relatively easy to detect and observe (Blair 1999), and respond rapidly to changes in landscape composition (Marzluff 2005), it is not surprising that they represent a significant proportion of published urban wildlife literature. Urban bird studies have significantly contributed to the field of urban ecology, and many of the patterns observed within urban systems are illustrated with birds (Blair 1996; Crooks 2004; Marzluff 2005; Aronson et al. 2014). Yet this research has primarily focused on patterns and processes at varying spatial scales, and most studies are conducted over relatively short time frames (1–2 years; Marzluff 2001). While studies of this nature fit within standard funding cycles or the length of a typical graduate program, longer-term studies are critical to better understand and predict how slow or subtle temporal processes, rare events, and complex phenomena influence urban bird populations and communities (Foster et al. 2002; Turner et al. 2004; Wolkovich et al. 2014).

The importance of long-term studies in ecology is well recognized, and reviews focused on the contribution of such studies in different ecological subdisciplines

abound (Strayer et al. 1986; Hobbie 2003; Likens 2004; Jackson and Fuereder 2006; Ducklow et al. 2009; Clutton-Brock and Sheldon 2010; Magurran et al. 2010). Although urban avian ecology is a relatively new and burgeoning field, the necessity for long-term ecological studies has also been recognized. Indeed, the seminal work by Marzluff et al. (2001a) has numerous suggestions for the inclusion of long-term studies in urban bird research including population-level studies that explore how birds respond to urbanization at different points along the urban-rural gradient, linking population demographics to urban bird community composition, and studies of non-synanthropic species. To determine if these suggestions have been addressed since that time, and to further evaluate the importance of and contributions provided by long-term ecological studies of urban avifauna, we reviewed the published literature for such studies to (1) explore and characterize the past and current focus of long-term urban bird research, (2) identify potential gaps in our knowledge base, and (3) make suggestions for future research directions.

9.2 Methods

We searched the published literature with two search engines, ISI Web of Science and Google Scholar, using all unique combinations of the search terms "*urban*," "long-term," "park," "bird*," "avian," "fragmentation," "time," and "temporal" that included at least one word associated with birds (i.e., "bird*" or "avian"). The "*" character was included within the "urban" and "bird" search terms so that iterations of these words such as suburban, ex-urban, urbanization, birds, or birding were also detected in the search. Each publication that resulted from this search was reviewed to determine if it met the criteria for inclusion. Given that most urban bird studies span 1–2 years (Marzluff et al. 2001b), publications were included if they represented original research on urban birds and collected data over at least a 5-year period. We chose a 5-year cutoff because we believe this is a conservative estimate of the length of time needed to represent a range of temporally varying conditions within an urban environment, such as wet or dry years. Furthermore, continuous collection of data over the length of a study was not necessary. For instance, a study would be included if it collected data on only two separate years provided they were at least 5 years apart. Following Marzluff et al. (2001b), we also searched the literature-cited section of each long-term study for additional empirical work on long-term urban bird research; all such studies were included if they met the criteria above.

Throughout this process there was some redundancy between studies as data from sites were used in numerous papers. For example, a series of studies were conducted over a period of about 150 years at the same sites in the Boston Metropolitan area (Brewster 1906; Walcott 1974; Strohbach et al. 2014). When these redundancies occurred, we considered research papers to be independent and original provided the questions asked and analyses performed differed. A total of 85 papers were found for this review (Appendix). We should note that our search technique may be less likely to detect research on temporal trends present in local

Fig. 9.1 The number of long-term urban bird studies published per decade since 1950
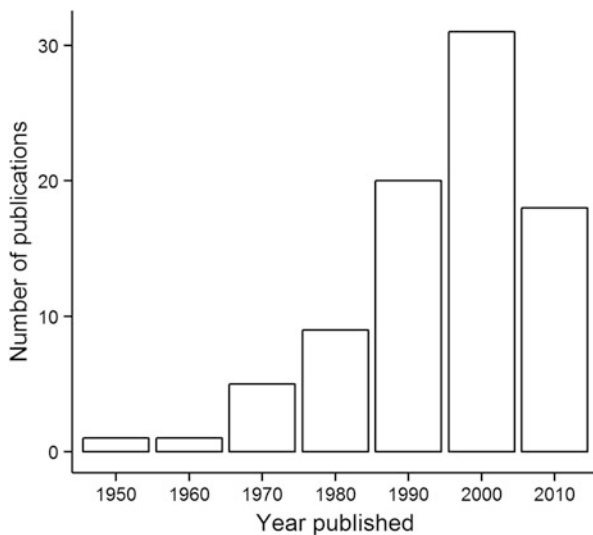
ornithological journals or in urban ornithological atlases (e.g., Luniak 2016). Furthermore, long-term studies that were not detected with our search terms and were not cited in papers found with these terms will inherently be absent from this review. We believe that these caveats do not change the overall perspective of long-term urban bird research in this review and that the papers we did review represent the vast majority of long-term urban bird research.

9.3 Results and Discussion

9.3.1 A Systematic Perspective of Long-Term Urban Bird Research

As with the field of urban ecology in general, the publication rate of long-term studies on urban avifauna is increasing (Fig. 9.1). The first published long-term study of urban birds we found was Cramp and Teagle's (1952) report on the abundance and distribution of the birds within inner London from 1900 to 1950. The London studies are particularly noteworthy because they are still ongoing (e.g., Oliver 1997), making this one of the longest temporal datasets of birds, urban or otherwise. However, studies that include data prior to 1960 are the exception, as a vast majority of the published research ($n = 62$, 72.9 %) initiated data collection from 1960 onward, illustrating both the sparseness of historical data and the relatively recent interest in urban wildlife research (Magle et al. 2012).

Although the length of long-term urban bird studies ranged from 5 to 175 years, the distribution is skewed heavily toward the shorter end, with 71.8 % ≤30 years in

Fig. 9.2 The frequency of
the temporal span of data in
long-term urban bird studies
in 5-year intervals. Most
studies (>70 %) were less
than 30 years in length
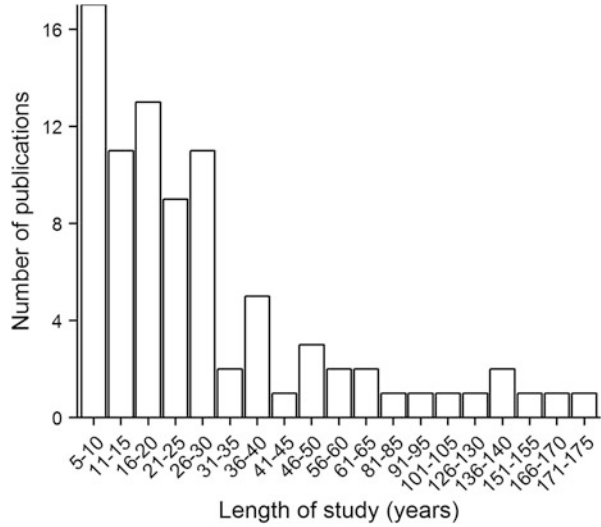
Fig. 9.3 Comparison of the
number of years sampled in
continuous and
discontinuous studies to
their overall length. The line
for continuous studies is a
simple 1:1 relationship,
while the line for
discontinuous studies is a
linear regression with
overall length as the
response variable and
number of years sampled as
the explanatory variable (r^2
$= 0.61, P < 0.0001$)
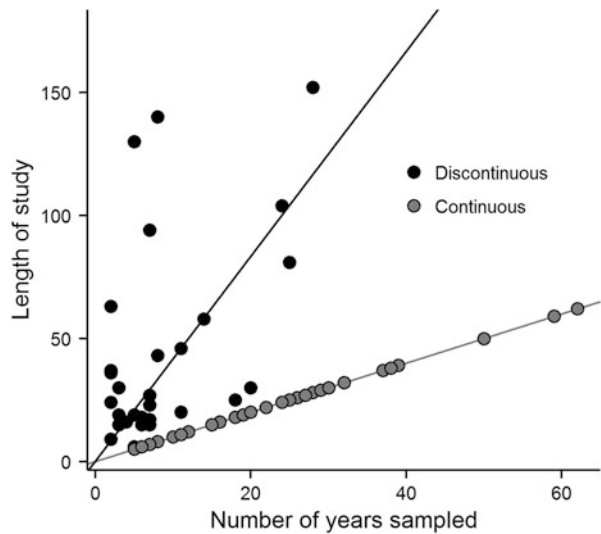
length and 20 % ranging from 5 to 10 years (Fig. 9.2). In discontinuous studies
(those that did not collect data yearly), very few were missing data for only 1–2
years (Fig. 9.3, e.g., Jokimäki and Huhta 2000), while most had large gaps between
subsequent observations (e.g., Jokimäki and Suhonen 1993; Parker et al. 1996;
Catterall et al. 2010). In some instances, studies had only 2 years of data separated
by multiple years (e.g., Aldrich and Coffin 1980; Kentish et al. 1995; Wood and
Recher 2004; Suhonen et al. 2009). However, discontinuous studies make up for a
lack of continuity with increased study duration (Fig. 9.3), as 76.5 % of the studies

Table 9.1 Mean and median study durations (years) of community-level and population-level long-term urban bird studies

	Study type	
	Community	Population
Mean study duration	39.32	30.49
Median study duration	27	19
Number of studies	34	51

we reviewed ≥40 years in length ($n = 17$), and all of the studies with ≥100 years in length were discontinuous ($n = 7$). Indeed, the longest continuous study was Batten's (1978) 62-year article on the immediate causes of blackbird (*Turdus merula*) mortality throughout England, while the longest discontinuous study on the temporal dynamics of wildlife in New England spanned 175 years (Foster et al. 2002).

Community-level studies were slightly longer in length than population-level studies (Table 9.1), though the difference was not significant; t_{83} (0.56), $p = 0.29$. Most long-term community-level studies quantified effects of urbanization on species richness or species turnover through time ($n = 15$, 45.5 %), with a majority of studies ($n = 12$) solely focused on the breeding bird community.

Only five community-level studies collected data on birds during all seasons (Recher and Serventy 1991; Jones and Wieneke 2000; Namba et al. 2010; Shultz et al. 2012; Ormond et al. 2014). For population-level studies, a large proportion was conducted on single species ($n = 30$, 68.2 %). Of those, almost every species studied was of larger body size and weighed ≥80 g. For example, 12 studies were conducted on birds of prey (e.g., Kauffman et al. 2003; Stout et al. 2007; Rutz 2008), three on the common blackbird (Batten 1973, 1978; Kentish et al. 1995), and three on a variety of gull species (Milone and Grotta 1983; Annett and Pierotti 1999; Pierotti and Annett 2001). The most commonly studied small-bodied bird is the ubiquitous and cosmopolitan house sparrow (*Passer domesticus*, $n = 6$; Balmori and Hallberg 2007; Dott and Brown 2000; Robinson et al. 2005; Liker et al. 2008; Bell et al. 2010; Murgui and Macias 2010). As this once incredibly abundant species has declined significantly in some parts of its range in recent decades, interest in its ecology and demography has increased recently (for a review see De Laet and Summers-Smith 2007).

Geographically, studies were most commonly conducted in North America ($n = 37$, 43.53 %), Europe ($n = 37$, 43.53 %), and Australia or New Zealand ($n = 8$, 9.41 %). This is generally unsurprising as temperate zones and wealthier countries tend to be overrepresented in the literature (Martin et al. 2012). Only 3 of the 85 studies were outside of these three geographic regions, with one located in the Caribbean (Fonaroff 1974) and two in Japan (Nihei and Higuchi 2002; Namba et al. 2010). We did not find any long-term studies of urban birds that spanned multiple continents, though short-term studies of this nature do exist (Aronson et al. 2014). As the geographic region of a study site can influence the patterns and processes observed, geographical biases in data collection can limit the extent to which findings from commonly studied urban systems can be applied to less common systems (Martin et al. 2012). Though there is currently a dearth of data from Africa and Asia (but see Symes et al. 2016), these areas are prime locations to

initiate long-term studies of urban avifauna. Over the next 35 years, both of these continents are expected to urbanize faster than other regions in the world (United Nations 2014), thereby providing opportunities for experimental, observational, and mensurative studies at a shifting urban-wilderness interface over time.

In summary, community-level studies disproportionately focus on breeding birds, while population-level studies tend toward large-bodied birds. Regardless of study type, studies in North America and Europe are much more common than other geographic locations. Most published research does not exceed 35 years in length. While this duration is likely adequate to determine how urbanization influences avian species with short generation times, it may not be enough time to study how long-lived species are impacted by urbanization. Moreover, studies that do exceed 35 years in length tend to have discontinuous datasets that integrate previous work. To highlight the important contributions that long-term studies have had on our understanding of how urbanization affects birds, we showcase a number of studies below. These particular examples have implications beyond their study systems and also provide a framework for future research directions.

9.3.2   Temporal Studies on Urban Bird Species Composition

The composition and richness of bird species are perhaps one of the most interesting parameters that evolve through time in urban environments. Short-term studies often report that species richness declines as urbanization increases (Tratalos et al. 2007), though levels may be highest at intermediate levels (Marzluff 2005; Catterall et al. 2010). Thus we may expect species richness to decrease as a single location becomes more urban over time. In our review, however, results were equivocal from studies that tracked species richness at urbanizing sites over time as studies alternately reported either no net loss in alpha diversity (Horn 1985; Jones and Wieneke 2000; Shultz et al. 2012), a slight increase in alpha diversity (Aldrich and Coffin 1980; Abs and Bergen 2008), or an overall decrease in alpha diversity (Batten 1972; Walcott 1974; Bezzel 1985; Biaduń et al. 2009; Catterall et al. 2010; Pidgeon et al. 2014; Strohbach et al. 2014). Given the wide range of responses we observed, we suggest that spatial differences observed along a gradient over short time frames do not adequately capture the many temporal forces that may subtly influence species richness, that different bird compositions may occur as urbanization increases through time, and that community composition may also be influenced by the rate at which urbanization increases. Thus, we consider here the complex ways time may influence urban bird communities.

Regardless of reported increases or decreases in species diversity, a high rate of turnover is a common trend in long-term studies with factors such as climate change (Travis 2003), the introduction of invasive species (Foster et al. 2002), maturation of local native or nonnative vegetation (Bloom and McCrary 1996; Jones and Wieneke 2000; Jerzak 2001; Gleditsch 2016), land-use legacies (DeGraff and Wentworth 1986; DeGraaf 1991), body size (Catterall et al. 2010), and habitat

fragmentation influencing species persistence, colonization, and extinction rates in complex ways (Butcher et al. 1981; Tait et al. 2005; Walk et al. 2010). Thus, although species richness may not change at a site over time, the composition of species present does. However, while the notion that urbanization may not decrease species diversity through time is encouraging, such a conclusion does not consider the relative values of particular species, the functional diversity of the urban bird community, or the type of habitat that is urbanized.

For instance, species diversity increased with urbanization in Aldrich and Coffin's (1980) 37-year study of a forest turned suburban lot, but this growth was the result of increases in common suburban species [e.g., blue jays (*Cyanocitta cristata*), northern mockingbirds (*Mimus polyglottos*), and American robins (*Turdus migratorius*)] and was at the cost of species more characteristic to the deciduous forests of Eastern North America [e.g., wood thrush (*Hylocichla mustelina*), red-eyed vireo (*Vireo olivaceus*), and scarlet tanager (*Piranga olivacea*)]. Indeed, this trend was often reported in long-term community-level studies that tracked bird communities in urbanizing forested regions (e.g., Bezzel 1985; Horn 1985; Catterall et al. 2010; Biaduń and Żmihorski 2011; Parody et al. 2001; but see Shultz et al. 2012). Urbanizing grasslands and deserts, on the other hand, may instead increase the richness of at least some non-synanthropic species by providing increased access to important limiting factors such as water, food, and nest sites (DeGraff and Wentworth 1986; Marzluff et al. 2001b). As such, when studying the effect that urbanization has on bird communities through time, it is crucial to explore how the community changes and to think critically about how urbanization alters the structural complexity of the environment.

Time since urbanization may also influence the composition of species at a site. Pidgeon et al. (2014) suggest that urbanization influences urban communities in two distinct temporal phases. The initial phase of urbanization increases habitat heterogeneity and provides novel resources, thereby creating more niches for species to occupy and increasing alpha diversity. However, species richness later decreases as housing density and habitat fragmentation increase through time, which extirpate many native species. For example, more recently developed regions in the United States with lower housing densities tend to have a greater diversity of forest-dwelling bird species (Pidgeon et al. 2014). Conversely, older, more developed ecoregions with higher housing densities have fewer species (Bezzel 1985; Pidgeon et al. 2014).

The rate at which urbanization occurs may also influence species richness, with more rapidly urbanizing habitats having lower species diversity. However, most studies ($n = 55$) did not report metrics that could adequately quantify the rate of change in their urban environment. Of those that did, direct comparisons are complicated as there is little consensus on what metrics to report or at what scales. Nonetheless, articles that reported decreased alpha diversity over time appeared to experience greater levels of urbanization per unit time over the course of the study (see Batten 1972; Strohbach et al. 2014) than those that saw no decrease (see Aldrich and Coffin 1980; Jones and Wieneke 2000). As such, this paradigm of

decline, with site-specific species richness dropping in response to rapid habitat loss via urbanization, may influence urban bird community composition.

Long-term studies provide compelling data on the dynamic nature of urban bird communities and indicate that temporal forces can have both positive and negative effects. While urbanization fragments natural habitats through time, which negatively influences many species, the maturation of landscaped vegetation or increased access to limiting factors (e.g., food and water) can positively influence others. The end result is often a high degree of turnover in species composition. At times, the species lost are those with more specialized habitat requirements (Aldrich and Coffin 1980; Jones and Wieneke 2000; Strohbach et al. 2014), but this is not always the case (see Shultz et al. 2012). As numerous forces may have time-lagged responses on the current urban bird community, much can be gained from including a temporal component into urban bird studies.

9.3.3   Temporal Studies on Urban Bird Demographic Parameters

Urbanization alters bird communities because species respond differently to human-dominated habitats, and therefore observed patterns in urban bird communities are a direct result of the mechanisms that influence populations of individual species. As such, community- and population-level studies can fit hand in glove, with well-designed population-level studies providing much needed mechanistic understanding to community-level patterns. At the population level, anthropogenic food sources have been cited as one of the most influential factors for urban birds, and long-term studies attribute it to higher breeding densities (Jerzak 2001), colonization rates (Raven and Coulson 1997; Rutz 2008), brood sizes (Gehlbach 1996; Solonen 2008), and survival rates (Gehlbach 1996). Given the large influence that anthropogenic food has on urban bird demography, it is of little surprise that supplemental feeding can have profound effects on urban avian assemblages (Fuller et al. 2007). However, anthropogenic food sources are not always beneficial to urban birds. Western gulls (*Larus occidentalis*) with diets rich in anthropogenic food sources hatch fewer young and breed for fewer years because such food sources may not provide adequate nutrition for nestlings or the formation of eggs during the breeding season (Annett and Pierotti 1999; Pierotti and Annett 2001). Furthermore, urban house sparrows are smaller and have worse body condition because urban nestlings may either receive a poorer diet or anthropogenic food sources allow birds in worse body condition to survive (Liker et al. 2008). While the presence of anthropogenic food sources is more dependent on spatial than temporal factors, long-term studies are able to link demographic parameters to population fluctuations, which is sorely needed in urban bird ecology.

In our review reproductive success was observed to be higher for many urban birds (Sodhi et al. 1992; Gehlbach 1996; Parker et al. 1996; Jerzak 2001; Kauffman

et al. 2003; Stout et al. 2007; Solonen 2008). Factors associated to these increased rates indicate that urban areas may provide more stable food sources (Gehlbach 1996; Jerzak 2001; Solonen 2008), nesting conditions (Solonen 2008; Stout et al. 2007), decreased predation (Gehlbach 1996), and at times decreased human persecution (Rutz 2008). These factors may in turn increase clutch sizes, nestling weights, and/or nestling survival rates (Sodhi et al. 1992; Gehlbach 1996; Parker et al. 1996; Kauffman et al. 2003; Stout et al. 2007). However, six of these seven studies were conducted on birds of prey, which limit the generality of this statement, and other reviews have noted that reproductive rates are higher in rural populations of other urban bird species (Chamberlain et al. 2009). Two additional studies we reviewed reported a decrease in urban bird reproductive success (Tella et al. 1996; Pierotti and Annett 2001). Urban lesser kestrels (*Falco naumanni*) delivered prey to nestlings at a lower rate than their rural counterparts, which resulted in greater nestling mortality due to starvation despite the fact that urban nests were predated less (Tella et al. 1996). Western gulls also fledged fewer young at urban colonies due to disturbance caused by workmen and a lack of shelter from the elements for chicks that left the nest (Pierotti and Annett 2001).

While population-level studies were more common than community-level studies (Table 9.1), the vast majority ($n = 38$, 74.51 %) did not report metrics on urban bird demography and primarily tracked the abundance of one or multiple species through time. Many of these studies correlated population trends to environmental factors (e.g., Robinson et al. 2005; Mazgajski et al. 2008; Żmihorski et al. 2010) but were unable to determine the mechanisms that caused these population changes. Long-term studies also did not explore how demographic rates change through time in urban environments and more so used long-term datasets to quantify differences between urban and rural populations. As species composition changes temporally, there is no doubt variation in demographic rates and studies that explore this variation are needed. Given the diversity of species in urban environments and the apparent bias toward studying the demography of birds of prey, there is also a knowledge gap as to what spatial and temporal factors influence species in other guilds.

9.3.4 Long-Term Studies of Rapid and Cultural Urban Bird Evolution

Cities are complex systems, constantly changing, which revise the selective pressures of the landscape over time. In response to this, urban birds tend to have higher rates of behavioral plasticity, the better to mitigate the varied and dynamic costs associated with human-dominated landscapes (Shochat et al. 2010). However, behavioral plasticity alone cannot account for species persistence and adaptation, and the novel abiotic components of the urban landscape can facilitate rapid evolutionary and cultural change in urban bird populations (Able and Belthoff

1998; Yeh and Huang 2009; Brown and Brown 2013). Marzluff's (2012) recent review of urban evolutionary ecology illustrates how urban noise, novel food sources, temperature, and pollution can all exert selective pressure on urban birds, and we encourage those interested in this topic to refer to it for a more detailed overview. However, we would like to emphasize the importance of long-term studies in documenting evolutionary change in urban bird populations, as even the most rapid of changes take considerable time. Thus, we highlight a number of such studies absent from Marzluff's review.

Automobiles are one component of the urban environment that exerts selection on urban birds in both direct and indirect ways, which can in turn alter species morphology and influence cultural evolution (Luther and Baptista 2010; Luther and Derryberry 2012; Brown and Brown 2013). For example, the wingspan of cliff swallows (*Petrochelidon pyrrhonota*) that nest under overpasses along highways has significantly decreased over time, making them more maneuverable and possibly more able to dodge fast-moving cars (Brown and Brown 2013). As a result, the number of road-killed cliff swallows decreased over this 30-year study, while the swallows still hit by cars as the study progressed had significantly longer wingspans than the population at large. Additionally, automobiles can influence urban birds through the noise they generate, and birds have exhibited an increase in song frequency and volume in response (Slabbekoorn and Peet 2003; Halfwerk et al. 2011). However, studies of this nature have typically been conducted across spatial gradients that vary in urban noise, while few have explored this relationship as urban noise increases through time. By comparing 36-year-old recordings of the song frequency and dialects of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) in San Francisco to their own recordings in the same locations, Luther and Derryberry (2012) confirmed that the minimum frequency of male white-crowned sparrow songs increased. While short-term studies that compare song frequencies of urban and rural bird populations clearly indicate that urban birds sing at higher frequencies, long-term studies conducted on populations over time reveal another equally important facet to this process: behavioral adjustment to urban noise over time influences cultural evolution.

9.3.5 Historical Perspectives in Urban Bird Research

Over the last 20 years, many compelling arguments have been made about the importance of including historical perspectives into ecology, and the subfield of historical ecology has emerged as a result (Egan and Howell 2005; Jackson and Hobbs 2009). Although this field may be relatively new, over 75 years ago, Aldo Leopold (1992) argued that even during his time "...research programs pay too little attention to the history of wildlife... We do not yet appreciate how much historical evidence can be dug up, or how important it can be in the appraisal of contemporary ecology." To add this historical perspective, previous publications are often a useful starting place, and different approaches have been employed to

add temporal breadth such as meta-analyses of results from the same geographic region (Bezzel 1985) or revisiting sites from previous studies and comparing results (Strohbach et al. 2014). However, a significant amount of data exists outside of published scientific literature, and a small number of the studies we reviewed incorporated data from nontraditional sources as well.

From newspaper articles and diaries to town records and museum collections, these nontraditional sources can greatly increase the temporal extent of a study and provide information on species abundance, presence, and distribution. The advantages of such historical datasets are great as they may provide baseline conditions before significant human impact and allow ecologists to explore subtle aspects of how humans influence birds over long time spans. Yet, these datasets can be difficult to analyze and interpret because they may be rife with geographic bias and contain reports from multiple observers using different methods, and data from different records likely vary in their grain and extent. Despite these constraints we argue that urban ecological research programs can greatly benefit by including historical perspectives from traditional and nontraditional sources alike.

Perhaps the most unique use of historical records, and by far the longest study we reviewed, is Foster and colleagues' (2002) 175-year study to determine how the physical, biological, and cultural changes within the New England landscape impacted wildlife assemblages. This particular study stands out in comparison to other publications due to the wide variety of sources the authors amalgamated to qualitatively analyze historical trends (e.g., explorers' accounts, museum collection, scientific studies, town records, harvest records, and newspapers). Furthermore, given the duration of this study, the authors were able to identify slow and subtle temporal processes that short-term studies could not.

Birds of prey, for example, have increased throughout New England due to improved cultural attitudes toward them and better water quality, a pattern also seen in other long-term studies that used more traditional methods (Walk et al. 2010; Shultz et al. 2012). Temporal shifts in habitat availability also had a profound influence on species abundance and turnover. While agricultural practices comprised a large proportion of the New England landscape during the mid-1800s, rates of farm abandonment at the time were high as farmers left the region for more fertile land west of the Appalachians (Askins 2002). This, in turn, created large amounts of suitable habitat for many grassland-dependent species, and populations skyrocketed as a result. At the same time, forest cover was at an all-time low, and many forest-dependent species were in decline. Conversely, the opposite pattern is observed today as the previously abandoned farmlands have slowly turned to forest, and grasslands have become less common. Subsequently, grassland-dependent species are now in decline, while a subset of forest-dependent species now thrive in the more abundant, though increasingly fragmented forests of New England (Butcher et al. 1981; Askins 2002; Foster et al. 2002).

Finally, historical records have shown that some species, certainly not all, have successfully adapted to the present landscape. A number of these were introduced, such as the European starling (*Sturnus vulgaris*) or house sparrow, but a few native species also responded favorably [e.g., northern mockingbird, northern cardinal

(*Cardinalis cardinalis*), and American crow (*Corvus brachyrhynchos*)]. This pattern has been observed throughout much of the world, with successful range expansions of invasive and native species alike (Sol et al. 2016). Common examples include the invasion of the common myna (*Acridotheres tristis*) to Australia (Jones and Wieneke 2000), Africa (Peacock et al. 2007), and Singapore (Yap et al. 2002) or the synurbanization of the blackbird throughout Europe (Batten 1978; Luniak and Mulsow 1988; Jerzak 2001). Indeed, historical records are an incredibly useful resource to explore different behaviors and range expansions in urban birds. Raven and Coulson (1997), for example, compiled data from other researchers, volunteers, and local governments to study the tremendous increase in the distribution and abundance of roof-nesting gulls in Britain and Ireland over an almost 30-year time period. While there currently are a small proportion of historical urban ecological studies, such work can greatly advance our knowledge of the long-term patterns and processes that change urban bird populations and communities.

9.3.6 Anthropogenic Change, Management Practices, and Urban Planning

From individual choices made by homeowners (Goddard et al. 2016) to management decisions made by city hall (Heyman et al. 2016; Meffert 2016), the cumulative effects of human decision-making influences bird community composition in complex ways (Alberti 2008; Belaire et al. 2014). Although variation in management practices inherently implies spatial differentiation in habitats, this process is also temporal. For example, the planting of trees in urban yards and parks has a time-lagged influence on birds (Bloom and McCrary 1996; Jones and Wieneke 2000; Jerzak 2001). As such, to better conserve, manage, and study biodiversity in urban areas, ecologists, land managers, policy makers, and conservationists should consider dynamic strategies that account for the rippling effects that current and past actions may have on urban bird communities (Hannah et al. 2002; Millar et al. 2007; Mcdonald et al. 2008).

One increasingly common aspect of city planning that benefits both humans and wildlife is the creation of urban green space (James et al. 2009; Fontana et al. 2011; Fuller et al. 2007; Murgui 2014; Szulczewska et al. 2014; Ferenc et al. 2014). Urban green space can open up the vertical dimension of cities by increasing tree and shrub cover, which over time can simultaneously raise urban bird diversity and people's experience of urban nature (Fontana et al. 2011; Fuller et al. 2007). Given the affinity that many urban bird species have for urban green space, it is unsurprising that city parks are often chosen as the sites for long-term studies. Studies in city parks often observe a general increase in the abundance of woodland-dependent species and a decrease in those that prefer more open habitats (Morneau et al. 1999; Murgui 2014). The shift in species composition in urban parks may be

in part due to changes in vegetation structure as planted trees and shrubs increase in size, but other local and regional processes likely influence community structure as well. For example, shifts in urban bird populations may also coincide with population trends at larger spatial scales (Murgui 2014) or in response to increases in supplemental feeding (Morneau et al. 1999).

Long-term studies also indicate that urban green space may provide bird species a somewhat more natural environment, or buffer space, to habituate to urban life over time. Magpies (*Pica pica*), a well-studied and ubiquitous urban species throughout Europe (see Jerzak 2001 and references therein), were largely dependent on city parks for breeding prior to 1970 but have now colonized almost the entirety of inner London (Oliver 1997). In Finland, hooded crows (*Corvus corone cornix*) initially nested in city parks before World War I but now primarily nest in city centers, suburbs, and residential neighborhoods (Vuorisalo et al. 2003). Northern goshawks (*Accipiter gentilis*) in Germany were commonly observed in city parks years before breeding pairs would settle there (Rutz 2008). In this way, city parks and urban green space can function as a stepping stone between the urban wild and the urban core that birds may use to habituate to increasingly urban environments.

Though many of the papers we reviewed contain bountiful information useful for wildlife conservation and management in urban areas, only a small subset of these papers considered the effect of management practices by including it as a variable during statistical analysis or discussing how management practices may have impacted birds throughout the study (e.g., Recher and Serventy 1991; Namba et al. 2010; Heyman et al. 2016). Yet, there is a significant opportunity for applied urban research programs to better incorporate city planning and management into their work which could then benefit researchers, urban planners, and urban bird biodiversity. For instance, predicting how species richness of varying bird guilds changes in response to future levels or patterns of urbanization can have clear and potentially profound implications on proposed policies of urban development and prioritize locations for conservation (Hepinstall et al. 2008). Given that future population growth and urbanization are unavoidable, there is a need for urban bird research to help direct development and sustain biodiversity. This will require work at a variety of spatial and temporal scales, and therefore long-term studies are a necessary component of urban bird conservation.

9.4 Future Contribution from and Challenges with Long-Term Studies

The potential for long-term bird studies is virtually unlimited, but such datasets do provide challenges. One of the most significant issues with long-term datasets is variation in sampling effort and standard protocols (or lack thereof, for a review of bird censusing in urban areas see Van Heezik and Seddon 2016), especially when

data collection is discontinuous (for a discussion of this see Strohbach et al. 2014). Because these data can be generated by multiple organizations, it is easy to introduce variation in the observational process through time, which can strongly bias results. Thus, it is important to ensure that historical data are comparable, and assumptions are made explicit as questions, statistical methods, and field techniques change. Here, we recommend a number of guidelines that can make future comparisons possible.

- Be as explicit as possible regarding the observational process. Common issues we observed include authors providing vague information regarding survey effort, number of observers, or the geographical boundaries of their study area. These issues make future comparisons impossible without making serious assumptions about the historical data.
- Include metadata. Datasets can become increasingly complex and large as time progresses. Having an effective "road map" to help interpret a dataset is necessary so others can make use of it in the future.
- Make published datasets accessible. All research is limited by access to data, and promoting an environment that rewards the sharing of high-quality datasets and comprehensive metadata will allow researchers to spend more time on analysis and reuse data meant for different applications.

Other challenges that arise include temporal autocorrelation and non-stationarity. Autocorrelation, or the propensity for single observations to share similarities with other observations, can be introduced temporally via cyclic patterns and trends, and many statistical approaches today can account for this. For example, generalized linear models can include temporal autoregression to address nonindependence in error terms and response variables (Chatfield 2013). Non-stationarity, or stochastic processes with probability distributions that change through time (e.g., climate change), can violate the assumptions in many statistical models if not explicitly addressed (Betancourt 2012). Wolkovich et al. (2014) speak at length on this matter, and we refer readers to their paper and references therein for techniques that address spatial and temporal non-stationarity.

Finally, very often temporal extent is traded for spatial extent in long-term studies. It is understandable that long time series are collected at a small number of sites, but this may preclude the possibility of hypothesis testing in some cases. Clearly, when designing a study with limited resources, it is difficult to simultaneously increase the spatial and temporal extent, and therefore any suggestion to do just that is of little use. Instead, we echo Strayer et al. (1986) and suggest that creating a flexible monitoring protocol allows researchers to study long-term processes while staying productive on the short term. This also forces researchers to maintain their long-term datasets, which should lead to better quality data and a more productive project. While the creation and management of long-term studies is difficult, and requires additional forethought, such datasets can yield many publications when used creatively and collaboratively.

Almost 15 years ago, Marzluff et al. (2001b) suggested that additional long-term bird research was needed, particularly studies that relate demographics to urban

bird community composition. Though the number of long-term studies has increased since 2001, we did not identify any studies of this nature. Such studies could be highly beneficial as they would allow ecologists to explicitly test the mechanisms that influence urban bird populations and therefore urban bird communities. Through the union of community- and population-level studies, hypotheses on exactly how urban bird communities assemble, persist, and shift over time may be addressed, and we can determine whether assembly rules are city specific or interface specific or if there exists an "urban wildlife syndrome" that influences all urban environments.

To date, demographic studies have been biased toward large-bodied birds, particularly birds of prey. As smaller-bodied birds (e.g., sparrows, titmice and chickadees, finches, swallows and swifts, etc.) may exist at different densities, use different food sources or nesting structures, and interact with the environment differently, future work exploring population dynamics of smaller species may help illustrate the full suite of impacts that urbanization has on avian fauna. Studies that relate bird diversity and demography to other taxa are sorely needed as well, as the interaction between birds and other species in urban environments has been relatively unexplored. Arthropod abundance and diversity, for example, varies by fragment size, age, and edge proximity in urban environments (Bolger et al. 2000), but empirical studies are needed to quantify how this may affect the foraging ecology, demographics, and abundance of bird species along an urban gradient.

There are clear opportunities for long-term investigations in understudied locations around the world at varying levels of urbanization, especially in Africa and Asia where the urban-wild interface is rapidly changing. Not only would such studies be able to observe how the initial processes of urbanization influences bird populations and communities, they could also be used to determine if results from other geographic regions are applicable in different environments. In conclusion, we encourage ecologists to keep long-term ecological phenomena in mind when constructing short-term studies. As many of the central questions in ecology revolve around predicting the mechanisms responsible for ecosystem responses, long-term studies are critical in that they are the primary way to validate theoretical models to reality (Franklin 1989). The benefit of urban ecological research goes beyond validating theory though, as better understanding bird-habitat relationships is a critical step toward reconciling the impact that urban environments have on wildlife communities.

Appendix: Long-Term Studies Reviewed

Author	Year published	Study type	Duration (yrs)
Able and Belthoff	1998	Population	37
Abs	2008	Community	43
Aldrich and Coffin	1980	Community	37
Annet and Pierotti	1999	Population	12
Askins and Philbrick	1987	Population	32
Baker	1980	Population	5
Balmori and Hallberg	2007	Population	5
Batten	1972	Community	140
Batten	1973	Population	8
Batten	1978	Population	62
Bell et al.	2010	Population	38
Bezzel	1985	Community	130
Biadun et al.	2009	Community	24
Biadun and Zmihorski	2011	Community	27
Bloom and McCrary	1996	Population	25
Boren et al.	1999	Community	24
Brown and Brown	2013	Population	30
Butcher et al.	1981	Population	23
Cannon et al.	2005	Population	8
Catterall et al.	2010	Community	15
Cramp and Agle	1952	Community	50
Cramp and Tomlins	1966	Community	15
Craves	2009	Community	15
Crosby and Blair	2001	Community	39
Decandio	2008	Population	138
DeGraff and Wentworth	1986	Community	5
DeGraff	1991	Community	5
Dott and Brown	2000	Population	18
Erskine	1992	Population	10
Faccio et al.	2013	Population	20
Fonaroff	1974	Community	8
Forman et al.	2002	Community	5
Foster et al.	2002	Population	175
Gehlbach	1996	Population	16
Hepinstall et al.	2012	Community	7
Herrando et al.	2012	Population	10
Horak and Lebreton	1998	Population	7
Horn	1985	Community	46
Jerzak	2001	Population	15
Jokimäki and Suhonen	1993	Community	20
Jokimäki and Suhonen	2000	Population	6

Author	Year published	Study type	Duration (yrs)
Jones and Wieneke	2000	Community	16
Kauffman et al.	2003	Population	24
Kauffman et al.	2004	Population	24
Kentish et al.	1995	Population	24
Kosiński	2001	Population	5
Liker et al.	2008	Population	10
Luther and Baptista	2010	Population	30
Luther and Derryberry	2012	Population	36
Mazgajski et al.	2008	Population	16
Milone and Grotta	1983	Population	18
Morneau et al.	1999	Community	15
Murgui and Macias	2010	Population	11
Murgui	2014	Population	15
Namba et al.	2010	Community	15
Nentwich and Paulus	1999	Population	12
Nihei and Higuchi	2001	Population	20
Nowakowski	1996	Community	25
Oliver	1997	Community	28
Ormond et al.	2014	Community	32
Parker et al.	1996	Population	17
Parody et al.	2001	Community	50
Pidgeon et al.	2014	Community	30
Pierotti and Annett	2001	Population	22
Raven and Coulson	1997	Population	19
Recher and Serventy	1991	Community	58
Robinsin et al.	2005	Population	29
Roth and Johnson	1993	Population	16
Rutz	2008	Population	59
Shultz et al.	2012	Community	94
Sodhi et al.	1992	Population	19
Suhonen et al.	2009	Community	9
Solonen	2008	Population	30
Stout et al.	2007	Population	12
Strohbach et al.	2014	Community	152
Suhonen and Jokimäki	1988	Community	27
Tait et al.	2005	Population	166
Tella et al.	1996	Population	6
Tryjanowski et al.	2013	Community	27
Vuorisalo et al.	2003	Population	81
Walcott	1974	Community	104
Ward et al.	2010	Population	26
Wood and Recher	2004	Population	63
Yeh et al.	2004	Population	19
Zmihorski et al.	2010	Population	26

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Chapter 10
Counting Birds in Urban Areas: A Review of Methods for the Estimation of Abundance

Yolanda van Heezik and Philip J. Seddon

Abstract Counts of birds can inform studies with different goals, such as estimating population size, monitoring populations over time and in response to environmental change, and estimating vital rates to model population dynamics. Because estimates need to be reasonably accurate and precise, considerable thought has gone into developing counting techniques that enable robust estimation of abundance, taking into account probability of detection, which can vary between species, land cover types and over time. In recent years these have been applied to over 60 % of studies estimating bird abundance conducted in non-urban landscapes. However, robust estimation techniques are not being similarly applied to studies in urban areas. We reviewed 162 articles in which birds had been counted and abundance and/or occupancy reported in urban areas, spanning the years 1991 to 2015, and found that only 11 % attempted to account for variable detectability; few of these had modelled detectability satisfactorily. There was no indication of increasing methodological rigour over time. Counting birds in urban areas poses significant challenges; robust techniques are constrained by limitations imposed by built structures, social factors and a mosaic of many small private parcels of land. We present a framework for estimating bird abundance and discuss the strengths and weaknesses of the different approaches, relating each to the urban context. Citizen science initiatives are considered as a good fit in urban areas and are increasing in number: sampling designed for all landscapes might be inappropriate in urban areas, but counting protocols should allow the modelling of detection probability.

Keywords Bird monitoring • Detectability • Distance sampling • Abundance estimates • Population assessment • Urbanisation

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10.1 Birds in Urban Areas

Birds are visible, charismatic and widely distributed and have long attracted attention from researchers and enthusiastic amateurs alike. Birds are counted for a wide variety of reasons: to estimate population size and monitor changes over time, to evaluate habitat requirements of species, to record distributions and how these might change in response to environmental modification and to provide estimates of vital rates that can be used to model population dynamics (Bibby et al. 1992). Estimates of the size and spatial extent of a focal population are necessary to investigate size-dependent or density-dependent relationships and assess the impacts of competition and predation on populations of interest over spatial and temporal scales (Williams et al. 2001). Abundance estimates are also particularly useful for evaluating the performance of a population model, by indicating whether important biological factors influencing changes in population status have been incorporated (Williams et al. 2001). Most conservation management programmes involve some manipulation of abundance, whether it is enhancing populations of species of conservation concern or controlling pest species, and a measure of population abundance is the basic metric that indicates whether a management action has achieved its goal.

In the last few decades, there has been a huge increase in interest in urban areas by ecologists and conservation biologists. The realisation that the accelerating growth of cities is responsible for many environmental and social problems today has created an urgency to improve our understanding of the ecology of urban landscapes, in order that we are in a better position to protect and enhance the biodiversity in the spaces where most of us lead our daily lives (McDonnell et al. 2009). There is also rapidly mounting evidence that regular contact with nature is essential for our physical and psychological wellbeing (Keniger et al. 2013; Russell et al. 2013; Lovell et al. 2014). Birds are a high-profile, popular, visible and well-described taxon and have been used extensively as proxies for other biological components of ecosystems (Warren and Lepczyk 2012). Counts of birds have been carried out to explore patterns of community structure and the mechanisms driving species' distributions along urbanisation gradients (Blair 1996; Clergeau et al. 1998; Sandström et al. 2006; van Heezik et al. 2008; Menon et al. 2014) but also to investigate the impacts of specific land uses, such as gardens (Gaston et al. 2005; Daniels and Kirkpatrick 2006; Goddard et al. 2016), housing developments (Mason 2006; Tratalos et al. 2007), parks and cemeteries (Latta et al. 2012) and urban woodlands (Donnelly and Marzluff 2004; Hedblom and Söderstrom 2010; Heyman et al. 2016) and wastelands (Meffert 2016). Long-term data sets allow the evaluation of how bird assemblages change over space and time (Catterall et al. 2010; Shultz et al. 2012), and comparisons between urban and regional populations of some birds of conservation concern have provided insights into the causes of population declines of some species (Fuller et al. 2009). More recently, studies have identified the relationships between the socio-economic and cultural characteristics of human populations and the abundance and diversity of birds (Kirkpatrick et al. 2007; Loss et al. 2009; Luck et al. 2013; van Heezik

et al. 2013). These factors drive bird assemblage structure and diversity and can be very important in urban areas. The use of birds as indicators of ecosystem health and change (see Herrando et al. 2016) opens up possibilities for engaging the public in data collection to inform understanding and management. Citizen science (i.e. the involvement of citizens from the non-scientific community in academic research (Tulloch et al. 2013), is a potentially powerful tool for counting birds in urban areas, with multiple benefits. On the one hand, it functions to engage and educate urban residents about the species with which they share their living space (McCaffrey 2005; Vargo et al. 2012), and it also enables the collection of wide-scale and long-term data on spatial distributions of birds in cities.

Urbanised landscapes are unique in terms of the extent of modification and degradation and in the heterogeneity and variety of different land uses (McDonnell and Pickett 1990). Direct ecological impacts include the replacement of native vegetation by buildings, roads and other structures; indirect impacts on vegetation composition and structure, which reduce habitat quality, are brought about through fragmentation and habitat degradation (Pennington and Blair 2012). Urban bird communities are also distinctive: as the degree of urbanisation increases, assemblages are composed of higher proportions of urban exploiters, species that form commensal relationships with humans, and in some countries, species which are non-native. Species that do not tolerate the transformed landscape (urban avoiders) drop out of the community, whereas urban adapters are often at their densest at intermediate levels of urbanisation (Blair 1996, 2004; Clergeau et al. 1998; McKinney 2006; Pennington and Blair 2012; Menon et al. 2014). The mechanisms behind these patterns are not well known, but local vegetation structure, availability of supplemental food, winter microclimate, proximity of remnants of native vegetation and human socio-economic factors all play a role in explaining the relative abundance of urban adapter species (van Heezik et al. 2008; MacGregor-Fors and Schondube 2011; Rodewald 2012; reviewed in Marzluff 2001).

Behaviour of birds also changes in response to urbanisation (Donaldson et al. 2007; Evans et al. 2010; Kitchen et al. 2010). Those species that thrive in urban environments, i.e. the urban adapter and exploiters, appear to possess behavioural traits that allow a more flexible response to high levels of disturbance and novel challenges (Møller 2010; Lowry et al. 2012 and refs within; Miranda 2016). Individuals of some urban species use human-subsidised resources and artificial structures, are less wary or more bold in temperament than their rural conspecifics (Vines and Lill 2014) and respond to increased year-round food resources by breeding earlier than their rural counterparts and by altering their foraging patterns and the food they eat (reviewed in Lowry et al. 2012). Some urban birds have also modified their behaviour in response to urban noise pollution, by shifting the frequencies and timing of vocalisations to improve communication (Lowry et al. 2012; Potvin and Mulder 2013; Potvin et al. 2014; reviewed in Macías-García et al. 2016). Finally, even the size and shape of birds that have adopted an urban lifestyle may differ from that of their rural counterparts: this might arise if bird populations in urban areas are established by a small number of individuals, and stochastic morphological divergence has arisen due to founder effects (Evans et al. 2009).

10.2   Objectives and Scope of the Chapter

Although the scope of research and the number of studies into the ecology and behaviour of urban birds has expanded hugely, the relative newness of the discipline raises the question of whether those studies relying on some estimate of the abundance of bird populations are applying appropriately rigorous methodology. Approaches for the estimation of bird abundance in non-urban areas might not be readily applied in urban regions. A key issue is detectability, the probability of counting a bird when it is present in the survey area. It cannot be assumed that detectability is perfect, that one species will be detected with the same certainty as other species or that a given species will be detected with the same probability in different habitats. In almost all situations, some individuals will be present but remain undetected, biasing metrics based on simple counts. The differences in behaviour that have been identified between urban and rural populations of the same species, such as flight distances (Møller 2008), have implications for detectability if comparisons are being made between populations. Moreover, the fine-scale heterogeneity of land uses typical of urban landscapes could cause detectability to vary within the same species across habitats. Counting birds in towns and cities is challenging: traditional robust methods are often constrained by limitations imposed by built structures, social factors and ownership of land. Here we present a framework for estimating the abundance of urban birds. We review the methods commonly used to count birds in urban areas and discuss the strengths and weaknesses of different approaches.

10.3   A Framework for Estimating Abundance

Population size is an appealingly transparent metric of population status, but its reliable estimation is fraught with difficulty. Ideally an estimate of abundance will be precise (low sampling variance) and accurate (unbiased). Precision will be improved through sampling intensity, recognising that it is virtually always impractical to conduct a true census (complete population count), and instead estimates of population size are based on some form of sampling. Accuracy may never be known since true population size is what is being estimated, but obvious sources of bias can be eliminated in any careful survey design, such as pre-count training of observers, and standardisation of survey conditions such as time of day and weather that take into account the behaviour of the target species. At the heart of any attempt to estimate animal abundance is the issue of detectability. Lancia et al. (1996) provide a concise categorisation of abundance estimation methods based on whether individual animals might not be detected during surveys. Figure 10.1 provides a simplified framework adapted from Lancia et al. (1996) for abundance estimation which first makes the distinction between methods to derive estimates of absolute abundance (population size (N) or density (D)) and methods that would
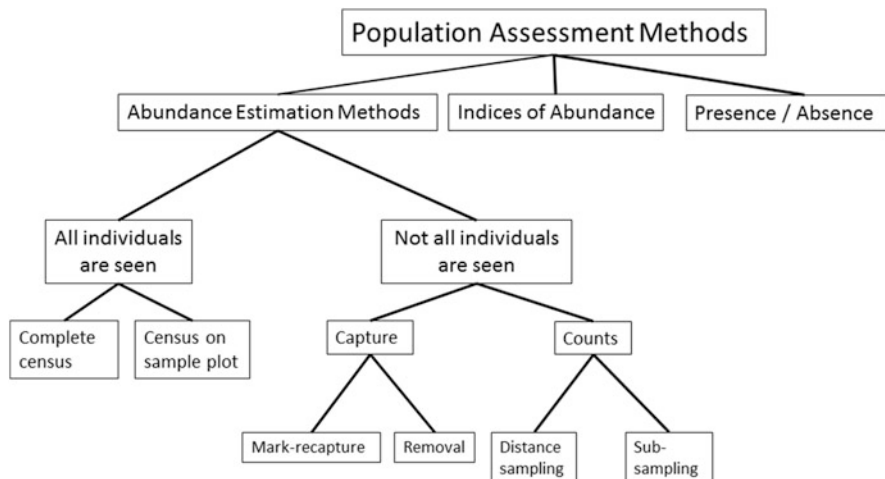
Fig. 10.1 A framework to assist in the estimation of abundance of urban birds, which distinguishes between methods that derive absolute abundance, indices of relative abundance, and presence/absence. Adapted from Lancia et al. (1996)

yield an index of relative abundance, or simple presence/absence. Indices and presence data, while apparently simpler than absolute abundance data, are not assumption-free.

10.3.1   Indices of Relative Abundance

An index of relative abundance is any measure that is correlative of absolute abundance. A typical bird count index would be the number of birds of focal species seen or heard during a defined survey period, from points or along transects, within an area of interest. A suitable index will have some positive relationship with absolute abundance. This relationship need not be linear but must be monotonic over all reasonable values of N (Williams et al. 2001). The utility of relative abundance indices is therefore dependent on the assumption of a constant probability of detection, although the method itself does not allow for the testing of this assumption (Norvell et al. 2003). Johnson (2008) defends indices by arguing that quantitative methods that account for variable detectability are limited in their practical application, particularly when extensive multispecies surveys are being carried out, and have their own shortcomings. However, indices are less likely to be adequate if comparisons are being made across habitats or between species when detectability rates are probably not similar, but they may be useful for monitoring populations if the variation in detectability is considerably less than the variation in population size sought to be detected, and is independent of population size (Johnson 2008). However, even when researchers are able to reduce the variability

in detectability through study design, such as standardising count times, durations, observer skills, weather conditions and habitat features, the assumption of constant detectability is consistently violated, making comparisons of relative abundance between years within a single species and a single habitat tenuous (Norvell et al. 2003). Although widely applied, indices are seldom validated against some robust estimate of abundance of the target population.

10.3.2 Presence/Absence Data and Occupancy Modelling

Presence-absence surveys seek to confirm the presence of a focal species within the survey area, so that the recording of even one individual would be sufficient to confirm the presence. Species absence, however, is much more challenging to confirm and becomes even more problematic where the intention is to quantify the occupancy of habitat patches by a focal species, i.e. the proportion of patches occupied within a landscape, otherwise expressed as the likelihood that the focal species is present within a given habitat patch. Traditionally presence/absence surveys have made the implicit and untested assumption that there is complete detection of the target species, i.e. if the species is present at a given site, it will be seen and recorded. But for many species, the probability of detection under virtually all survey regimes will be imperfect (Gu and Swihart 2004). The failure to record a species as present when it is actually there will result in overestimation of absences and underestimation of the proportion of the patches occupied. Reliance on simple presence/absence survey data can bias estimates of changes in even relative abundance, since it is impossible to exclude the possibility that recorded colonisations arise through the misclassification of a patch as vacant in earlier surveys (Hanski 2002; Moilanen 2002).

Models have recently been developed to estimate the proportion of sites occupied by a species when the detection probability is less than one (MacKenzie et al. 2002, 2003, 2006; Royle and Nichols 2003). The basis for these modelling approaches is the repeated survey of a sample of sites within a relatively short time frame, during which it is assumed there have been no systematic changes in the occupancy state of sites. These models can be applied to data collected over a single time period, e.g. 1 year, to assess the status of the population (MacKenzie et al. 2002; Royle and Nichols 2003) or to data collected over longer time frames, such as multiple years, to assess trends in occupancy and to estimate localised extinction and colonisation rates (MacKenzie et al. 2003). The model consists of N sites being visited on T sampling occasions. The presence or absence of the species is recorded at each visit, and the detection histories for each site are then constructed and site occupancy rates estimated (MacKenzie et al. 2002, 2003, 2006).

10.3.3   *Measures of Estimating Absolute Abundance*

For count-based evaluation and modelling of a population, indices and presence/absence data will not suffice and some estimate of N (abundance) or D (density) is necessary (Krebs 1999).These absolute abundance estimation methods may be divided into those where the probability of detecting an animal is one, and those where incomplete detectability is likely, i.e. some proportion of the population will be missed during surveys. In the unlikely case that the entire target population can be detected and counted, this would constitute a census. A more likely scenario would involve the complete count of all individuals within a sample plot, in which case the usual sampling considerations of sample unit placement and number will apply. In most cases however, it is reasonable to expect that not all animals will be seen in any given survey, thus most of the development of abundance estimation theory has concentrated on estimating detection probability and using this to account for the missing (undetected) proportion of a population and to adjust survey data.

10.3.3.1   Capture Methods

The robust estimation of detection probability can be approached in two main ways: capture-based methods and count-based methods. Capture methods may entail the systematic capture and removal (often killing) of individuals to derive an estimate of N, not surprisingly most often used on common, harvested and pest species (Pierce et al. 2012). For most other situations, estimates are based on the capture, marking and recapture (or resighting) of individuals over short time periods. The simplest case would be the capture, marking and release of some unknown proportion of a target population and the subsequent capture of a second sample comprising a mix of unmarked animals and those captured previously (Greenwood 1996). This two-sample ($k = 2$) mark-recapture estimator is known as the Lincoln-Petersen estimator and is the basis for other mark-recapture methods; more precise estimates are possible where $k > 2$ (Krebs 1999). Mark-recapture methods of abundance estimation make some important assumptions relating to capture probability; a detailed discussion is given in Williams et al. (2001). Spatially explicit capture-recapture models, which incorporate information about the likelihood of animals being captured in "traps", are a relatively new addition to the literature on abundance estimation (overviewed in Borchers 2012), with "traps" including detection devices that do not actually catch the animal.

10.3.3.2   Counting Methods

Count-based methods either directly estimate the detection probability or collect data that enables the modelling of detection probability. Direct estimation methods

require an appropriate subsample of the focal population and take the form of either double sampling or the use of a radio-tagged subpopulation. In double sampling a large number of survey units are counted using some rapid low intensity effort, such as direct counts during an aerial survey, and a random subsample of the same units are counted intensively, equivalent to a census on a sample plot. The counts obtained from the subsample can then be used to estimate the proportion of animals seen during the wider survey, and this relative probability of detection can be used to correct the abundance estimates for the whole survey region (Pierce et al. 2012). Double sampling assumes that the subsample units have been truly censused and that the two sets of counts are sufficiently close in time as to sample the same population. With a radio-tagged subsample of animals, it is known precisely how many animals are available to be counted and how many of these are missed using any rapid survey method. As for double sampling, the ratio of the counts from the rapid method to the counts from the subsample provides an estimate of the proportion of animals seen.

Strip transects and fixed radius point counts apply the implicit assumption that all objects of interest are detected within a predefined strip each side of a transect line or within a fixed distance from a point. In this way the area of interest is readily calculated, and estimates of density can be derived. However, the critical assumption of perfect detectability within the defined area is seldom tested explicitly. Failure to meet this assumption will result in overestimation of abundance where fewer detections are made at greater distances from the line or point. The problem of decreasing likelihood of detection with distance from the observer led to the development of distance sampling, now one of the most widely used methods for abundance estimation (Buckland et al. 2008). Distance sampling involves the modelling of a detection function using information on the distance at which animals are detected, by sight or sound, from a point or perpendicular to a transect line. The limits of detection do not need to be defined or constrained during surveys. There are four assumptions of distance sampling: that objects directly on the point or on the transect line are never missed, that objects do not move before detection, that detections are independent of each other, and that distances are measured accurately.

The major advantage of distance sampling is that it takes into account the decreasing ability of the observer to detect objects with increasing distance. As objects are detected, their distance from the point of observation or perpendicular distance from the transect line is recorded, and through the fitting of a detection function to the distance data, an estimate of density can be made (Buckland et al. 1993). If the size of the sample area is known, density estimates can be converted into estimates of sample population size. Examination of the detection functions for even highly visible species indicates that detection probability declines rapidly with distance, further casting into doubt the validity of estimates from strip transects and fixed radius points; an accessible introduction to distance sampling is provided by Buckland et al. (2001).

10.4 Counting Techniques in Urban Areas: Current Practice

10.4.1 Methodology

To obtain an overview of the ways in which researchers have sought to estimate the abundance of birds in urban areas, we combined the results of searches on the Web of Science (https://webofknowledge.com), cross-checked with searches on Google Scholar (https://scholar.google.co) and Wildlife and Ecology Studies Worldwide (http://web.b.ebscohost.com) using the search terms $Urban + Bird + Abundance$. We included only peer-reviewed papers, and did not restrict the search to specific journals, but focussed on the last ~24 years of research as there are relatively few papers on urban birds prior to 1991, and earlier studies would not have been able to apply techniques developed in recent decades. The resulting list is therefore not an exhaustive summary of all urban bird counting studies but is indicative of the range of approaches applied.

10.4.2 Results

We found 162 articles published in 68 journals in which birds had been counted, and abundance and/or occupancy reported in urban areas, spanning the years 1991 to 2015 (details available upon request to the authors). The context of the studies was very variable, including urban/rural gradients, altitudinal gradients, urban farmland, forest, riparian areas, gardens, golf courses, green walls, housing developments, parks, cemeteries, prairie fragments, railways, streetscapes, suburbs and grasslands. Abundance was reported using a wide variety of terms: only one study reported that a census had been made, some reported occupancy, others proportional abundance, relative abundance or an index of abundance. Density was also reported on one occasion as relative density.

Of the five studies that reported occupancy, three accounted for detectability in the calculation of the estimate; however, only 17 of the 160 studies that reported abundance (11 %) made any attempt to account for detectability. We separated the studies into those published between 1991 and 1999 ($n = 13$), between 2000 and 2010 ($n = 87$) and between 2011 and 2015 ($n = 61$), but there was no evidence of a real increase in the proportion of studies accounting for variable detectability over the 24-year period (Fig. 10.2).

10.4.2.1 Measuring Detectability

A number of studies acknowledged that variable detection might be an issue, but justified in a variety of ways not having modelled detectability, e.g. asserting that
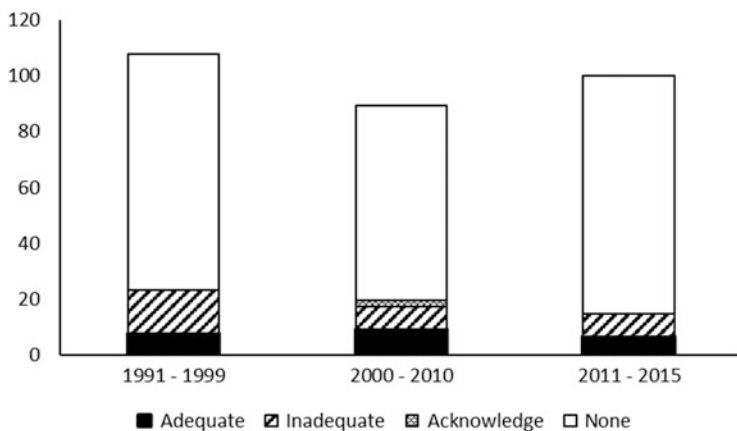
Fig. 10.2 Review of 162 articles published between 1991 and 2015 in which birds had been counted and abundance and/or occupancy reported in urban areas, with regard to whether variable detection was accounted for: adequate = variable detectability accounted for in study design and analytical methods; inadequate = methods adopted inadequate to account for detectability; acknowledge = variable detection acknowledged as a potential problem but not addressed; or none = neither acknowledged nor addressed

their methodology ensured that variation in detection probabilities was less than the variation in population size, that long sampling periods (e.g. 20 min) maximised the probability of detection of birds or that although the detectability of the species counted could differ among the habitats, a comprehensive study plot survey method meant that it was safe to assume that the observers were able to observe all individuals present during the survey period, and therefore habitat-related differences in the detectability did not significantly influence results. However, even when counts are made over longer periods of time, it is still possible to miss individuals, and it is more likely that individuals are counted more than once. A short count duration reduces the potential influence of evasive movements by the animals counted in response to the observer (Scott and Ramsey 1981). For these reasons standardised point counts recommended by different institutions are usually 5 min in length, and if they extend to 10 min, the data should be separated into time intervals (Ralph et al. 1993, 1995).

Some authors claimed that modelling detectability was not an issue because their study focused on within-species differences across habitats. In fact detectability of the same species can vary across habitats, and counts that do not account for detectability might arrive at erroneous conclusions through underestimating abundance in some habitats relative to others. The authors of one study compared two counting techniques (area search and strip transects) and concluded that both failed to provide 100 % detectability. One study adopted the approach of carrying out some pilot studies, and from these concluded that there was no significant difference in detection of bird species, so modelling of detectability was not warranted. Some authors acknowledge detectability, but made no attempt to model it, whereas

others measured distances to detections or counted birds within detection bands, but then did not appear to use this information to model detection probabilities.

10.4.2.2   Use of Relative Abundance and Indices of Abundance

A number of studies in our review ($n = 14$, 9 %) reported they had measured relative abundance, relative density in one case or an index of abundance. By doing so they acknowledge that their counts were not designed to estimate absolute abundance. In fact the 89 % of studies reviewed that did not estimate detection probability were effectively presenting an index of abundance, but without acknowledging they were doing so. Standardised point count surveys have been recommended to provide data resulting in indices of abundance that are comparable across years, habitats and studies and that can be used for monitoring populations (Ralph et al. 1993, 1995). Recently Matsuoka et al. (2014) called for a revival of common standards in point count surveys, after a review by them of 125 studies across Northern America revealed a large variability in point count technique— only 3 % of the counts carried out over the period 1992–2011 followed recommended standards for count duration and radius. We also found considerable variability in duration and radius of point counts. Durations ranged between 3 and 30 min, and radii between 25 and 100 m and in some cases were unlimited. Longer count periods may be necessary to enhance detectability of songbird species if the gap between songs exceeds 5 min, but for species that move during the duration of the count, longer durations result in birds being detected more than once and birds absent from the count area initially, can enter it during the count period resulting in an overestimation of density (Buckland 2006; Johnson 2008). For example, density estimates of birds were 22–56 % higher for a 10-min count than for a 5-min count (Granholme 1983). Buckland (2006) recommend the adoption of the snapshot approach to address the problem of bird movement, which involves the observer detecting and following movements of birds at the point, and then defining a moment when the distances from the point are recorded.

There are a number of variables that can influence bird counts, such as the observer's ability to detect and correctly identify birds, environmental conditions that affect bird behaviour and observer efficiency and the physical and behavioural attributes of the birds that make them conspicuous, all of which can vary over time (reviewed in Rosenstock et al. 2002). Some studies in our review justified the absence of detection modelling by claiming that because counts were made by only one observer in similar weather conditions and because they were only interested in within-species differences in abundance across habitats, detection modelling was not necessary. To be reliable, index counts must demonstrate a positive correlation with actual bird density that is consistent across habitats and in different conditions (Rosenstock et al. 2002). Nichols (2014) argues that there are good reasons to expect variable detection probabilities when making comparisons across species, locations and times; these non-random differences are likely to preclude any consistent correlations and therefore argue against the use

of count-based indices. While standardisation might reduce the influence of these factors, it is unlikely that detectability is constant (Nichols et al. 2000). In a review of studies testing for constancy of detection, Kellner and Swihart (2014) found that 86 % of studies reported significant variation and suggested that it is prudent to assume that detection probabilities differ, and therefore investigators should provide evidence of their equivalence before using indices. Indices of abundance also lack any measure of precision, without which comparisons might yield spurious results (Rosenstock et al. 2002). Point counts can be designed to account for imperfect detection and yield abundance estimates with measured precision that are comparable across time and space. Despite this only a very small proportion of the studies we reviewed used this methodology.

10.4.2.3 Use of Mark-Recapture Estimates

Abundance estimation by mark recapture was not used in any of the urban studies we reviewed. While capturing birds at locations across the urban landscape is possible, recoveries of marked birds that have dispersed across the city can be very difficult due to problems regarding access to private parcels of land, which make up most of a city's surface. Radio-tracking birds in urban areas would also be challenging for the same reason. However, spatially explicit mark-recapture methods are certainly an option to estimate the abundance of localised populations of birds in parks, reserves and other green spaces. The "captures" can be actual captures in traps or mist nests, but birds can also be captured acoustically or on camera (Borchers 2012), and spatially explicit mark-recapture analysis can be applied to incorporate information on the location of traps relative to animals to address the question of what area the traps cover (Efford 2004; Borchers 2012) and hence to estimate bird density.

In many cases the majority of detections recorded when counting land birds are based on auditory cues; however, the ability of observers to detect bird vocalisations varies significantly according to the amount of vegetation and background noise (Pacifici et al. 2008). Localisation of singing birds can be imprecise (Alldredge et al. 2007, 2008), and accurate measurement of distances to birds is one of the assumptions underlying distance sampling (Buckland et al. 2001). Dawson and Efford (2009) explore the use of an array of microphones to enable a spatially explicit capture-recapture analysis (SECR) of bird calls to produce density estimates. This approach requires that cues of individual birds are able to be distinguished and that all individuals vocalise during the sampling period. This methodology has been further developed to address some of the assumptions of Dawson and Efford (2009) that are unlikely to always hold and has been generalised for use in many situations (Stevenson et al. 2014). The various methodological approaches using passive acoustic data to estimate density are reviewed in Marques et al. (2013). None of the studies reviewed here used acoustic surveys and SECR, and careful consideration is necessary when applying this technique in urban areas. Problems associated with background noise and impacts of vegetation volume and

built structures are particularly pertinent. Traffic and other urban noise could overlap with parts of the acoustic frequencies of some bird calls (Potvin et al. 2014). As the signal-to-noise ratio decreases, the signal becomes less detectable, and a threshold should be selected that is high enough to ensure detection irrespective of noise (Dawson and Efford 2009). Given that as few as two microphones can be used to collect necessary data, it could be feasible to carry out a study in an urban landscape, but the method remains to be tested.

10.4.2.4   Use of Distance Sampling

Distance sampling was the approach most commonly used in the 11 % of studies ($n = 17$) in our survey that accounted for detectability when estimating density or population size. In these studies practitioners typically counted birds from a point and either measured distance to each detection or measured them into a number of bands. While point counts are less efficient and less accurate than transects at counting birds, and errors in estimating distances or violations of assumptions generate more bias (Buckland 2006; Johnson 2008), point counts are the only feasible option across large parts of the urban landscape, because they are more likely to be able to be placed randomly with regard to the animals' distribution, which is one of the preconditions behind distance sampling (Buckland et al. 2001). If transects were placed randomly with respect to the landscape, they are unlikely to be able to be traversed as they would inevitably cross many parcels of private land and built structures. Studies reviewed here using transects sought to circumvent this problem by placing transects parallel with roads; however, any data collected in this way are likely to be unrepresentative of the surrounding area (Thompson et al. 1998; Buckland et al. 2008).

One of the limitations of distance sampling in multispecies studies is that detectability can be modelled only in species for which there are sufficient numbers of detections, perhaps as few as 30, but guidelines suggest 60–100 (Buckland et al. 2001; Rosenstock et al. 2002). Avian communities are typically composed of a relatively small number of common species and a much larger number of rare species. The strategy adopted in ten of the reviewed studies was to model detectability on species pooled according to similar morphology and behaviour, assuming that these species had similar detection characteristics. The use of surrogate species is not well studied. Surrogates should be sympatric with the uncommon species of interest, and be similar with respect to all factors influencing detectability, i.e. microhabitat use, behaviour, size, vocalisation type and pattern (Rosenstock et al. 2002). In two of the studies reviewed, surrogates were matched to rare species for habitat type and ease of detectability and comprised only a small proportion of the total. However in two other studies, surrogate detection functions were used on the majority of species, while in one study the reporting of methods was not sufficiently detailed to determine the extent of use of surrogates. Abundance estimated in this way should be treated with caution because detectability patterns may differ between the pairs of species (Buckland et al. 2008). Assumptions about

detectability can be tested in distance by including the species as a covariate and conducting a multiple covariate distance sampling analysis (Buckland et al. 2008). We found only two multispecies studies which were sufficiently rigorous to the extent that they limited their density estimations to species for which they could model detectability.

Given the small proportion of urban bird studies that addressed variable detection, it was not surprising that none adopted any of the strategies proposed for difficult species (Buckland et al. 2008). For example, distance sampling can be combined with mark recapture in double-observer methods for both point and line transect sampling in situations where it is likely that not all animals at the point or on the transect are detected (Borchers et al. 2012), an assumption underlying distance sampling (Buckland et al. 2008). By using two or more observers, a combination of mark recapture and distance sampling can be used: both observers record overlapping detections independently of each other, or alternatively one of the observers is unaware of the detections made by the other, and the birds detected by both observers are considered as recaptures with the distance from the animal to the observer recorded as a covariate (Borchers et al. 2012). This spatially explicit capture-recapture model can then allow inferences about animal abundance and density.

10.4.3 Summary and Recommendations

10.4.3.1 Use of Presence/Absence

Simple presence/absence surveys can provide the basis for quantitative resource selection analyses, without any associated estimation of abundance, but there are formal methods available to consider incomplete detectability to derive estimates of the occupancy of discrete patches in an urban matrix. These could also be used to evaluate extinction and colonisation probabilities.

10.4.3.2 Use of Indices of Relative Abundance

It is important to recognise that any index of relative abundance is not assumption-free, in that it assumes that the metric being quantified varies positively and monotonically with actual abundance. Any index needs to be validated against some species-specific estimate of abundance, perhaps derived from a subset of the survey region.

10.4.3.3   Use of Censuses

Total counts of all individuals of interest over the entire survey area are probably justified only on very small plots. Extrapolation from plot-based census counts can be used to derive an estimate of total population size or mean density, taking into account inter-plot variability. However, extreme heterogeneity and issues of restricted access in urban areas make the placement of random or fully representative plots problematic, and plot size is likely to have to be challengingly small in order to have confidence that all birds were detected.

10.4.3.4   Estimation of Actual Abundance with Incomplete Detectability

In spite of the range of methods for estimating the probability of detection, surprisingly few of the studies we reviewed accounted for imperfect detection. In a survey published in 2002 on methods used to count land birds across all landscapes, in 224 papers from nine major journals, 95 % of studies relied on index counts (area counts, points, strip transects, mapping techniques), and only 13 % of studies (total proportions were >100 % because many studies used more than one method) used empirical modelling approaches (variable distance transects, variable circular plots or distance sampling; Rosenstock et al. 2002). Only 4 % of studies used distance sampling (Rosenstock et al. 2002). More recently, a literature review of 537 articles from 10 journals, published between 1970 and 2011, that estimated abundance of a range of taxa across various scales and landscapes, reported that just 23 % accounted for imperfect detection (Kellner and Swihart 2014). The proportion of studies addressing imperfect detection increased over time, from <25 % in 1971, 1981 and 1991, to 29 % and 35 % in 2001 and 2011, respectively, but for birds was over 40 % in 2001 and over 60 % in 2011 (Kellner and Swihart 2014). Our figure of 11 % of studies accounting for imperfect detection in urban landscapes is significantly lower than that for studies in non-urban landscapes. Urban ecology is a relatively recent discipline, and it is possible that its newness has engendered a lack of rigour that should be addressed in future studies.

10.5   Citizen Science and National Bird-Monitoring Programmes

The popularity of citizen science, whereby volunteers are involved in the collection of data for research and monitoring, has increased hugely in recent years, aided by the integration of the internet into daily lives and the use of new phone technologies (Tulloch et al. 2013; Dickinson et al. 2010; Bonney et al. 2014). Benefits derived from citizen science are broad: the data collected can facilitate the investigation of ecological processes over broad geographical scales, on private land and over long

time scales (Howe 2006 in Tulloch et al. 2013; Dickinson et al. 2010), resulting in information that would otherwise be unaffordable (Tulloch et al. 2013). The participation in citizen science programmes can also deliver significant social outcomes, such as educating the public about science (Brosshard et al. 2005), but also documenting information to inform sustainable management of harvests, protected area establishment and environmental air quality (Bonney et al. 2014). The oldest and most common citizen science projects are bird-monitoring schemes, for example, the National Audubon's Christmas Bird Count, running since 1900 in the USA (Greenwood 2007). Bird monitoring can be categorised as cross-sectional surveying, e.g. atlases (for a review of bird atlases in urban areas, see Luniak 2016), and longitudinal surveying, e.g. breeding bird surveys (reviewed in Tulloch et al. 2013). Citizen science initiatives often span many landscapes, including urban environments (see Goddard et al. 2016; Herrando et al. 2016), but most frequently provide information on the presence of birds rather than abundance. Citizen science has been described as a "good match" for the field of urban ecology (Dickinson et al. 2010): large numbers of potential volunteers live in urban areas and are able to access the private land which comprises the greatest proportion of the urban landscape. However the design and analysis of data from citizen science projects can be challenging, and designs that have been implemented to improve the reliability of the data do not always work well in urban areas.

Many citizen science-based bird-monitoring programmes do not take species' detectability into account. Murgui Pérez (2011) compared four independent estimates of bird population sizes in Spain obtained through citizen science and found large differences between the estimates for most species, sometimes up to 30-fold and particularly in urban areas. He attributed these to a lesser extent to differences in observer skills (professionals versus amateurs), a possible effect of field methods (transects versus point counts) and differences in study design (bias in the sites selected to be counted) and to a greater extent on whether detectability was taken into account. In one programme, which estimates national population sizes for common birds (SACRE, Seguimiento de Aves Comunes Reproductoras en Espaňa), an effective census radius was calculated for each species, with the assumption that all records of each species would fall within that effective sampling area (Carrascal and Palomino 2008). Not surprisingly population estimates using the SACRE data were higher than from data where detectability was not modelled, as has been observed elsewhere (van Heezik and Seddon 2012). Murgui Pérez (2011) also speculated that extrapolations of data collected from limited habitat types to non-surveyed areas could have resulted in overly conservative estimates for some species, whereas the SACRE data were based on 22 habitat types and not subject to the same degree of cautious extrapolation. However some of the SACRE estimates appear too large to be likely, compared to total European bird populations, casting doubt on the reliability of applying the effective census radius to model detectability (Murgui Pérez 2011). The effective census radius approach might have been species-specific but also needed to be habitat-specific. Regional population estimates of jackdaw *Corvus monedula* in Spain using the technique of Carrascal and Palomino (2008) resulted in large discrepancies when compared with

figures obtained through careful censuses, in this case depending on the time of year counts were made (Blanco et al. 2014). Urban environments are typically comprised of high heterogeneity of habitat types, and so researchers should make sure that detectability for each species does not vary between habitats and seasons before applying a general effective radius width.

The British Breeding Bird Survey (BBS), which was introduced in 1994 and covers a range of landscapes including urban, serves as an example of how large-scale citizen science data collection can still be carried out in a fairly rigorous manner to monitor population trends of a broad range of breeding birds in the UK (Newson et al. 2005). The BBS generates large numbers of detections of many species, by citizens who are usually experienced bird watchers. By recording birds in distance categories, the BBS allows the evaluation of detectability, and from this habitat-specific estimates of density and population size can be derived. However because birds are counted into only three distance intervals and the data from the third interval are often not used, there may be too little information on the shape of the detection function to allow goodness-of-fit testing (Buckland 2006). Newson et al. (2005) validated the estimates from the BBS by comparing them with those generated by other studies and found good agreement for most species. However the BBS design used transects to count birds, and while these may work well in most landscapes, in urban landscapes they invariably follow roads, and as such do not allow the robust estimation of density.

There are a few examples of specifically urban bird-monitoring programmes using citizen science: these include the Smithsonian Institute's Neighborhood Nestwatch Program, five studies on urban birds coordinated by the Cornell Lab of Ornithology, and the Tucson Bird Count (McCaffrey 2005). The Tucson Bird Count is a volunteer-based project using skilled observers to survey breeding birds at hundreds of sites across Tucson, using 5-min unlimited-radius point counts, with no assessment of detection probability, and primarily producing distribution maps rather than abundance indices (Turner 2003). Herrando et al. (2012) used bird-monitoring data collected in two cities, Barcelona and Brussels, to develop a multispecies indicator for each city to be used to evaluate responses of birds to environmental changes in urban habitats in other European cities. The data from Brussels were collected using point counts at 98 sites with no estimate of detection probability, and in Barcelona birds were surveyed using eight 3 km transects. The study concluded that values provided by urban indicators can differ depending on the conceptual approach (Herrando et al. 2012); however, other factors relating to study design most likely also contributed to the variation; a reliable index should be based on similar study design and should evaluate detection probability.

10.6 Final Comments

Despite significant advances in the theory of animal abundance estimation, the development of accessible quantitative tools for abundance estimation and the robust application of these tools to estimate bird abundance in natural areas, a majority of the studies reporting on bird counts in urban areas apply methodology that most likely results in biased estimates. Virtually no method is free from some assumptions around the probability of detection of individuals of the target species. Indices of relative abundance should be validated against some estimate of actual abundance, complete detection in any census should be confirmed and occupancy estimation, or capture- or count-based estimates of actual abundance (whether expressed as density or number), should apply the appropriate tools that incorporate explicit modelling of detection probability.

While distance sampling has most commonly been applied to address problems of variable detectability, surveys based primarily on auditory cues often violate the basic assumptions of this approach, as do double-observer approaches (reviewed in Schmidt et al. 2013). Moreover, in recent years researchers have drawn attention to the existence of two detection probabilities (Newson et al. 2005; Schmidt et al. 2013). Distance sampling allows the estimation of the number of animals available for detection during the survey; however, it is possible that some animals in the area being surveyed are not available for detection, e.g. in an urban area, birds might be situated behind a built structure, or the point counts might be made of vocalising birds that do not call at all during the period of the count (Nichols 2014). Two detection probabilities can therefore be estimated: the probability that an individual bird is potentially detectable (availability), and the probability that it is detected, given that it is available at some time during the count (Nichols 2014). Schmidt et al. (2013) found that variation in detection due to the presence and availability was large and differed between species of birds counted in Denali National Park, Alaska. A number of methods can be employed to estimate the probability of availability for detection: Schmidt et al. (2013) suggest that repeated count surveys and mixture models for analysis would improve the sensitivity and effectiveness of many passerine-monitoring programmes. Most importantly, the investigator needs to be aware of the different approaches and choose the one that best suits the questions being addressed. For rare species, low numbers of detections might prohibit robust estimates using distance sampling methods, and the use of surrogate species might seem appealing; however, the appropriateness of surrogates should be explicitly tested.

While a number of studies address the issue of how to deal with error and bias in citizen science data sets (Bird et al. 2013; Tulloch et al. 2013; Isaac et al. 2014), trade-offs between data quality and quantity, quantification and standardisation of sampling effort and methods and mismatches in skills and expectations of data collectors and users (Robertson et al. 2010), as well as the study design itself, are all fundamental to how reliable the data collected will be. Design needs to be such that some evaluation of detection probability is possible. Urban citizen science

bird-monitoring programmes that wish to evaluate abundance should use point counts and count either into distance bands (preferably greater than three) or record distances to all detections. When sufficient data are collected, habitat- and species-specific effective radii could be modelled and validated across a range of cities.

Mirroring the accelerating growth of urban areas and their human populations has been a rapid proliferation of studies conducted on urban bird populations as well as on other urban taxa, including those based on citizen science data. At present the majority of investigators are not applying sufficiently rigorous techniques when estimating urban bird abundance. While some recent studies have accounted for imperfect detection in a rigorous manner, there is still considerable scope for an improvement in abundance estimation techniques and also for trying approaches other than conventional distance sampling when estimating urban bird population size.

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Chapter 11
Urban Ornithological Atlases in Europe: A Review

Maciej Luniak

Abstract For half a century regarded as the most appropriate methodological approach for censusing wild animals and plants, the atlases are also used for presenting the distribution of avifauna in European towns and cities. This chapter looks at ornithological atlases concerning solely an urban area and not in a much more extensive region of which that area is just a small part. To date (2014) at least 77 avifauna atlases have been published for 66 towns and cities in Europe. In Italy (44 atlases), Poland (12) and Germany (8), this is currently the usual way of describing the distribution of bird species within an entire urban area. The cartographic basis for presenting the material is usually a grid of cells based on Universal Transverse Mercator (UTM) or some other system like the Gauss-Krüger. Less commonly, the grid is defined by geographic coordinates, and, exceptionally, a mosaic of irregularly shaped plots may be used, as in the Turin and Warsaw atlases. The majority of atlases relate exclusively to breeding birds, the maps showing the probability of breeding and/or the number of breeding in the grid cells. Only a few urban atlases supply cartographic information on wintering birds or their year-round status. Repeat editions of atlases include maps comparing present and past distributions. For most cases each atlas cell was surveyed ca four times per season. The fieldwork usually lasted 1–2 years in small towns but from 3 to 10 years in larger ones. The number of observers was often independent of the size of the area to be surveyed: in some cases up to a dozen or so experienced ornithologists were involved, but usually a large number (50–60 to over 100) volunteers took part. Compared with traditional verbal descriptions, an atlas mapping the distribution of birds in an urban area is of greater use as a scientific document, as a source of data for urban planning and for popularising wildlife among its inhabitants. It ensures better coverage of the area, comparability and transparency of the data and is more useful for municipal administration purposes.

Keywords Urban birds • Avifauna of European cities • Methods of bird inventory • Ornithological cartography

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11.1 Introduction

The atlas as a way of describing the distribution of species of flora or fauna in a given area based on a specific cartographic formula, came into general use since around middle of twentieth century. In this form data from censuses of plants and animals were found to be better applicable (especially with use of computer techniques) in urban planning and nature conservation; as a scientific record, it also satisfied the requirements of rigour and comparability.

This method of describing bird life came into use in 1970, when the first ornithological atlas in Europe was compiled for the West Midlands region of England (Lord and Munns 1970). A few years later, however, four national atlases were published: for France (Yeatman 1976), Britain and Ireland (Sharrock 1976), Denmark (Dybbro 1976) and then West Germany (Rheinwald 1977). They opened a new chapter in European avifaunistics; in the development of which a leading part came to be played by the European Bird Census Committee (EBCC). The Atlas of European Breeding Birds (Hagemeijer and Blair 1998) was published under the auspices of EBCC. A similar working group is active in North America (North American Ornithological Atlas Committee). At present many European countries have ornithological atlases covering the whole state, a region or a smaller local area. Two reviews of such atlases have been published recently: that by Gibbons et al. (2007) is based on more than 400 of these atlases published between 1976 and 2005 in nearly 50 countries, while the one by Dunn and Weston (2008) analyses the content and utilisation of 272 atlases that appeared in print or on the Internet in 50 countries up to 2007. The latter review ignores, with three exceptions, ornithological atlases of towns and cities as separate entities.

The first bird atlas of a city is generally regarded as the one for the London area (Montier 1977). However, as this atlas covers an area of 3424 km^2 and encroaches far into rural areas, one would be justified in treating it as a regional atlas—a detailed version of a section of the UK atlas (Sharrock 1976) that was being compiled at the same time. Instead, the bird atlas for the West Berlin (Witt 1984) is actually the first one of its type.

This chapter, an extended and updated version of an earlier paper (Luniak 2013), focuses on atlases for which the area surveyed is the city itself and not a much wider area within which the city occupies just a small part. This premise therefore excludes regional atlases, even if they include large cities like Basel (Blattner and Kestenholz 1999), Bonn (Reinwald et al. 1984), Essen (Przygodda 1988) or Hamburg (Holzapfel et al. 1984). The first edition of the Moscow atlas (Kalyakin and Volzit 2006), for example, related to a vast area of some 47,000 km^2, in which the city itself, even within its widest administrative boundaries, covered a mere 1000 km^2. In the case of the two editions of the London atlas (Montier 1977; Hewlett 2002), the disproportion between the city's area and that covered by the atlas is much smaller, and therefore it is generally cited as an "urban" one. In contrast, the Paris atlas (Malher et al. 2010) covers only the fairly small central part of this metropolis. In similar vein, the atlases for Voronezh (Numerov et al. 2013)

and Brussels (Rabosee et al. 1995) do not include the extensive suburbs of these cities. A monograph, in non-atlas form, of the avifauna of 16 European cities was published by Kelcey and Rheinwald (2005).

11.2   The Spread of Urban Ornithological Atlases

At least 77 urban ornithological atlases have been published for 66 towns and cities in Europe since the appearance of the first ones for London (Montier 1977) and West Berlin (Witt 1984), and work is well advanced on a number of others. Atlases of this type appear to be specific to Europe; on other continents, e.g. North America, the preference is for regional or local atlases in which towns and cities make up just a fraction of a larger area surveyed. In Africa just one urban ornithological atlas has been produced—for Bloemfontein in the Republic of South Africa (Kopij 2001).

Italy is the absolute leader when it comes to urban bird atlases. By 2014 there were 44 such atlases for 38 Italian towns and cities (Fig. 11.1) and work is under

Fig. 11.1   Towns and cities in Italy for which ornithological atlases have been published. Off the map are two other cities with atlases—Caltanissetta in Sicily and Cagliari in Sardinia. *Underlined*—the cities for which there are repeat atlases

way on a number of others (M. Dinetti in litt. 2014). Urban atlases constitute the majority of all (70 or so) bird atlases which have appeared in Italy (Gibbons et al. 2007). This has been achieved by the Italian national working group which since 1980 has been inspiring and coordinating this kind of work (Fraissinet and Dinetti 2007). So great is the interest in Italy in urban bird surveys that a handbook on "urban ornithology" was published (Dinetti and Fraissinet 2001), probably the first such work in the world literature. Florence is the only city in the world that can boast three editions of bird atlases (Dinetti and Ascani 1990; Dinetti and Romano 2002; Dinetti 2009), compiled in consecutive decades. Five other Italian cities— Naples (Fraissinet 1995, 2006), Livorno (Leghorn) (Dinetti 1994; Dinetti et al. 2013), Milan, Cremona and Grosseto—have two editions of atlases (Dinetti 2009), and the repeat atlas for Rome (Cignini and Zapparoli 1996) is in preparation (M. Dinetti in litt. 2014). Most of the atlases for Italian cities are discussed in the reviews by Fraissinet and Dinetti (2007) and Dinetti (2009).

Poland is the country with the second largest number of urban ornithological atlases. To date (2014), 12 have been published for 11 towns and cities (Fig. 11.2), and further two are in preparation. They are for towns with less than 100 thousand inhabitants (Świebodzin, Sulechów, Gorzów, Leszno, Przemyśl, Jasło) and the two largest Polish cities—Warsaw (Luniak et al. 2001; Nowicki 2001) and Łódź (Janiszewski et al. 2009). Two atlases have been compiled for Warsaw, one covering the entire municipal area (494 km^2, Luniak et al. 2001) and the other giving the results of a more detailed survey of just the city centre (52 km^2, Nowicki 2001). The urban bird atlases for Poland are listed by Luniak (2013). Since 1990 only three non-atlas monographs on urban avifauna have appeared in Poland; the results of urban bird censuses in this country are thus published mainly in atlas form.

For **Germany** there are 8 bird atlases for **7** towns and cities (Fig. 11.3) This is not a lot considering the advanced state of avian faunistics in this country, where some 50 regional and local atlases have been compiled (Gibbons et al. 2007). A pivotal role was played by the West Berlin atlas (Witt 1984), which became a point of reference and inspiration for other works of this type in Europe. This particular atlas was a reflection of the political situation of the time: it could embrace only the western part of the city. On the other side of the Berlin Wall, another bird atlas was compiled for that part of the city lying within the borders of the German Democratic Republic (Degen and Otto 1988). Happily, history brought this artificial division to an end, and a bird distribution atlas for the whole of Berlin (Otto and Witt 2002) was compiled by two of the authors formerly separated by the Wall. Another German atlas worthy of note is the one for Hamburg (Mitschke and Baumung 2001). The remaining German atlases (Fig. 11.3) are for smaller towns and cities— Bielefeld (Laske et al. 1991), Halberstadt (Nicolai and Wadewitz 2003), Chemnitz (Flöter et al. 2006), Emden (Retting 2007) and Regensburg (Schlemmer et al. 2013).

Elsewhere in Europe urban ornithological atlases are rare (Fig. 11.3), even though the atlas, as a way of depicting bird distributions, is common. Among over 50 regional and local bird atlases for the **United Kingdom** mentioned by Gibbons et al. (2007), only two are for cities—London (Montier 1977; Hewlett

Fig. 11.2 Towns and cities in Poland for which ornithological atlases have been published. The *small dots*—towns with populations below 100,000

2002) and Leeds (Fuller et al. 1994). In **France** only two of the 21 bird atlases (Gibbons et al. 2007) are strictly urban atlases: one is of the central districts of Paris (Malher et al. 2010) and the other is of the small town of Douai (Boutroille 2005). Work is in hand on atlases of "Grand Paris" (762 km^2, F. Malcher in litt. 2014) and Marseille (240 km^2, E. Barthelemy in litt. 2014). In **Spain** there are 25 bird atlases (Gibbons et al. 2007) but none as yet for urban areas was published. The first one, which included information about breeding and wintering bird fauna was carried out in Valencia, is awaiting publication (E. Murgui in litt. 2014); Breeding Bird Atlas of Barcelona (2012–2014) is in the process of publication (see Herrando et al. 2016). For other countries in Western Europe, there are two editions of the Brussels atlas (Rabosee et al. 1995; Weiserbs and Jacob 2007) and the Amsterdam atlas (Malchers and Daalder 1996). In central and southern Europe (apart from Poland and Italy), there are two atlases from the Czech Republic—for Prague (Fuchs et al. 2002) and Pardubice (Vranova et al. 2007)—and one from Bulgaria—for Sofia (Yankov 1992). In Russia and the countries of the former Soviet Union, there is the atlas for St. Petersburg (Khrabryi 1991) and the more
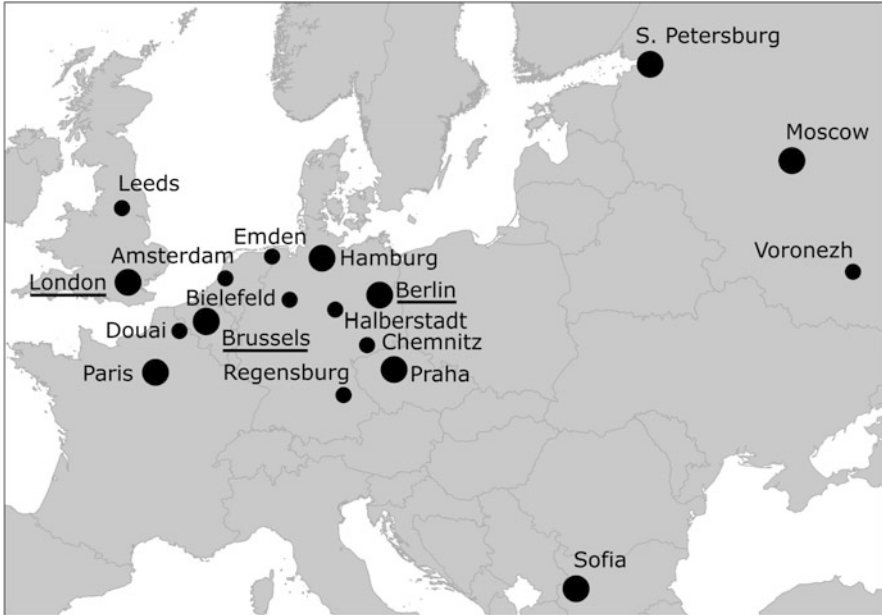
Fig. 11.3 Towns and cities in Europe (excluding Italy and Poland) for which ornithological atlases have been published. The *large dots*—cities with populations of more than one million. *Underlined*—the cities for which there are repeat atlases

recent ones for Moscow (Kalyakin et al. 2014) and Voronezh (Numerov et al. 2013). The atlases for Lviv in Ukraine (A. Bokotey in litt. 2014) and Kaliningrad (E. L. Lykov in litt. 2014) are awaiting publication.

Of the at least 66 European towns and cities for which bird distribution atlases have been published, repeat editions reflecting newer records (3 for Florence!) have been published for 9 of them. This makes up 14 % of all urban atlases, a proportion similar to that given for ornithological atlases of all kinds worldwide—12 % (Gibbons et al. 2007, $N = 411$) and 13 % (Dunn and Weston 2008, $N = 272$).

11.3 Cartography

In urban ornithological atlases, as in other faunistic or floristic atlases, various systems are used to map the records.

UTM Grid (Universal Transverse Mercator). This is based on a "flat" projection of a geographical area with divisions into squares, as well as wedges that compensate for the convexity of the earth's surface. It is used mainly in Italy, except in the earlier atlases for Florence and Turin. Elsewhere, this system has been used for the atlases for Sofia, Pardubice, Voronezh and Moscow, but not in the atlases for towns

and cities in Poland and Germany. In Italy, the UTM grid was based on 0.25 km^2 squares in the atlases of the smaller towns and on 1×1 km (1 km^2) squares in those of the larger cities. In contrast, 2×2 km (4 km^2) tetrads were used for the Moscow atlas. Gibbons et al. (2007) estimate that some 75 % ($N = 252$) of ornithological atlases use the UTM grid or other grids based on a kilometre system (see below).

Other Types of Grid Using Rectangular Cells These were used in earlier atlases, e.g. those of St. Petersburg and some towns in Poland, and the system would often be the same as that used for national atlases, as in the London atlas. The largest such cells were applied in both London atlases (2×2 km) and the St. Petersburg atlas (1.5×1.5 km). In other atlases of large and medium-sized urban areas, as in the UTM system, the use of 1 km^2 squares was standard practice. In the atlases for small Polish towns, 200×200 m (0.04 km^2) and 500×500 m (0.25 km^2) squares were the norm. With the exception of the West Berlin atlas, all the atlases of German towns and cities use the national Gauss–Krüger grid (1 km^2).

Grids Based on Geographical Coordinates The West Berlin atlas (Witt 1984) was the first to use this approach and became a model for some later atlases. There,

Zięba

Fringilla coelebs

występowanie lęgowe

ponad 30 par / km^2

11 - 30

4 - 10

0,1 - 3

0   2.5   5 km
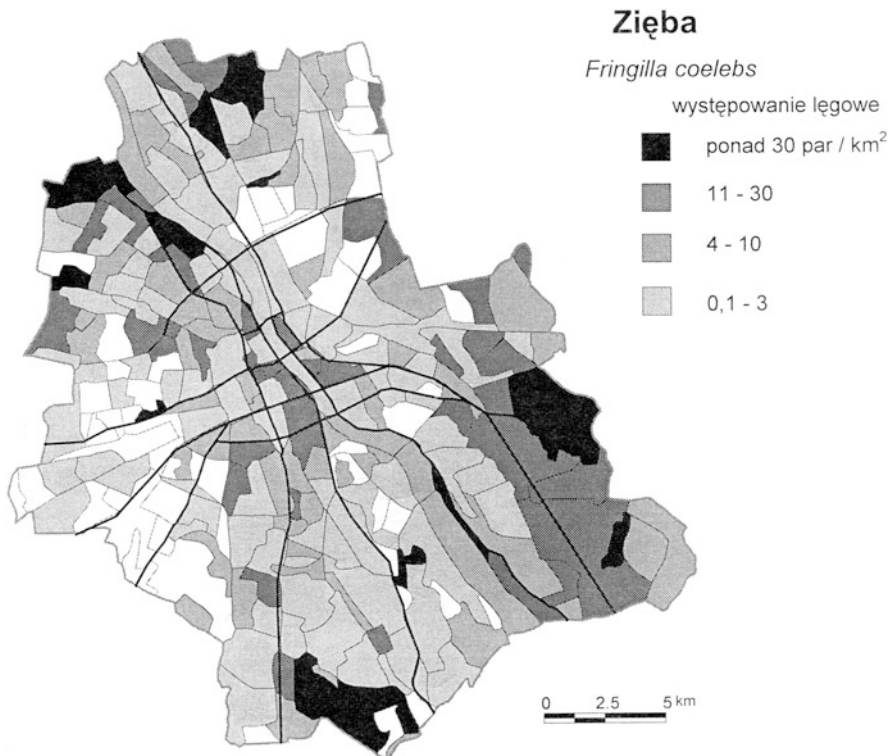
Fig. 11.4 An example of a species distribution map with irregularly shaped plots—the Warsaw atlas (Luniak et al. 2001)

the grid cells were delineated by 0.5 min of latitude and 1 min of longitude, i.e. 922×1132 m (1.04 km^2). This system was also used (exceptionally for Italy) in the first two editions of the Florence atlas (1990 and 2002), and more recently for the Polish city of Łódź (Janiszewski et al. 2009). According to reviews of ornithological atlases worldwide, this system is used in 20 % (Gibbons et al. 2007) and 32 % (Dunn and Weston 2008) of such works.

Division into Irregular Units This is based on the topography of environments and urban structure, e.g. streets, administrative divisions, etc. (Fig. 11.4). This system has been used in just two atlases, the ones for Turin (Maffei et al. 2001) and Warsaw (Luniak et al. 2001; Nowicki 2001). Drawbacks of this method include the difficulties in establishing criteria for dividing the area into atlas cells and in the workup and comparability of data relating to bird numbers in different cells. On the other hand, it is coherent with city maps, so it is better applicable in an administrative context. In the case of Turin, the atlas units were from 1.2 to 3.7 km^2 in area, whereas in Warsaw, their size ranged widely, from 0.26 km^2 (a small city centre park) to 9.62 km^2 (a suburban forest park).

11.4 Information on the Maps

The way in which information is displayed on the species distribution maps is specific to ornithological atlases, although obviously, the maps are accompanied by longer or shorter textual descriptions characterising the presence of particular species in an area and by chapters of a more general nature. The atlases under discussion here present the following parameters of a species' occurrence in the grid cells in a standard cartographic form, sometimes on several maps for that species.

Breeding Status and Season of Occurrence The great majority of atlases relate only to breeding birds. Breeding status on species distribution maps is often represented by three categories of probability, i.e. confirmed, probable or possible (Fig. 11.5), in accordance with the criteria applied in the European atlas (Hagemeijer and Blair 1998). The Moscow atlas (2014) uses a fourth category: "species observed during the breeding season but no evidence of breeding". The map legend usually summarises the number of squares with a given category of breeding probability. Only a few atlases provide maps of the occurrence of species outside the breeding season. The presence of a species in winter is given on separate maps only in the atlases for Moscow, Warsaw, Jasło (Stój and Dyczkowski 2002) and a few Italian cities, e.g. Naples, Venice and Bergamo. Data relating to the whole of the year outside the breeding season are given only in the atlases for Genoa, Milan and Turin (Dinetti 2009) and Moscow (2014). According to Dunn and Weston (2008), 81 % of ornithological atlases worldwide relate solely to breeding birds. Similarly, Gibbons et al. (2007) state that 12 % of such atlases
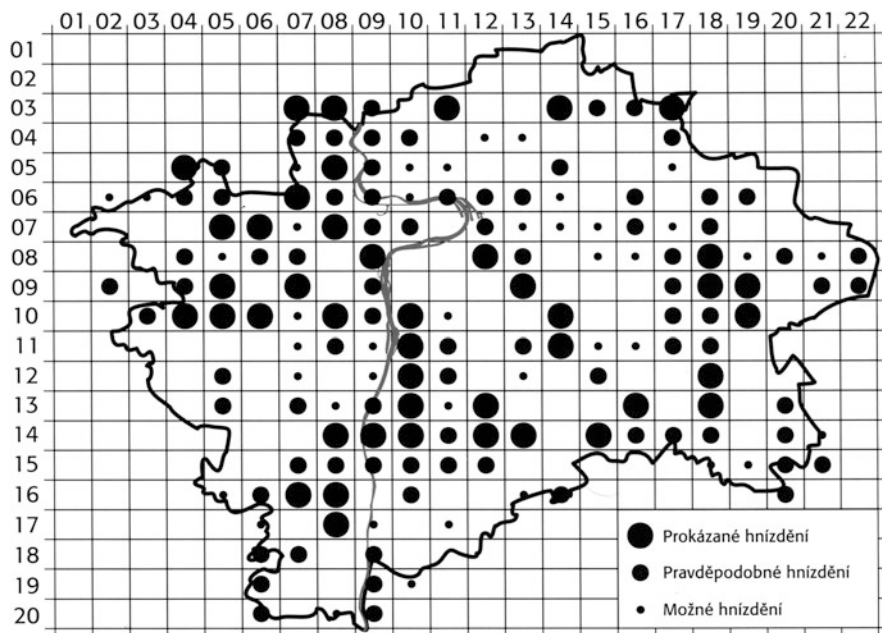
Fig. 11.5 A map showing the three categories of breeding probability—the Prague atlas (by courtesy of the authors—Fuchs et al. 2002)

contain data on overwintering and 7.5 % contain year-round data. The proportions in urban bird atlases are similar.

Bird numbers are taken into account in most of the recent urban bird atlases, although the two reviews of these atlases state that only 30 % (Gibbons et al. 2007) and 46 % (Dunn and Weston 2008) provide such information (for a review of census methods in urban areas, see van Heezik and Seddon 2016). Showing numbers of birds on the maps usually means forgoing the differentiation of breeding probabilities, e.g. in the atlases of Hamburg, Warsaw and Florence. In line with tradition, however, a few of the recent atlases—London (2002), Naples (2006), central Paris (2010) and Częstochowa (Czyż 2008)—show only the probability of breeding. The very recent atlases for Livorno (2013) and Moscow (2014) show both parameters—the degree of breeding probability and numbers of birds—on the same map; only the Prague atlas provides two separate maps with these data. Other recently published atlases, e.g. Voronezh (2013), Łódź (2009) and Regensburg (2013), give only numbers on the maps, usually on a logarithmic scale. The Regensburg atlas does not illustrate graphically the number intervals: the maps give absolute figures pertaining to pairs in different localities. The different cell sizes in the Warsaw atlas required (for common species only) relative numbers to be given as territory density per 10 ha. Italian atlases, e.g. Naples and Turin, show the numbers of birds outside the breeding season, the quantitative parameter being

the sighting frequency of a species. In contrast, the Moscow atlas (2014) states the maximum number of birds recorded outside the breeding season, and the atlases for Jasło (Poland) and Warsaw give the average number of birds per 10 ha per survey visit.

Distribution in Habitats Recent advances in colour printing have made it possible to map the distribution of bird species against the background of the main habitats in the city. The most advanced atlas in this respect is the one of Hamburg: instead of using a uniform environmental background for all the maps, just the habitats essential to a particular species have been selected. This approach shows more clearly how its distribution in an urban setting is determined by particular habitat.

Changes in Occurrence Atlas surveys of birds have been repeated in eight European towns and cities (13 %, $N = 63$), and in Florence such surveys have taken place three times, at 10-year intervals (Figs. 11.1 and 11.3). This proportion is similar to the one given by Gibbons et al. (2007) for all bird distribution atlases worldwide (12 %, $N = 411$). The repeat editions of the atlases supply additional maps of the past distribution of a species next to the main maps showing its present distribution. The second edition of the London atlas (2002) gives an additional map for each species showing the difference between the present distribution and that after the earlier census. The maps in the atlas for Olsztyn, Poland (Nowakowski et al. 2006) address the historical aspect by showing earlier (up to the year 2000) localities of a species, abandoned before the atlas census took place.

   The context of a species' occurrence in a particular country in map form is shown only in the recent atlas for Pardubice (Vranova et al. 2007), which contains species distribution maps taken from the national atlas of the Czech Republic.

11.5   Fieldwork

No standardised census methodology is used in urban bird atlases. Only in Italy is all such fieldwork carried out in accordance using a national standard (Fraissinet and Dinetti 2007). In general, however, atlases follow the recommendations set out in the EBCC atlas (Hagemeijer and Blair 1998), particularly as concerns the categories of probability of breeding of a species. In the great majority of cases, each grid cell was surveyed 4 (rarely 3–5) times during a single year. The recommendation for the London atlas (2002) was that the fieldwork in each tetrad (2×2 km square) should last for a total of 12 h during the 4-month-long breeding season. For the Moscow atlas (2014), observers were required to monitor each tetrad for a total of 6 h in each month of the breeding season, and at the observer's discretion, at other times of the year. A more or less simplified version of the cartographic method was used for counts of particular species in the grid cells, especially species occurring in large numbers. Such counts are often done in only selected parts of grid cells, but they are then more intensive. In some atlases,

e.g. St. Petersburg and Voronezh, transect and point counts were done. For the Hamburg atlas, it was recommended that intensive counts should be done in one-third of a grid cell.

The **duration (years) of fieldwork** in atlas projects varied a great deal and was not always proportional to the size of the area to be studied. The shortest—1–2 years (seasons)—was usual in the smallest towns, such as Livorno, Parma and Gorzów Wielkopolski (Poland), but also in some larger ones, covering an area of 50–100 km^2, such as Regensburg, Florence and even Milan. Projects lasting 3–4 years were carried out in both smaller towns, e.g. Chemnitz, Pardubice (Czech Republic) and Jasło (Poland), and some of the largest cities like Rome or Hamburg. Quite frequently the atlas projects lasted for 5–10 years not only in large cities (Berlin (2002), Moscow (2014), St. Petersburg, Prague, Warsaw) but also in much smaller ones (Częstochowa, Padua, Voronezh). Examples of even longer studies are rare: the projects in Amsterdam and Turin lasted for 12 years. Sometimes, the atlas was published long (more than 10 years) after the fieldwork had been carried out, e.g. Warsaw, Prague, Olsztyn.

11.6 Project Participants

The atlas form of carrying out bird censuses is more labour-intensive than the traditional descriptive form as it requires complete coverage of the area to be surveyed. Hence a large number of field workers are needed for gathering basic data. But the advantage is that this collective work could be done according to a standardised methodology passed on to participants in fairly simple instructions.

The **features specific to urban atlases** mean that such projects are admirably suited to the involvement of volunteer observers:

- In most towns and cities, there are usually groups of birdwatchers who are familiar with the area and the local bird life. This makes it easy to recruit volunteers for the project, for whom such participation brings satisfaction and the opportunity to widen their ornithological experience.
- The impoverished avifauna in the urban landscape also makes it easier to carry out such a project. Likewise, since the study area is "close to home" and is usually smaller than one that has to be covered for a regional atlas, the fieldwork can be more intensive but less costly.
- In urban areas people and the media usually show a greater interest in their local bird life. This factor stimulates such projects and improves the chances of obtaining funding for them. It also contributes to the popularisation of ornithology and raises the awareness of nature among the local community.

The **number of participants** in bird atlas projects was not always proportional to the area to be covered. For example, only 40 recorders did the fieldwork for the extensive area of Berlin—892 km^2 (Otto and Witt 2002), while 130 worked in the much smaller area covered for the Brussels atlas—162 km^2 (Rabosee et al. 1995).

Large numbers of observers also took part in the fieldwork for the atlases of Prague ($532 km^2$)—154 participants, Venice ($414 km^2$)—155 (M. Dinetti in litt. 2014), Amsterdam ($432 km^2$)—103 and Hamburg ($747 km^2$)—89. The number of observers was the largest in the case of the Moscow ($972 km^2$) atlas (2014): here, 313 people supplied data, 112 of whom carried out standardised field censuses in the grid cells. Only in a few cases was the fieldwork done by one or a few authors of the atlas, usually professional ornithologists, as in Sofia, Olsztyn and Przemyśl. The largest area of such "elite" fieldwork was St. Petersburg (ca $500 km^2$), where the records were gathered by a dozen or so fieldworkers. For the Voronezh atlas ($189 km^2$), the basic fieldwork was done by just 11 observers, but records were accepted from some 400 people.

11.7   The Use of Urban Ornithological Atlases

In Italy, Poland and Germany, the atlas form is currently the most common means of describing of avifauna of cities. In a review of 270 such atlases from the worldwide ornithological literature, Dunn and Weston (2008) mention as many as 15 ways of applying the information they contain. Authors above in their assessment of 97 publications generated from atlases in Britain and Ireland, Southern Africa and Australia indicated that majority of considered papers concerned distribution of birds (27 %), planning and land management (27 %) and ecology (21 %). In Europe examples of use of atlases as a source of data for faunistic and ecological analyses of an urban avifauna are works of Ferenc et al. (2014), Herrando et al. (2012, 2016), Murgui (2009) or Witt et al. (2005), and in the global scale—the work of Aronson et al. (2014). In spite of those examples, Dunn and Weston (2008) conclude that "…atlas data seem underutilised". Similarly, Murgui (2009) claimed that "…the potential of studies mapping the distribution of birds in cities probably has not fully developed".

The **significance and applications** of urban bird atlases, especially in comparison with the traditional descriptive approach, are mainly justified by the following arguments:

- Such atlases are scientific documents of the bird life of a town/city; they ensure complete coverage of the area to be surveyed and better comparability of data over time (in monitoring programmes) and in relation to different areas.
- Compared to the descriptive approach, atlases present the relevant information in a more transparent, concise form, which is readily comprehensible to a reader unfamiliar with the language they are written in.
- They are a source of data for knowledge of specific ecological and behavioural relationships of birds in an urban setting, e.g. the synurbisation (Luniak 2009) of urban populations, and the changes they are subject to. Such information is more difficult if not impossible to obtain from regional atlases, in which the town/city makes up just a small part of the area explored.

- They provide information for urban planning and other applications in an administratively friendly form.
- They activate and integrate the local birdwatching community and enhance the ornithological expertise of its members.
- They contribute to nature education and increase the awareness of birds among the inhabitants of an urban area, its administrators and the media. In cities there is a special need for data on its birdlife in a form friendly to town planning and the popularisation of ornithology.

It is why an atlas form should be recommended for works describing composition and distribution of the avifauna of urban areas.

The **drawbacks of the atlas form**, compared to the traditional descriptive approach, are that it requires a greater intensity of fieldwork in order to achieve complete coverage of the study area, specialist data processing and a greater financial outlay for printing the maps. In the case of an urban atlas, however, these difficulties should be easier to surmount, since local sponsors are more likely to support a local undertaking; the costs of the fieldwork will be lower, too.

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Part IV
Anthropogenic Factors

Chapter 12
Pollutants in Urbanized Areas: Direct and Indirect Effects on Bird Populations

Jaana Kekkonen

Abstract Industrialization, traffic, intensification of agriculture, and development of human lifestyle in general during the last century have resulted in elevated levels of various chemical compounds in our environment. Especially in urbanized areas, harmful substances are produced in such quantities that they can have a deleterious effect on the development, survival, and reproduction of organisms. Many bird species have adapted to living alongside with humans and even discovered new resources within the urban lifestyle. However, these birds are in greatest risk of being harmfully effected by various chemicals.

This chapter reviews the effects of heavy metals and organic pollutants on avian populations in urban areas. Case studies are brought together in order to gain comprehension on how well we understand the role of these pollutants as factor influencing the well-being of urban bird populations. The examples highlight the fact that pollutants do not have only direct physiological effects but also indirect effects through, e.g., decreased food availability. As populations of many urban bird species are declining, new research developments for pollution studies are also proposed.

Keywords Pollution • Heavy metals • Organic compounds • Biomonitoring

12.1 Introduction

Industrialization, traffic, intensification of farming, and development of human lifestyle in general during the last century have resulted in elevated levels of various chemical compounds in our environment (Candelone et al. 1995). As humans alter the environment drastically, other species are also affected and need to adapt to the potentially deteriorating conditions. Especially in urbanized areas, harmful substances are produced from traffic, housing, energy production, construction, and production of goods in such quantities that they can have deleterious effects on the development, survival, and reproduction of organisms. This has become a

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particularly large-scale problem given that more than half of the world's human population now lives in urban areas with a projected 68 % (6.3 billion people) expected to live in cities by 2050 (World Urbanization Prospects 2012). Organisms that have become closely associated to human housing are at greatest risk of being affected. Bird populations in urban environments represent upper trophy levels of food chains consuming both plants and other animals. Thus, as many pollutants bioaccumulate as they pass between the trophy levels, birds are likely being affected both directly and indirectly by pollutants (Burger 1993; Furness and Greenwood 1993). Harmful substances can, for instance, reduce breeding performance (reduced fertility, hatching failure), delay growth and development, cause damages in organs, and in the end hamper survival (Romanowski et al. 1991; Burger 1993; Janssens et al. 2003; Eeva et al. 2009). On the other hand, pollutants also decrease the availability of, for example, invertebrates that the urban birds feed on (McIntyre 2000). Urbanization has therefore created opportunities and new living environments for bird species but, on the other hand, also deteriorating conditions and challenges. As many bird species nowadays have declining trends (BirdLife International), the role of pollution should also be considered (see also Macías-García et al. 2016).

Pollution in this chapter is defined as chemicals produced by human activities into the environment. In urban environments, also light and noise pollution are growing concerns (Fuller et al. 2007; Barber et al. 2010; Kempenaers et al. 2010; Dominoni 2016). The scope here, however, is on chemicals because they already form a highly problematic issue. The two main groups of pollutants studied in birds are heavy metals and organic pollutants. Since the beginning of industrialization, their amounts have increased almost exponentially in the urban habitats (Candelone et al. 1995). Even though many regulations and cleaner production techniques have helped to regulate and even decrease some of their amounts these days, the ever growing human population and its demands make it difficult to stay on top of the situation (Järup 2003). Pollutants which have already been banned over the years remain problematic due to their persistent nature, and they tend to stay in the environment for very long times (Beyer et al. 1996; Agarval 2009). Thus, studies on how the pollutants accumulate in food chains, how they affect different development stages of urban birds, and, in the end, population demographics are needed to evaluate for potential conservation actions.

For these reasons, it is very important to conduct research not only in laboratory conditions but on wild populations (cf. Burger and Gochfeld 1997). Environmental pollution has without a doubt a role in the declines of many bird species, but it is not always easy to demonstrate the causal relationships as there are many other factors affecting simultaneously in urban environments (Lepczyk and Warre 2012). In this chapter I bring together some of the case studies done in urban environments and, this way, bring forth on what is already known and what may be the gaps where more research should be focused on. I aim to present the various chemical compounds potentially found in urban environments, introduce interesting case studies of pollution-influenced urban birds, and suggest directions for future studies.

12.2 Different Pollutants

12.2.1 Heavy Metals

Heavy metals occur naturally in the environment in small quantities. However, due to human actions, excessive amounts of heavy metals have ended up in the ecosystems. Heavy metals are especially problematic for biological organisms due to their accumulative properties and persistent nature. Some of the heavy metals are even necessary to organisms as small amounts (Valko et al. 2005). For instance, copper and zinc are essential for the immune system and iron for transportation of oxygen (Percival 1998; Prasad 1998). However, other metals are biologically not needed at all (e.g., cadmium, lead, mercury, nickel, arsenic). Moreover, heavy metals can even bind to important molecules preventing biologically important processes. Since heavy metals are known to have long lasting toxic effects that will not easily biodegrade, chronic exposure can have harmful effects (Ikeda et al. 2000; Dauwe et al. 2006; Nam and Lee 2006). In some cases the damages may appear only after several years (Furness 1996).

Large proportion of heavy metal pollution is airborne. Atmospheric concentrations of heavy metals primarily result from burning of urban and industrial wastes, mining, smelting processes, gas emission from motor vehicles, and combustion of fossil fuels (Harrop et al. 1990; Mohammed et al. 2011). Heavy metal pollution is thus spread effectively both at local and regional levels. Heavy metals access water systems and soils from which they effectively accumulate in the food chains (Suedel et al. 1994; Kaminski 1995; Labare et al. 2004). The heavy metals often studied in birds are, e.g., lead, cadmium, zinc, iron, copper, and chromium.

Lead is probably the most measured one possibly because lead poisoning can have so many physiological and behavioral impacts. Physiological effects include anemia, emaciation, weakness, and poor growth and development (Franson 1996; Kaminski and Matus 1998), which all affect overall body condition and survival. Behavioral problems can include increased aggressiveness (Janssens et al. 2003) and difficulties in flying and walking (Sanderson and Bellrose 1986). Also breeding can be affected from lowered ability to attract a mate, build a nest, and adequately feed nestlings (De Francisco et al. 2003). Previously, one of the main sources of lead pollution was leaded fuel, but since the 1970s, most of the industrialized countries have restricted the use of lead additives in motor fuels (Ancillotti and Fattore 1998). As a result, the amount of atmospheric lead has reduced significantly, but the lead residues have persisted in the soils. Moreover, lead is still produced as a by-product in several industries like ore and metal processing, piston-engine aircraft operating on leaded aviation gasoline, glass and chemical industries, and energy production (Agarval 2009).

Cadmium poisoning in birds can cause growth retardation, anemia, and testicular damage as well as renal failure which affects the calcium balance causing proteinuria and bone decalcification (Larison et al. 2000). Cadmium pollution comes

mainly from enrichment of zinc and steel industry and energy production (Agarval 2009).

Birds can regulate *zinc* effectively within a wide range of exposure. However, when the exposure is too high, they exhibit symptoms like abnormalities in their exocrine pancreas and decreased motor function (Zdziarski et al. 1994). The main sources of zinc pollution these days are energy production, traffic, and metal industry (Agarval 2009).

Physiological signs of *copper* toxicosis include weakness, anemia, and decreased egg production, body and tissue weight, and feather growth (Stohs and Bagchi 1995; Isanhart et al. 2011). Sources of copper include, e.g., copper sulfate, antifouling paints, mining and metal industries, and coal-using power plants (Christian Franson et al. 2012).

When accumulated in tissues, *iron* can increase hemosiderosis, i.e., iron deposits in local tissues (Cork 2000). Most important sources of iron pollution are iron and steel industries (Agarval 2009).

High levels of *chromium* can cause altered growth patterns and reduction in survival. Moreover, there can be mutagenic, teratogenic, and carcinogenic effects (Eisler 2000). Phosphate fertilizers, industrial and sewage wastes, landfill dumping chromium-containing consumer products, and atmospheric emissions are main sources of chromium pollution (Fishbein 1981; Outridge and Scheuhammer 1993).

There are many studies which measure the amounts of heavy metals in birds in urban habitats and compare them to birds from rural habitats. However, it is not always easy to show which levels result in deteriorated survival or reproduction and, moreover, population declines. However, as the amount of studies increases, these causality relationships can be determined more easily. Moreover, in urban habitats when the amount of one heavy metal is increased, often also other heavy metals are more pronounced. Thus, there are cumulative effects which may not be easy to measure but surely affect the well-being of organisms living in the cities.

12.2.2   Organic Compounds

Organic compounds are produced in immense varieties by human housing, industrial processes, and the production of a range of goods (Harrad 2009). Some of the compounds are harmful already in small amounts, but at least excess amounts make many of these compounds harmful to living organisms. The pathways and effects of these contaminants in ecosystem level are not well known. However, some more recent studies also on bird populations are shedding light into these important issues since these compounds are being produced increasingly especially in urban environments (Beyer et al. 1996).

Of particular interest is the chemical group of organohalogens, which constitutes of thousands of compounds. Interestingly, some of them occur naturally in the environment. However, the artificially excessively produced compounds have become problematic in the nature. The occurrence of organohalogen pollutants

has been of great concern because of their persistent, lipophilic properties, bioaccumulative nature, capability of long-distance transportation, and adverse effects on variety of different taxa (Beyer et al. 1996; Yu et al. 2014). Thus, we need to be concerned of both humans and wildlife sharing the urban environments. The use of some of these persistent organic pollutants (POPs) has been restricted by international treaties. For example, the Stockholm Convention (United Nations Environment Programme 2001) had 179 countries to agree to restrict and/or eliminate the production and use of the compounds classified as POPs as well as to study and potentially list new ones. However, many of the already restricted pollutants will still persist for a long time in the environment. Moreover, other compounds are still being produced, and thus information on their effects is needed.

The organic pollutants mostly studied in birds include pesticides and herbicides like aldrin, dieldrin, endrin, hexachlorobenzenes (HCBs), hexachlorocyclohexanes (HCHs), mirex, chlordanes (CHLs), and dichlorodiphenyltrichloroethane (DDTs) and its metabolites, heptachlors, and toxaphenes (Beyer et al. 1996). Moreover, chemicals like polychlorinated biphenyl (PCB), polybrominated diphenyl ether (PBDE), and hexabromocyclododecanes (HBCDs) are used, for example, as solvents, synthetic polymers, flame retardants, insulants, and intermediates in the preparation of dyes and pharmaceuticals (Hale et al. 2006; Marvin et al. 2011).

The harmful effects of these organic compounds are often related to reproduction in birds. DDT through its metabolite DDE causes thinning of eggshells by inhibiting calcium metabolism. The eggs break more easily and embryo mortality increases. Moreover, DDTs are involved in reproductive impairment and affect thyroid hormones, i.e., metabolic activity (Ratcliffe 1967; Hickey and Anderson 1968; Fry 1995). PCBs reduce clutch sizes, lower hatching and fledgling rates, and cause hormonal disruptions as well as embryonic and offspring abnormalities. Thus, increased levels of PCBs reduce the overall reproductive success of birds (Fry 1995; Fernie et al. 2001).

PBDEs can affect the birds to delay the timing of reproduction, lead to fewer copulations, cause longer egg-laying intervals, and reduce clutch sizes. Birds may lay smaller eggs which have reduced fertility (Marteinson et al. 2010; Winter et al. 2013). HBCDs affect hormonal levels like increasing testosterone and reducing thyroxine levels. Birds affected by HBCDs also present less active courtship, produce eggs with reduced mass, have lower incubation temperatures, and may present less active parenting behavior (Marteinson et al. 2010, 2012).

One of the first and most famous examples of harmful effects on birds is the discovery of relationship between introduction of DDT as a pesticide and the thinning of eggshells of birds of prey. This was linked to decreased reproductive success (Ratcliffe 1967; Hickey and Anderson 1968). These types of studies showed such clear causalities between organic compounds and deleterious effects that they have contributed in banning the use of those compounds. However, there are so many others produced and new ones developed from which the effects in different trophy levels are not fully known and that these types of studies are needed to fill the gaps that exist now.

12.3   Sampling and Analysis Methods

Sampling designs vary between studies depending on the questions asked, the geographical scale covered, and the type of samples aimed for. As birds are capable of moving distances exceeding urban boundaries, the source of the pollution is not always easy to pinpoint (i.e., point-source pollution like a factory). On the other hand, the interest may not even be on the particular source but measuring the general pollution level in the environment. However, in all studies, there needs to be some type of references for the measured levels of pollutants in the birds. These can be, for example, references measured from laboratory animals (e.g., Beyer et al. 1996; Burger and Gochfeld 1997). Many studies also use comparisons between samples from urban and rural sites (Table 12.1). Thus, I would like to stress that when sampling of any pollution-related study is designed, these issues need to be considered carefully so that the samples gained best describe the issues the researchers wish to address.

Moreover, pollutants can be analyzed in many types of samples from birds depending on the research questions. First of all, sampling can be done on dead or live birds and, secondly, on different development stages, i.e., eggs, nestlings, or adults. The potential differences between sexes in adult birds need to be taken into account as well (Burger and Gochfeld 1992; Eeva et al. 2009). Eeva et al. (2009) suggested that due to their higher reproductive effort, females might be more susceptible to the negative health effects of pollution stress. Another possible reason would be that because of differences in dispersal, sexes would have experienced different environments as young. Also ages need to be taken into account in adult birds as we did, for example, in Kekkonen et al. (2012).

Tissues that are most interesting for pollution studies are the liver, kidney, lungs, and blood. Blood samples can be taken from live birds. However, the pollutant levels in blood are considered to generally reflect more recent exposure (Furness and Greenwood 1993). The intestine organs represent a longer term accumulation and thus can present different information. However, noninvasive sampling is increasingly done by determining pollution levels also from the feathers of birds (Jaspers et al. 2007). Birds can reduce their body burden of toxic substances by excretion in their feathers (Dauwe et al. 2000; Dauwe et al. 2003). Pollution levels in feathers reflect the conditions and diet during the period of feather growth, when the feather is connected to the body with blood vessels. Feathers grow for few weeks and thus they represent longer term pollution levels than blood samples (Furness and Greenwood 1993). When birds are molding, they tend to stay in a confined area, and thus, feather pollution levels also represent quite local pollution (Fasola et al. 1998; Burger et al. 2007).

Very interesting information is also gained by linking nestling growth rates, survival, and potential deformities to amounts of pollutants. Developing organisms have a potentially elevated susceptibility to pollution compared to adults. Eggs can also be sampled for levels of pollution because females sequester pollutants into them (Gochfeld 1997; Fasola et al. 1998). Concentrations in eggs typically reflect

Table 12.1 Pollutant levels measured in birds in urban and rural habitats

Pollutant	Measured from (unit)	Concentration urban	Concentration	Significance	Problematic level	Other results	References
Lead							
Gray catbird	Blood (ppm = µg/g wet weight)	0.09	0.01	<0.05	0.2 poisoning, 0.5 sub-lethal (15, 16)		1.
Gray catbird (nestling)	Blood (ppm)	0.10	0.01	0.001		Neg linked to body condition	1.
American robin	Blood (ppm)	0.26	0.08	<0.05			1.
Northern cardinal	Blood (ppm)	0.11	0.29	<0.05			1.
Northern mockingbird	Blood (ppm)	0.19	0.01	<0.05			1.
House sparrow	Blood (ppm)	0.15	0.02	<0.05			1.
Song sparrow	Blood (ppm)	0.05	0.02	<0.05			1.
Carolina wren	Blood (ppm)	0.07	0.03	Non-sign			1.
Blackbird	Blood (ppm)	0.15	0.05	<0.05	0.2 poisoning, 0.5 sublethal	Earthworms higher Pb in urban	2.
House sparrow	Liver (µg/g dry weight)	0.54	0.10		20.0 indicate toxicosis (17)	Potential link to pop declines	3.
House sparrow	Liver (µg/g dry weight)	37.60	18.00		20.0 indicate toxicosis		4.
House sparrow	Liver (µg/g dry weight)	3.70	2.70		20.0 indicate toxicosis		5.
Feral pigeon	Liver (µg/g wet weight)	2.30	1.80	<0.05	20.0 indicate toxicosis	Urban nestlings a bit smaller	6.
	Kidney (µg/g wet weight)	4.10	3.00	<0.05			

(continued)

Table 12.1 (continued)

Pollutant	Measured from (unit)	Concentration urban	Concentration	Significance	Problematic level	Other results	References
	Bone (µg/g wet weight)	30.00	11.00	<0.05			
	Egg (µg/g wet weight)	1.60	1.10	<0.05			
Rook	Egg (ppm)	4.11	2.90	<0.05			7.
House wren	Feather (ppb → ppm)	~0.70	~4.00	<0.001	4 ppm (18)		8.
White stork (nestling)	Blood (µg/L)	0.11	0.02	<0.001			9.
Cadmium							
Feral pigeon	Kidney (µg/g wet weight)	1.10	0.43	<0.05	2.0 exposure, >100 toxic (19, 20)		6.
House sparrow	Liver (µg/g dry weight)	0.16	0.09		3.0 exposure, >100 toxic	Potential link to pop declines	3.
House sparrow	Liver (µg/g dry weight)	0.07	0.07		3.0 exposure, >100 toxic		4.
House sparrow	Liver (µg/g dry weight)	1.31	0.48		3.0 exposure, >100 toxic		5.
Copper							
House sparrow	Liver (µg/g dry weight)	4.03	3.69			Potential link to pop declines	3.
House sparrow	Liver (µg/g dry weight)	38.20	27.00				4.
House sparrow	Liver (µg/g dry weight)	42.00	61.80				5.
House wren	Feather (ppb → ppm)	~6.50	~4.50				8.

						Potential link to pop declines	
Zinc							
House sparrow	Liver (μg/g dry weight)	21.10	18.40			Potential link to pop declines	3.
House sparrow	Liver (μg/g dry weight)	121.00	97.00				4.
House sparrow	Liver (μg/g dry weight)	205.00	154.00				5.
House wren	Feather (ppb → ppm)	~160.00	~150.00				8.
Iron							
White stork (nestling)	Blood (μg/L)	386.90	269.60				9.
House wren	Feather (ppb → ppm)	~370.00	~60.00				8.
Chromium							
House wren	Feather (ppb → ppm)	~1.20	~0.30				8.
DDTs							
Eurasian tree sparrow	Muscle (ng/g)	92.00	150–1400				10.
Little egret	Egg (ng/g)	1170–40,200	4320–11,400			Comparably high DDT	11.
pp'-DDE							
Peregrine falcon	Egg (ng/g)	4040–12,400	1380–3930	Nonsign	2800 (ng/g) (21)		12.
Eurasian dipper	Egg (ng/g)	2541	1085		2800 (ng/g)		13.
PCBs							
Eurasian tree sparrow	Muscle (ng/g)	44.00	59–88.00				10.
Peregrine falcon	Egg (ng/g)	4910–12,500	3250–12,800	Nonsign			12.

(continued)

Table 12.1 (continued)

Pollutant	Measured from (unit)	Concentration urban	Concentration	Significance	Problematic level	Other results	References
Eurasian dipper	Egg (ng/g)	946.00	2491.00	<0.0001		High for passerine eggs	13.
PBDEs							
Eurasian tree sparrow	Muscle (ng/g)	28.00	32–250				10.
Peregrine falcon	Egg (ng/g)	32.80	126–354	Nonsign			12.
Eurasian dipper	Egg (ng/g)	387.00	1714.00	0.0002		High for passerine eggs	13.
HBCDs							
Eurasian tree sparrow	Muscle (ng/g)	2.8–51	Not detected				10.
Light-vented bulbul	Muscle (ng/g)	15.0	2.8			Diet differences between species	14.
Long-tailed shrike	Muscle (ng/g)	8.6	–			Diet differences between species	14.
Oriental magpie-robin	Muscle (ng/g)	16.0	380.0			Diet differences between species	14.

The reference for each study is given as numbers. Harmful levels of toxicity are given if there are known examples from the literature which can be used as indicative value. However, because these levels are from the same tissue but most often from different species, they are merely indicative and should be considered with great caution. The reference for the clinical value is given in parenthesis

References: 1. Roux and Marra (2007), 2. Scheifler et al. (2006), 3. Kekkonen et al. (2012), 4. Swaileh and Sansur (2006), 5. Gragnaniello et al. (2001), 6. Nam and Lee (2006), 7. Orłowski et al. (2014), 8. Hofer et al. (2001), 9, De la Casa-Resino et al. (2014), 10. Yu et al. (2014), 11. Lam et al. (2008), 12. Potter et al. (2009), 13. Morrissey et al. (2013), 14. Sun et al. (2013), 15. De Francisco et al. (2003), 16. Sanderson and Bellrose (1986), 17. Shealy et al. (1982), 18. Burger and Gochfeld (2000), 19. Scheuhammer (1987), 20. Larison et al. (2000), 21. Lam et al. (2008)

both circulating levels of contaminants in the blood as well as the stored reserves of the females at the time of egg formation (Burger and Gochfeld 1996).

There is great variety of laboratory analysis methods to determine the levels of different pollutants in different sample types. Whichever procedure is used, it should be properly executed following certified protocols and laboratory conditions. For heavy metals, in many cases so-called EPA methods are used (US Environmental Protection Agency test methods) or other approved procedures for chemical pollutants. After careful preparations, the concentrations are most often measured using a type of mass spectrometry. Laboratory reagent blanks, metals standard reference material, and replicate samples should be analyzed with every batch of samples. For organic pollutants, the laboratory analyses are compound specific, but in each case a certified protocol and conditions should be also used. In a recent review, Tang (2013) covered recent developments in sample preparation, separation, and detection in analysis of persistent organic pollutants under the Stockholm Convention. This review provides good guidelines for future studies, but as main points (a) gas chromatography is still a prominent chromatographic technique for nonpolar POPs, and (b) mass spectrometry is prevailing in sensitive, selective detection in POPs measurement (Tang 2013). Based on clinical laboratory studies, there are benchmark values for the harmful levels for some of the substances in the tissues. However, these levels depend very much on the species and developmental stage, and thus these are not available for all case studies (some presented in Table 12.1).

12.4 Different Effects Found in Bird Studies

Chemical pollutants can have an impact on body condition, behavior, survival, breeding performance, and even DNA of avian fauna. Based on my literature search, I present here some of the intriguing case studies to demonstrate the variety of effects and, on the other hand, the challenges within the research field of urban birds facing environmental pollution.

12.4.1 Pollutant Levels Discovered in Urban vs. Rural Adult Birds

Based on the literature search, most of the studies have measured the levels of different pollutants in different tissues of the birds, and either compared the results to levels found from other studies or to benchmark values that relate to subclinical, clinical, or lethal effects (Franson 1996; Pain 1996; Friend and Franson 1999). Further, several studies have done comparisons between urban and rural sites. These studies give very important information on what are the actual levels that

the birds have to deal with in the urban habitats and whether these levels could be harmful for individuals' survival or reproduction. This helps to evaluate whether there could be consequences for population level demographies.

In an interesting study linking body condition and lead pollution, Roux and Marra (2007) measured lead concentrations in blood samples of seven passerine species in urban and rural environments. They used both adults and nestlings and assessed their body condition based on body mass in relation to length. They determined soil lead concentrations on rural to urban gradient in the Washington DC study area. Expectedly, the soil lead concentration was significantly higher in urban sites compared to rural ones. Accordingly, urban adult and nestling birds had significantly higher blood lead concentrations than rural ones. Interestingly, ground-feeding birds had higher differences between urban and rural birds than canopy/shrub feeding species. However, from the seven passerine species studied, only gray catbird *Dumetella carolinensis* nestlings were found to have lower body condition due to lead contamination. The levels of lead in adult urban birds of all species ranged between 0.01 and 0.08 ppm in rural sites and between 0.07 and 0.26 ppm in urban sites. In general, the level of blood lead considered as lead poisoning is confirmed at 0.2 ppm and above (De Francisco et al. 2003) and sublethal at 0.5 ppm (Sanderson and Bellrose 1986). Here, despite urban birds were found to have blood lead concentrations at and above the 0.2 ppm benchmark value, no negative impact on body condition was found in adults. Birds may be able to remove pollutants by excreting them throught vascular system or into feathers. Moreover, e.g., protein- or calcium-rich diets can reduce the absorption of lead (Sanderson and Bellrose 1986). With nestling birds, however, gray catbirds with higher blood lead concentrations were also found to be in poor physical condition.

Lead concentrations were measured also in a study on blackbirds *Turdus merula* and one of their main prey, earthworms (Scheifler et al. 2006). Sampling was done in Besançon, France, and in a rural reference site. Blood samples, washed and unwashed outermost tail feathers and breast feathers were collected from the blackbirds. Individual body condition index was determined based on body mass and tarsus length. Results showed that the lead concentrations in earthworms were significantly higher in urban individuals than in rural ones. Moreover, concentrations in outermost tail feathers, breast feathers, and blood were significantly higher in urban than rural blackbirds. The use of washed and unwashed outermost tail feathers allowed estimating the external contamination from, e.g., dust as opposed to internal contamination. The result was that 37 % of the total lead concentration was from external sources and the remaining 63 % can be linked to food chain. The blood concentrations in urban blackbirds were on average 0.15 ppm which is similar than what was found by Roux and Marra (2007). As the benchmark value of 0.20 ppm for subclinical and physiological effects was not exceeded, it was not so surprising that body condition did not vary with lead concentration. Nevertheless, this study shows that even though the atmospheric lead emissions have been reduced dramatically globally, urban birds remain exposed to lead pollution. Moreover, food transfer from soil invertebrates may be an important route of lead exposure.

The causal relationships between pollutants and urban bird populations may indeed be quite complex, and the indirect effects of the pollutants should be also considered. In a previous study, I and my collaborators studied levels of eight heavy metals in house sparrows *Passer domesticus* in urban and rural habitats in Finland (Kekkonen et al. 2012). The house sparrow has declined >60 % during the last couple of decades. One suggested reason for this decline (especially in cities) is heavy metal pollution. A museum collection from the 1980s was used to investigate the accumulation of heavy metals (Al, Cr, Mn, Fe, Cu, Zn, Cd, Pb) in the livers of these birds. Significantly higher heavy metal concentrations were found in the livers of urban than rural birds which could support this hypothesis. Heavy metal levels in urban birds were, however, not as high as in other house sparrow studies by, e.g., Gragnaniello et al. (2001) and Swaileh and Sansur (2006). Nevertheless, in their study in the area of West Bank, Swaileh and Sansur (2006) found also clearly more copper, lead, and zinc in the organs and tissues in house sparrows from urban areas. When considering the Finnish house sparrow, the heavy metal pollution is unlikely to be a sole cause of the severe declines. However, pollution is more pronounced in cities and could thus contribute to declines through indirect effects, such as insect availability, as shown for the house sparrow in Leicester, UK (Vincent 2005; Peach et al. 2008). Along with other environmental factors, heavy metals decrease the amount of some invertebrate groups in cities (Pimentel 1994; McIntyre 2000) that are used as nestling food in many bird species. Vincent (2005) found annual productivity (the number of fledged young) to be lower in urban areas due to starvation of chicks when their diet contained a high proportion of vegetable material or ants instead of, e.g., spiders. Moreover, Peach et al. (2008) reported that years of poor reproduction were characterized by, e.g., high concentration of air pollution from traffic.

Besides the heavy metal studies, information is increasing on organic pollutants and urban birds. For example, Sun et al. (2013) linked diet and concentrations of hexabromocyclododecane (HBCD) and its enantiomeric distributions on passerines. These chemical compounds were determined in muscle and stomach contents of three terrestrial birds from e-waste (electrical waste) and urban and rural locations in South China. The study species light-vented bulbul *Pycnonotus sinensis*, long-tailed shrike *Lanius schach*, and oriental magpie-robin *Copsychus saularis* are all resident birds which have quite small-scale territories and foraging areas, making them interesting for bioindicator monitoring of local pollution. Urbanization and industrialization were found to relate to levels of HBCD. In turn, birds from the rural site had the lowest concentrations of HBCD, urban site the highest, and e-waste site the second highest. The diet seemed to be the most important pollutant source for the birds. Moreover, the concentrations of HBCD were highest in the oriental magpie-robin in all habitats which could indicate differences in their diet. The oriental magpie-robins often feed in urban gardens and cultivated areas which are likely more polluted by HBCD.

Yu et al. (2014) also studied contamination of organohalogen pollutants, including DDT and its metabolites, PCBs, PBDEs, decabromodiphenylethane (DBDPE), hexabromocyclododecanes (HBCDs), and dechlorane plus (DP) in Eurasian tree

sparrows *Passer montanus* and common magpie *Pica pica*. They had three metropolises of China (Beijing, Wuhan, and Guangzhou) and a reference rural site. The results were very similar to Sun et al. (2013), i.e., levels of the organohalogen pollutants were in general lower in the reference site than in the urban sites. There were some differences between the urban area concentrations in the muscle samples. The levels of DDTs were higher in Wuhan, whereas flame retardants dominated in Guangzhou and Beijing. PCBs exhibited different homologue profiles among different sites which is a likely result of different dietary sources of the bird species. In general, PCB concentrations were at the low end of worldwide figures which was not unexpected because PCBs are not used as much in China as in other parts of the Northern Hemisphere. PBDE levels, however, were in the same range as those of North America, and generally higher than in Europe.

Based on these examples, markedly increased levels of pollutants have been found from urban birds compared to rural ones in many studies and different taxa. In some cases, a link to the diet was established, and possible deteriorating effects could be evaluated based on benchmark values. However, I consider that more research on testing the effects on individual condition, survival, and breeding parameters could be done. Even though a direct causal relationship to population declines has not been established in many cases so far, all of the research done so far are important pieces adding up to growing knowledge. When considering environmental pollution, it is very important to remember that there are likely combined effects which need to be taken into account. This means that environmental, population demographic or other anthropogenic factors might interplay with the effects of pollutants.

12.5 Effects of Pollution on Eggs and Nestling Stages in Urban Areas

Earlier developmental stages of organisms may be more vulnerable to environmental effects and thus give different points of view also on pollution studies. Egg characteristics such as egg size and eggshell thickness were the early signs of detrimental effects of pollution on reproduction, growth, and nestling survival of birds (Ratcliffe 1967; Bize et al. 2002). Both egg and nestling stages have been studied in urban birds, and their importance in monitoring bioaccumulation of contaminants in the human-inhabited environment has been quite well established.

Orłowski et al. (2014) studied the concentrations of chromium, nickel, cadmium, and lead in rook *Corvus frugilegus* eggshells from rural and urban areas of western Poland. They found that eggshells in large industrial cities had significantly higher concentrations of chromium, nickel, and lead than crook egg shells collected from small towns and villages. They highlighted the importance of taking into account also local habitat effects when considering population declines. In another heavy metal study, Nam and Lee (2006) investigated the heavy metal accumulation on

breeding feral pigeons *Columba livia* in South Korea. They compared the egg size, eggshell thickness, and reproductive parameters in colonies from cities of Seoul and Ansan and found that the concentrations of lead in the bone and cadmium in the kidney of adult pigeons in Seoul were three times higher than in Ansan colony. No significant differences were, however, observed in egg characteristics, clutch size, incubation periods, or hatchability of eggs between the two study sites. Body size measurements of nestlings from Seoul were somewhat smaller, but the difference was not statistically significant. Nestlings at Seoul fledged significantly later and with a lower success than in Ansan. As Seoul is more polluted than Ansan, these results indicate that heavy metal pollution may have negative effects on feral pigeon breeding.

Organohalogen compounds were measured in urban birds of prey in two studies by Dell'Omo et al. (2008) and Potter et al. (2009). In both cases the eggs contained organohalogen pollutants but the effects on, for example, population level are unclear. Dell'Omo et al. (2008) studied PCBs and DDTs in Eurasian kestrel *Falco tinnunculus* eggs in Rome, Italy. Organohalogen congeners were determined from 27 unhatched eggs in years 1999 and 2005. The authors concluded that the concentrations were not so high as compared to other kestrel study from earlier period, and as the animals in the study area do not perform long migratory movements, the contamination levels in the eggs are likely to present local pollution levels. Potter et al. (2009) measured also organohalogen concentrations in 23 eggs of the peregrine falcon *Falco peregrinus*. These eggs were obtained between 1993 and 2002 from 11 locations in the Chesapeake Bay region, USA. Different congeners of PBDE and PCB as well as PBB153 and 4,4'-DDE were measured. In general, the levels or organohalogen compounds detected were similar to other birds of prey studies in Europe and the USA (Potter et al. 2009). When considering the habitat effect, only BDE 209 concentrations were significantly correlated with the human population density of the area surrounding the nest. The authors considered that urban falcons may feed on prey which has less of the last mentioned compounds than their rural counterparts but the mechanism for this is not clear.

On contrary, as Lam et al. (2008) measured a great variety of organohalogen compounds (aldrin, dieldrin, endrin, hexachlorobenzene, mirex, chlordanes, DDTs, heptachlors, toxaphenes, PCBs, PBDEs, dioxin-like equivalents (TEQH4IIEluc)) in eggs of the little egret *Egretta garzetta* and black-crowned night heron *Nycticorax nycticorax*, they found some physiologically significant levels of pollutants. The study was done in three Chinese harbor cities: Hong Kong, Xiamen, and Quanzhou. Concentrations of DDTs, PCBs, and chlordanes were significantly greater than concentrations of other residues, and all in all DDTs were found to be most abundant. The high levels of these compounds indicate that they pose likely physiological health risks to the study populations.

Organohalogen compounds were also studied in the eggs of a river passerine, the Eurasian dipper *Cinclus cinclus* (Morrissey et al. 2013). Among other pollutants, compounds like PCBs and PBDEs are ending up into the urban streams and from there secreted by female birds to the eggs. Morrissey et al. (2013) sampled dipper eggs from 33 rural and urban rivers in South Wales and the English borders and

found that concentrations of both total PCBs and PBDEs were positively related to urbanization, whereas organochlorine pesticides such as *p,p′*-DDE, lindane, and hexachlorobenzene were found in higher concentrations at rural sites. Levels of PBDEs in urban dipper eggs were among the highest ever reported in passerines, and some pollutant levels were even sufficient for causing adverse effects on development. In another study, Morrissey et al. (2014) studied also dipper nestlings for early development in respect to the same pollutants. They measured breeding performance, as well as nestling growth, condition, and plasma thyroid hormones in 87 nests on urban and rural streams. They collected also invertebrate prey data for knowledge on potential food scarcity. Interestingly, clutch sizes and egg fertility were similar in both habitats and nest success was even higher at urban sites (food abundance was not reduced). However, urban nestlings were significantly lighter than rural ones, and brood sex ratios were increasingly male biased. In addition, increased amounts of PCBs and PBDEs in urban sites were found to be linked to reduced levels of thyroid hormones (T3) and poorer body condition. The authors concluded that pollutant levels recorded from urban streams could have detrimental effects on dipper nestling development.

These case studies show how studies on egg and nestling stages complement the knowledge gained from monitoring bioaccumulation of pollutants in adult birds.

12.6 Interaction Between Pollutants and Pathogens in Urban Birds

It has been noted that pollutants can affect epidemiology of wildlife diseases, but the studies in this field have focused so far more on the function of immune systems. Interestingly, pollutants can also potentially affect ecological interactions between species like hosts and their pathogens or parasites. This approach was taken by Gasparini et al. (2014) on Parisian pigeons *Columba livia*, who found that heavy metals can indeed affect the epidemiology of diseases especially in the urban environment. They used feathers of the pigeons to measure concentrations of copper, cadmium, lead, and zinc. Moreover, they did cloacal swabs from the pigeons to estimate prevalence and intensity of the parasite *Chlamydiaceae* and blood smears to estimate the prevalence and intensity of haemosporidian parasites. The study revealed that copper or cadmium levels in the feathers were not correlated with parasites, but elevated levels of zinc were associated with both low prevalence of *Chlamydiaceae* (ornithosis disease) and low intensity of *Haemosporidian* parasites. However, high concentrations of lead in the feathers were linked to high blood pathogen intensities. The interesting results from this study give indications on heavy metal pollution having a role in host-parasite interactions and encourage for further research.

12.6.1 Behavioral Effects

Direct physiological effects are most often measured in pollution studies, but there can be other types of indicators in bird populations on environmental contaminants. In an interesting study, Gorissen et al. (2005) examined the expression of dawn singing behavior in male great tits *Parus major* in relation to environmental pollution. They compared the singing behavior of the males from an area extremely polluted with heavy metals (in particular lead), with that of males from less-polluted ones. However, all the sites can be considered to be located in an urbanized environment near Antwerpen, Belgium. Males at the most polluted site had a significantly smaller repertoire size in their singing. They also produced a significantly lower total amount of song during the dawn chorus than the males at a distance of 4 km from the pollution source. Effect of age was also accounted for as older birds have a larger repertoire. These results may be linked to a lowered male quality at the polluted site. Lead pollution is known to have adverse effects to brain development (e.g., Burdette and Goldstein 1986), and this decreased ability of a male to invest in brain tissue has been suggested to be an important physiological mechanism that links singing repertoire size to male quality (Garamszegi and Eens 2004). Thus, the expression of singing behavior could potentially be a used as an indicator of environmental stress at the population level in birds. Moreover, there could be other behavioral indicators which could be used for similar purposes (Miranda 2016).

12.6.2 Effects on DNA

One of the latest developments in pollution studies with birds is the investigation of effects to DNA. Pollutants which are genotoxic cause chemical and/or physical modifications to the DNA, and this may lead to, for example, reduced fitness (through gene and protein dysfunction), tumor initiation, growth impairment, embryonic malformations, or reduced fecundity (Sadinski et al. 1995; Theodorakis 2001). Skarphedinsdottir et al. (2010) studied adult and young herring gulls *Larus argentatus* in Sweden and Iceland to find out whether there is a link between polycyclic aromatic hydrocarbons (PAH) measured in nearby surface sediments and indications of genotoxic effects. They determined (a) the level of DNA adducts (piece of DNA bonded to the chemical) and (b) the frequency of micronucleated erythrocytes (red blood cells which have DNA disrupted outside nucleus). They used blood, liver, kidney, and intestinal mucosa of the gulls. The results indicated that both Swedish and Icelandic herring gulls are exposed to genotoxic pollution. Urban samples had higher levels of DNA adducts than rural ones, and also the levels of PAHs were higher in the urban sites. The frequency of micronucleated erythrocytes was slightly elevated in all the sampling sites, reflecting a significant background exposure. This study showed that the DNA adducts and potentially

micronucleated erythrocytes can be useful as biomarkers for genotoxicity in birds. However, there was no direct measurement of pollution levels in the tissues of the gulls. Nevertheless, this study provides an interesting start for future studies, and it can be used as a basis when designing next level research.

12.7   Future Directions for Studies on Urban Birds and Pollution

Based on the literature search, there is growing number of research on chemical pollution on birds in urban areas. However, as the study cases presented here show, there are still many unanswered questions regarding the potential role and mechanisms pollutants have on survival and breeding of individuals and, in particular, how these issues may be linked to changes in population demographic level.

In order to tackle these issues more in depth, future studies in my opinion would need to combine measuring mere levels of pollutants with other types of data like body condition, survival indices, or breeding performance. These aspects need to be considered already during project planning. Secondly, when possible, data on food availability, environmental factors, population demographies, and anthropogenic factors would be good to include. This way combined effects with other factors could be mapped. Implementing many different factors is by no means easy but can provide important new insights into, e.g., declining bird species.

There are also new research developments which open possibilities in this field. Studying oxidative stress as a response to heavy metal pollution has been quite recently lifted as one very potential way also to measure effects of environmental pollutants. This response capacity of antioxidant defense plays an important role in the protection of organisms against toxic-induced oxidative stress. Indeed, the maintenance of a high antioxidant capacity in cells may increase tolerance against different types of environmental stress (reviewed by Koivula and Eeva 2010). Herrera-Dueñas et al. (2014) studied house sparrows in two differently polluted areas and found that oxidative stress markers, hemoglobin (Hb) and total antioxidant capacity (TAC), were both lower in urban populations. Analysis methods are quite well established in this field, but it has not been implemented much for urban fauna in particular. Moreover, the rapid development of genomic methods can also provide new ways to gather information on responses to environmental stress. Effects of pollutants on DNA are studied in some field examples so far (e.g., Baos et al. 2006; Eeva et al. 2006), but not too much is yet known. Some heavy metals and organohalogens are known be mutagenic, and thus in highly polluted urban environment, there might be local effects. Moreover, DNA studies can reveal it is possible to adapt to urbanization in terms of pollution and how this differs between bird species.

One important factor which comes up frequently in these studies is the suitability of birds to be used as bioindicators of environmental pollution (e.g., Cui et al. 2013;

Valladares et al. 2013). The use of avian populations as biological monitors can be an effective method in quantifying the overall health of the ecosystem since they represent the upper trophy levels. Previously, raptors were the main focus because they are in the highest level of food chains, but more often nowadays other species are acknowledged as well. As seen from the case studies in this chapter, many passerine species are of interest nowadays. Residential passerine species are especially suitable to reflect local contamination because of their small home ranges, territories, and foraging areas whereas passerines with widespread populations enable large geographical-scale monitoring (Dauwe et al. 2006; Van den Steen et al. 2009). Water fowl are also used since they indicate the pollution in water bodies (Pereda-Solís et al. 2012). Sampling designs depend on the study questions, but feathers are increasingly used as a noninvasive source of samples for biomonitoring of all sorts of pollutants (e.g., Malik and Zeb 2009; Hofer et al. 2010; Padula et al. 2010). All in all, the techniques and knowledge are available for executing multifaceted pollution studies of urbanized environments in the future.

12.8 Concluding Remarks

This chapter highlights the importance of studies on urban bird populations and the threats which are posed to them by environmental pollutants. Despite the many restrictions that have already been made for production of harmful substances, many heavy metals and persistent organic pollutants will not be phased out from the urban environment for a very long time. This is another stress factor that urban fauna needs to deal with. Moreover, new chemical compounds are being developed. Bird studies will not only help to understand the underlying mechanisms between population demographics and environmental pollutants but the results can be linked to protecting other taxa. Moreover, we humans share the urban living environment with the birds, and thus, biomonitoring them will be of great benefit for us as well. As a positive concluding remark, however, I want to end with a study from Eeva and Lehikoinen (2000). They found that after a copper smelter was closed and the side product lead decreased in the environment, the breeding success of two bird species markedly increased as a result. These types of positive examples should encourage researchers to gather in-depth data and bring forth the potential causal relationships when studying organisms in our urbanized environments.

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Chapter 13
Ecological Effects of Light Pollution: How Can We Improve Our Understanding Using Light Loggers on Individual Animals?

Davide M. Dominoni

Abstract Light pollution has become an important theme of both scientific research and policy-making. Although in recent years we have seen a boost of research on this topic, there is still surprisingly little knowledge on the levels of artificial light at night that wild animals really experience. I made use of miniature light loggers attached to individual free-living European blackbirds (*Turdus merula*) to measure the light intensity to which these birds are exposed to in forest and urban areas. I have first shown that male blackbirds living in a city are indeed exposed to higher levels of light at night compared to forest conspecifics, but these levels are substantially lower to what can be measured underneath typical street lamps. Recently I have offered new perspectives by estimating the subjective day length to which urban and rural blackbirds are exposed to and by analysing the overall light intensity to which blackbirds are exposed daily. In a series of studies, I have interpreted these data in the context of daily patterns of activity as well as seasonal biology. European blackbirds which were exposed to a longer photoperiod than their rural counterparts extended their activity into the night and showed reduced levels of melatonin production in the early morning, suggesting that this could be the biophysical process underlying the early onset of daily activity, but also the advanced breeding season observed in many avian species that successfully colonize urban areas. Indeed, I found a remarkable similarity between the difference in the photoperiod experienced by rural and urban blackbirds and the difference in timing of reproduction and onset of daily activity between my two study populations. I will discuss these findings and underlie several outstanding questions that still remain unresolved.

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13.1   Introduction

Light pollution is a global phenomenon of increasing importance. Indeed, as urban areas are the fastest growing land cover type around the world, the impact of artificial light at night on natural and anthropogenic ecosystems will likely increase, too. The dramatic change in the outdoor light environment recorded since the large-scale deployment of electric lights has the potential to impact a broad array of organisms. The increasing recognition of lightscapes as important environmental features has stimulated great scientific interest which has resulted in a unique amount and quality of ecological research published on this topic in the last decade (Rich and Longcore 2006). In this chapter, I will first highlight the importance of considering the light environment as a key driver of temporal biological processes, focusing on different levels of organismal responses, from genes to physiology to behaviour (Dominoni et al. 2016). I will then review the studies that have analysed how light pollution alters the natural lightscapes, including temporal and spatial global trends. Last, I will focus on my personal research, which has focused on analysing individual-based recordings of exposure to light at night using miniature light loggers mounted on free-living songbirds tagged at different urban and rural sites. In a series of papers, I used this information to define the light environment to which birds are exposed to in cities and compared it to the conditions of dark, forest areas. In addition, I also examined how the variation in exposure to light in and away from a city relates to the temporal (daily and seasonal) patterns of behaviour and physiology.

13.2   Natural and Artificial Changes in the Light Environment

To understand what the potential impacts of light pollution are on the biological functions of organisms, we must first understand how the presence of anthropogenic night light alters natural lightscapes. With respect to the physical properties of light, there are at least two important features that need to be considered.

Light Intensity Huge changes (10 orders of magnitude) in the amount of light that reaches the ground occur between day and night, and this is the most obvious property of the light environment that organisms use (Roenneberg and Foster 1997). But more subtle, short-term variation in the light intensity detected by an organism can also occur, for instance, as a consequence of cloud cover, moving through thick vegetation or directly looking at the sun. During the night light intensity can also vary depending on the moon phase, which some organisms synchronize to, especially in tidal environment where moon phase can have a great influence on the time and amplitude of tides (Kronfeld-Schor et al. 2013). Thus, long-term light sampling or integration over time is required to bypass these
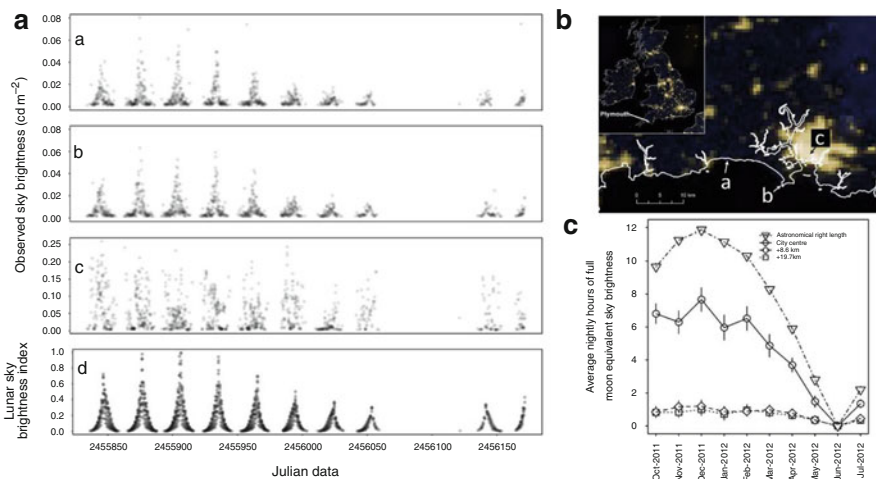
Fig. 13.1 (**A**) Observed regimes of night-time sky brightness (*grey points*) recorded 19.7 km (a), 8.6 km (b) and 0 km (c) from Plymouth city centre are compared to the predicted natural regime of lunar sky brightness (d). *Darker areas* indicate denser aggregation of points. (**B**) Map of sampling locations and relative light pollution. (**C**) Annual variation in night length compared to the annual variation in the number of hours per night when sky brightness was observed to be greater than the third quartile sky brightness observed in each month at a dark sky location when the moon is close to full. Graph reproduced with permission from Davies et al. (2013b)

small local fluctuations in the light environment. Light pollution can alter both spatial and temporal features of night light intensity in several ways. First, a recent study conducted in and around the city of Plymouth, UK, has shown that the average light intensity at night is six times higher in the city than in suburban and rural areas (Fig. 13.1) (Davies et al. 2013b). The major implication of such increase is that natural regimes of moonlight are masked. In particular, the amount of full-moon equivalent hours is increased, and the seasonal variation in nocturnal light intensity is almost lost. The consequences of such change for both diurnal and nocturnal organisms could be huge. In addition, several analyses of long-term satellite images have revealed a global trend in increasing night brightness overall the last 50 years (Bennie et al. 2015). However, recent work has highlighted that while the increasing trend is true for most regions in Europe, there are also areas in developed European countries that have experienced large decreases in night-time brightness, mostly because of a switch towards less industrial production and/or the implementation of new policies to contain the economic costs of night-time illumination (Bennie et al. 2014).

Spectral Composition Sunlight covers a wide range of wavelength, but spectral changes occur during the day. For instance, twilights phases are normally enriched in short wavelengths (Roenneberg and Foster 1997). As moonlight is pretty much all reflected sunlight, a lunar spectrum looks very similar to a solar spectrum. However, the introduction of different sources of anthropogenic night light has

altered not only the amount/intensity of light experienced at night but also its spectral properties (Gaston et al. 2012; Hale et al. 2013). As different wavelengths have the capacity to impact different biological functions and ecological processes to different extent, (Aubé et al. 2013; Davies et al. 2013a), this is an important issue to be considered if we want to understand the response of organisms to anthropogenic light, as well as its mechanistic underpinning. For instance, as the light action spectra for the circadian response of mammals and birds peak at mid- to low wavelengths (Davies et al. 2012), blue-rich light bulbs have been found to affect the expression of circadian behaviour and physiology the most, for instance, decreasing nocturnal levels of the hormone melatonin (Aubé et al. 2013).

While in the last 15 years several studies have quantified how light pollution affects lightscapes, we still have a limited understanding of how such changes in the light environment are perceived by wild organisms. For instance, as night-time light levels in urban areas might even be constantly above that of moonlight, are urban exploiters exposed to a 24-h day? How does the nocturnal light intensity that reaches an organism's photoreceptors compare to that provided by anthropogenic light? And how does the light intensity perceived by an animal relate to its activity? In order to try to answer these questions, we need individual-based measurements of light intensity. Recent technological advances in telemetry have given us the possibility to tag individual organisms and follow them over a relative long period of time. After briefly reviewing the known effects of light pollution on the daily and seasonal activity patterns of animals, I will focus on my own work on wild European blackbirds (*Turdus merula*), where I used light loggers to record the amount of light intensity to which urban and rural blackbirds were exposed to at night, and relate it to several parameters of daily activity recorded with automated radiotelemetry.

13.3 Light Pollution and Biological Rhythms

All organisms have evolved in a rhythmic world and respond to periodic changes in the environment driven by cycles of light, temperature, food availability and many other parameters. However, the natural alternation of day and night is probably the most constant feature of the planet Earth, and photic information is used by virtually all organisms to synchronize their activity to the best time of day and year in order to maximize their fitness (Foster and Kreitzmann 2004). Moreover, organisms have evolved morphological structures and physiological mechanisms to detect and interpret light stimuli (Foster and Kreitzmann 2004). For instance, different organisms possess different photoreceptors in different tissues of their body, and the sensitivity of these photoreceptors varies greatly among taxa (Peirson et al. 2009; Dominoni 2015). At the same time, the most common visual reception organ, the eye, also shows great variability in size and structure which largely depends on whether the organisms are diurnal, nocturnal or crepuscular.

As artificial light at night changes the temporal regimes of night-time light intensity (Davies et al. 2013b), it comes with no surprise that organisms living in light-polluted areas show a remarkable shift from their natural temporal patterns of daily and seasonal behaviour and physiology. Such changes have been documented in a vast array of species, from plants to invertebrates to birds and mammals (Rich and Longcore 2006; Kempenaers et al. 2010; Rotics et al. 2011; Dominoni et al. 2013b; van Geffen et al. 2014). Several reviews have already covered this topic; thus, my intention here is rather to highlight the general findings of these studies, their limitations and the promising areas for future research.

The response to light at night and its potential ecological consequences seem to depend not only on the temporal activity strategy of the species but also on its sensitivity to light and its feeding ecology. Many diurnal species, especially those which are also active at dawn and dusk, seem to be prone to extend their activity into the night. For instance, in songbirds, only those species that display a very early dawn chorus show a significant advance of its onset in light-polluted areas, suggesting that only species that are sensitive to low light intensity levels can afford to be active at night when anthropogenic light is present (Kempenaers et al. 2010). In nocturnal species, however, the response to light pollution seems to be largely species specific. In bats, while the common pipistrelle (*Pipistrellus pipistrellus*) has been found to increase its activity (Spoelstra et al. 2015), lesser horseshoe bats (*Rhinolophus hipposideros*) tend to avoid bright areas while commuting at night (Stone et al. 2009). However, although several studies in the last decade have reported these and similar effects, we still lack a deep understanding of the consequences of such temporal shifts in activity at basically all levels of biological organization, from the individual to the species, to populations and to ecosystems. A recent study has highlighted that the reproductive timing as well as the breeding success of wild songbirds is affected by an experimental manipulation of the night light environment and that this effect may also depend on the wavelength of light, with white lights being the more impacting light source (De Jong et al. 2015). The temporal shifts in activity timing will likely impact the time and modality of social encounters between individuals of the same species, but this has been rarely investigated. A landmark study on blue tits (*Cyanistes caeruleus*) has shown that a small advance in the time of male dawn song can increase annual reproductive success considerably by allowing males to gain more extra-pair youngs (Kempenaers et al. 2010). Thus, encounters between male and females of different breeding pairs of this species seem to be increased in the early morning under light pollution. In addition, interspecific relationships, for instance, the temporal overlap in activity timing between predators and preys, might also be affected, but these trophic effects are largely unknown. Spoelstra and collaborators have examined the activity of wood mice (*Apodemus sylvaticus*) and common pipistrelle under different light at night treatments in the wild, and they showed that mice activity was reduced and bat activity was increased under light pollution, with red light having the smallest impact (Spoelstra et al. 2015). However, the activity of mice's main predators, howls, and pipistrelle's main prey, mosquitoes, was unfortunately not monitored, leaving a black hole in our knowledge about how

the change in temporal activity strategy caused by light pollution can cascade across trophic levels.

13.4 How Light Loggers Can Help Us in Understanding the Impact of Light Pollution on Animals' Behaviour and Physiology

13.4.1 How Much Light Pollution Are Animals Exposed To?

The amount of artificial light that organisms are exposed to will greatly depend on their behaviour. For instance, male songbirds have been reported to perform dawn chorus directly under, or even on top, of streetlamps (Stephan 1985). Under these circumstances, light exposure can reach very high levels, even above 20 lux (Dominoni, unpublished data). Mammals that rely on visual cues to forage, such as mice, foxes and certain species of bats, are also likely to be exposed to considerably high levels of light pollution. These levels can vary depending on the type of bulbs used in streetlamps, but they are usually between 6 and 20 lux when measured at the ground and directly under the light source (Miller 2006; Kempenaers et al. 2010; Rotics et al. 2011; Dominoni et al. 2013b). When moving away from the direct light source, however, light intensity decreased exponentially and rapidly (Kempenaers et al. 2010). Thus, animals that spend the night in borrows or nest boxes, or that roost in very thick vegetation, are likely to be exposed to very low levels of light intensity (Dominoni et al. 2013b). Despite this evident link between behavioural modes and light exposure, most studies on the ecological effects of light pollution have measured light intensity in the environment surrounding the territory of an animal, but little consideration has been made on which part of the habitat the animal is more likely to use and when. Without detailed measurements at the individual level, it is difficult to make strong inference on the spatial and temporal variability in the exposure to light pollution.

I tried to overcome this limitation by deploying miniature light loggers on individual male European blackbirds breeding in the city of Munich, south-east Germany, and in a forest 40 km south-west from the city centre (Fig. 13.2). Blackbirds were caught at dawn using mist-nets, tagged and then immediately released in their territory. The tag I used was a combination of two devices: a light intensity micro-logger and a radio-transmitter (Fig. 13.3). Light loggers were used to record light intensity during day and night, while the radio-transmitters were used to record activity rhythms of the animals (see below). The locations where blackbirds were caught vary considerably in the amount of light intensity present in the environment (Dominoni et al. 2013a). Indeed, I used two light loggers as stationary loggers and deployed them on tree branches at the two extremes of the urban gradient. These loggers recorded data for approximately 3 weeks, and the data are shown in Fig. 13.4. While during daytime light intensity does not seem to

Fig. 13.2 Study sites. (**a**) Overview map. Birds were sampled in the city of Munich and in the forest of Raisting, 40 km south-west of Munich. (**b**) Map of nocturnal light intensity in the city of Munich and locations where birds were caught (*green circles*, business district; *red circles*, urban parks). Notice the higher light intensity in the areas surrounding the business district compared to the other two locations. This picture is by courtesy of Franz Kurz, DLR, Oberpfaffenhofen, Germany

vary significantly between urban and rural areas (panel a), night-time light intensity is considerably higher in the city centre of Munich (panel d). Interestingly, light intensity in the first half of the night is double as high as in the second half, probably due to the fact that fewer cars are around late at night, most bars close and many streetlights are turned off in the middle of the night.

But how much of this night light are blackbirds really exposed to? Figure 13.5 shows the median and maximum light intensity calculated from the light loggers retrieved from blackbirds captured in the city of Munich. Median light intensity was lower than 0.3 lux, while maximum light intensity was between 1 and 2.5 lux (Dominoni et al. 2013b). Thus, urban blackbirds are exposed on average to a night-time light intensity 20 times lower than what could be measured underneath a representative streetlamp in our study sites and around the level of a full-moon night. This suggests that although urban songbirds are only rarely exposed to very high levels of light pollution, nevertheless the nocturnal lightscape they live in masks the natural variation in night light due to the moon. As I will explain in the following section, this can potentially have important consequences for the photo-period that birds experience in urban habitats. I showed this data expressed in lux the sake of consistency and comparison with most animal studies conducted in the wild and in captivity.

However, lux is a measure of illuminance based on the sensitivity of the human eye and thus does not really apply to birds, as they are able also to see ultraviolet light. I have therefore calibrated the lux measurements using a pyranometer (Dominoni et al. 2014), an instrument able to record light radiance expressed as the amount of energy (radiant flux) incidence on a surface per unit area. Irradiance is often expressed as "intensity" in watt/m^2. Figure 13.6 shows irradiance data during the early and late night in the three different study sites. I have split the urban habitat into two different subtypes depending on the size of the study area and human presence (see Dominoni et al. (2014) for more details). Although the data

Fig. 13.3 Bird tagging. (**a**, **b**) Blackbirds were tag using a "backpack". This consisted of two devices, a light logger and radio-transmitter, stuck together using shrinking tubes and then attached to the animal with rub and cotton harnesses pulled through the legs. (**c**) Light logger (Sigma Delta Technologies, Australia). The loggers weighed 2.4 g and were composed of an electric circuit linked to a photodiode, whose spectral responsivity ranged from 300 to 1100 nm, with a peak around 780 nm. They recorded and stored light intensity every 2 min for the entire time. We calibrated the loggers against a photometer (LI-1400 and LI-2100, LI-COR, USA) in order to convert frequency into lux (illuminance) and watt/m^2 (irradiance) values

from stationary light loggers might have suggested that exposure to light pollution may vary between the early and late night, the data from loggers mounted on individual blackbirds did not show any significant differences between separate phases of the night in any of the study locations (Dominoni et al. 2014). Light intensity was, however, significantly higher in the business district compared to the rural forest and the suburban parks, justifying the splitting of the urban sites. Moreover, it is worth to highlight that not only absolute levels of light intensity were higher in the business district but also between-individual and within-individual variation was higher in the most urban locations (Dominoni et al. 2014). This suggests that (1) different individuals are exposed to a very different amount of light pollution within the same business district sites, and (2) individuals in the business district can be exposed to large differences in light pollution during subsequent nights. Therefore, variation at the level of the micro-habitat occupied by each individual is crucial for the understanding of how avian behaviour and physiology might be influenced by light at night. On the other side, behaviour in the form of temporal activity patterns can obviously have produced the
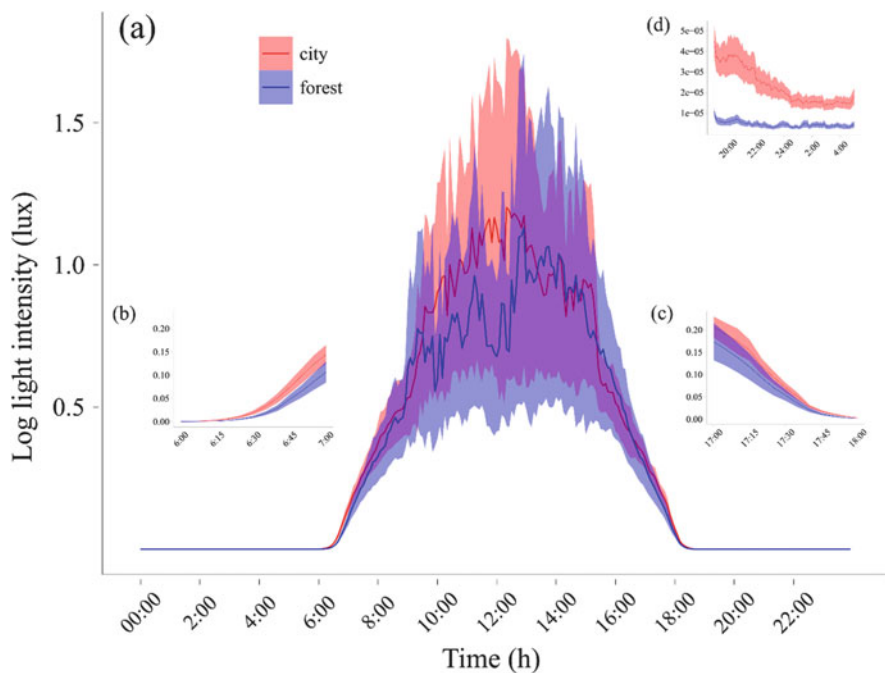
Fig. 13.4 24-h light profiles of the urban and forest study sites. Light was recorded between March 4 and 20, 2011, using stationary light loggers. Two loggers were placed at a height of ~2 m on tree branches at the edge of a forest patch (rural site) and a botanical garden (urban site). *X*-axis represents time, and *Y*-axis represents log-transformed light intensity. *Lines* depict mean light intensities for the entire recording period, *shaded areas* are s.e.m. (**a**) Complete 24-h profile. (**b**) Morning twilight phase (6:00–7:00). (**c**) Evening twilight phase (17:00–18:00). (**d**) Night (20:00–4:00)

patterns of light exposure recorded by the light loggers. I will go in more details about this topic later in the chapter.

13.4.2   Are Urban Birds Exposed to a Longer Day Length?

As I mentioned in the introduction, photoperiod is a crucial environmental cue that animals use to synchronize their daily and seasonal activities to the best time of the day and year, and its importance often overrides that of other cues such as temperature and food availability. For instance, many animals can be "tricked" to reproduce at any time of the year by subjecting them to long days, which simulate the approaching spring and summer and therefore the breeding season (Follett et al. 1967; Lambrechts and Perret 2000; te Marvelde et al. 2012). Therefore, one of the key questions when we aim at investigating the effects of light pollution on wild organisms is whether the presence of artificial lights might affect the detection
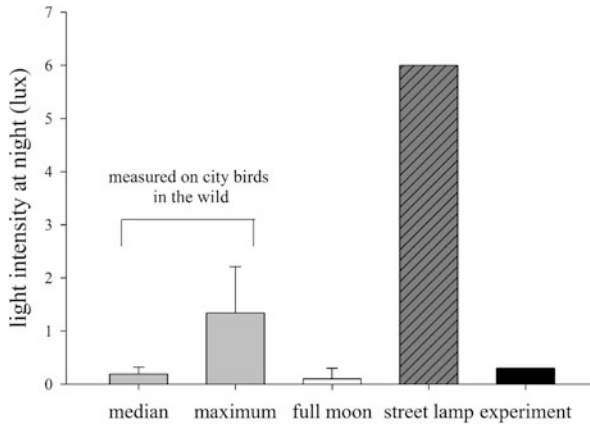
Fig. 13.5 Natural exposure to light at night of free-living city European blackbirds. *Light grey bars* represent data obtained from loggers deployed on individual birds in their natural urban environment. For each city bird ($N = 28$), we calculated the median and maximum of the third quartiles of all nights and used the mean of those values from all birds (mean $= 0.2$ lux) for presentation in the figure. Data are represented as means $\pm$ SEM. *White bar* represents full-moon light intensity (0.1–0.3 lux). *Dark grey striped bar* represents the light intensity measured under a representative street lamp of our study site (~6 lux). *Black bar* represents the light intensity (0.3 lux) we used in the captive study to simulate urban exposure to light at night in the experimental treatment group (see text and Fig. 13.11)

of day length. More specifically, I hypothesized that in light-polluted areas, birds will be exposed to a longer day length than in rural areas free of artificial lights. I avoid using the word "perceive" because without proper physiological and neuro-endocrinological measurements, it is not possible to state with certainty than birds perceive a longer day length. But it is logical to assume that if birds are exposed to a pattern and intensity of light at night that mimic those of a longer photoperiod, they will also physiologically perceive a longer day.

But what does define day length? In laboratory studies, photoperiod is easily defined by the fact that lights are usually turned on and off sharply. But during a natural dawn, light intensity increases gradually before reaching its maximum only around midday (Fig. 13.4). So when do animals begin realizing that the day is starting and they should get ready with their business? Within the same taxa, animals can have a considerably high variation in sensitivity to light (Thomas et al. 2002; Kempenaers et al. 2010). Thus, they likely have different thresholds of light intensity that need to be met to signal the onset or end of the day. This could depend on several ecological and physiological factors, including eye size (Thomas et al. 2002). Indeed, among songbirds, there is a clear separation between families based on when species start their dawn chorus relative to the beginning of twilight, with early rising species having on average larger eyes relative to body size (Thomas et al. 2002). Light pollution could therefore impact day-length detection differently depending on sensitivity to light. Indeed, Kempenaers and collaborators have shown that among five different species of songbirds, those belonging to the
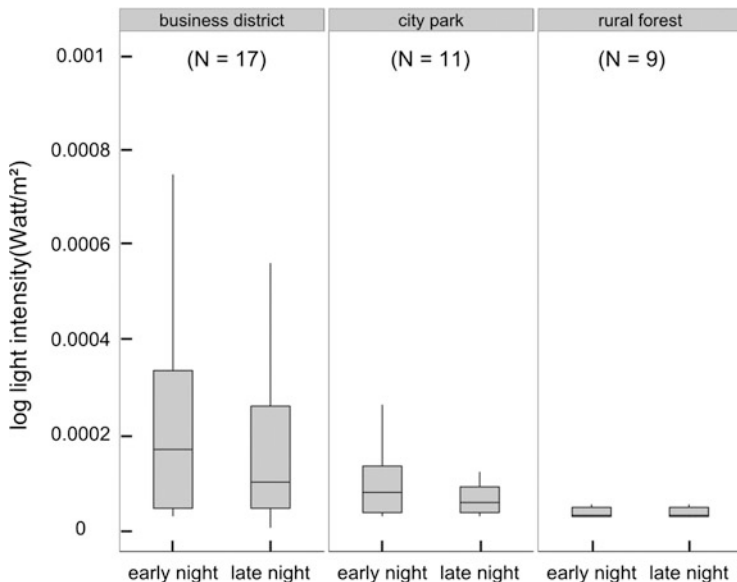
Fig. 13.6 Variation in exposure to light at night in adult male European blackbirds recorded at three study sites differing in the degree of urbanization, using light loggers deployed on individual blackbirds. We calculated the median light intensity in the early night (10:00–00:30) and in the late night (00:30–3:00) and averaged these values for each bird. *Box plots* represent, from bottom to top, one standard deviation (SD) below the mean, lower quartile, median, upper quartile and one SD above the mean

family Turdidae seem to be much more affected from light pollution than species of the families Paridae and Fringillidae (Kempenaers et al. 2010).

Based on these considerations and on how light pollution can alter the natural regimes of sky brightness at night (Fig. 13.1), my recent work has been devoted to understand whether birds in urban environment are exposed to patterns of light at night that may be perceived as a longer day length (Dominoni and Partecke 2015). In particular, assuming that the highest naturally occurring light intensity at night is produced by full moon, I defined "subjective day length", or simply "day length", the duration of time in minutes between the time that light intensity passes the level of full-moon light intensity in the morning and the time when that happens in the evening. This is exemplified in Fig. 13.7. I hypothesized that birds in light-polluted areas will be exposed to a longer subjective day length than rural conspecifics.

I tested this hypothesis using the same data collected by the light loggers and presented in Fig. 13.6. As a threshold for the full moonlight intensity, I used a value of 0.3 lux, which corresponds to 0.0025 W/m^2 as measured at ground level during a full-moon night in my forest study site. Based on this assumption and on the procedure to calculate subjective day length explained in Fig. 13.7, I analysed the variation in day length as well as in the onset and end of the subjective day across the different study sites. Subjective day length was significantly longer in the
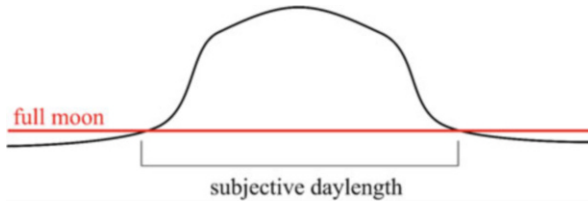
Fig. 13.7 Schematic representation of the concept of "subjective day length", which was used to test the hypothesis that urban birds are exposed to a longer day length than rural conspecifics. Briefly, full-moon light intensity (0.3 lux) was used as reference threshold level to which we compared each light intensity time series recorded on individual free-living blackbirds using light loggers. The times at which the series crossed full-moon intensity in the morning and evening were recorded, and the duration in minutes between these two time points was defined as subjective day length

business district compared to both the rural forest and the urban park, which were not significantly different between each other. This difference was equally explained by an earlier onset and a later end of the subjective day in the business district compared to the other two sites (Fig. 13.8). Thus, birds breeding in highly light-polluted areas appear to be exposed to a longer day length than birds inhabiting darker areas. On average, this difference is 52 min. In the Munich region, this equals approximately to 19-day difference in photoperiod during the late winter/early spring, the time at which blackbirds start to reproduce (Partecke et al. 2005). I will get back to this concept later in the chapter, where I will discuss the effect of light pollution on the reproductive biology of urban blackbirds.

13.4.3 Does Variation in Exposure to Light at Night Relate to Activity Patterns?

Several studies in the last decade have linked light pollution to both an earlier onset of dawn song and a later offset of dusk chorus in birds. This has been shown not only in European blackbirds but also in several other songbird species such as great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), European robin (*Erithacus rubecula*), American robin (*Turdus migratorius*) and song thrush (*Turdus philomelos*) (Miller 2006; Fuller et al. 2007; Dominoni et al. 2013b, 2014; Nordt and Klenke 2013; Da Silva et al. 2014, 2015). However, these studies have either measured the average night light intensity in the areas where the birds were recorded or record birds in areas with or without light pollution. Thus, our understanding of the relationship at the individual level between the timing of dawn and dusk song and the amount of night light was limited. I tried to overcome this using the data collected by both light loggers and automated radiotelemetry on the European blackbirds. Indeed, as the blackbirds carried radio-transmitters on their back, I was able to use automated receiving units (ARUs) to record the activity
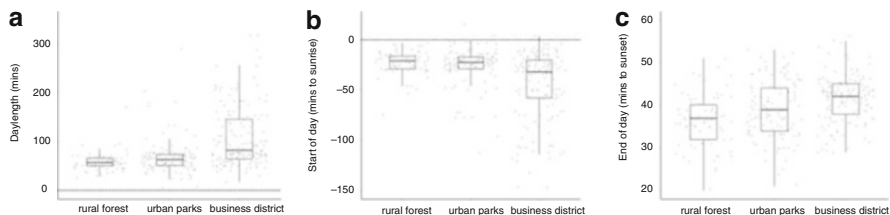
Fig. 13.8 Full-moon light intensity (0.3 lux, or 0.0025 W/m^2 at 500 nm in the rural forest) was used as threshold value to calculate the time at which the light intensity time series (recorded by light loggers deployed on individual male blackbirds) passed this value in the morning and evening and defined those times as onset (**b**) or end (panel **c**) of day. The "subjective day length" was calculated as the difference between the onset and end of day (**a**). We standardized the measurements to the natural variation in day length, the horizontal line at time 0 (**a**, total day-length hours; **b**, sunrise; **c**, sunset). Each *dot* represents one single day of recording for a specific bird, whereas *box plots* represent median and s.d. values for each study site. Sample sizes: rural forest $N = 8$, urban parks $N = 11$, business district $N = 12$

patterns of one specific bird. The ARUs recorded the signal strength emitted by the transmitters every minute. By looking at the variation in signal strength over time, these data were used to infer the activity state (active vs. nonactive) of the animal, although not its exact position. The basic assumption of this methodology is that variation in signal strength signals movement of an animal (Cochran et al. 1965). Conversely, when variation in signal strength is minimal, the animal is assumed to be inactive (Fig. 13.9). Together with Dr. Bart Kranstauber (Max Planck Institute for Ornithology, Germany, now at the University of Zurich, Switzerland), I have developed a statistical methodology to objectively quantify switches in activity state without using arbitrary threshold levels (Dominoni et al. 2014). I used this methodology to estimate the time at which a bird started its activity in the morning and ceased it in the evening and called these onset and end of activity.

These data were collected in the three study sites on several individual blackbirds which simultaneously carried light loggers on their back, thus allowing a direct comparison between light exposure and activity patterns. As for light exposure, I used the average light intensity recorded during the true night, thus excluding the twilight phases. The reason behind this approach is that I wanted to avoid using periods of the night when the light intensity recorded by the light loggers could be highly influenced by the behaviour of the animals, as blackbirds are very active during twilights. Rather, I wanted to estimate the average nocturnal light environment to which blackbirds were exposed to, and the data were already shown in Fig. 13.6. I used these data as explanatory variable in different linear mixed models that aimed at testing the effect of several environmental variables (including noise, temperature, cloud cover, rainfall and season) (Dominoni et al. 2014). In all these models, light intensity at night was a significant predictor of the onset of activity in the morning: the higher the light intensity to which an animal was exposed to at night, the earlier the onset of its daily activity (Fig. 13.10). A trend was also found for the end of the daily activity (not shown), such as birds breeding in highly
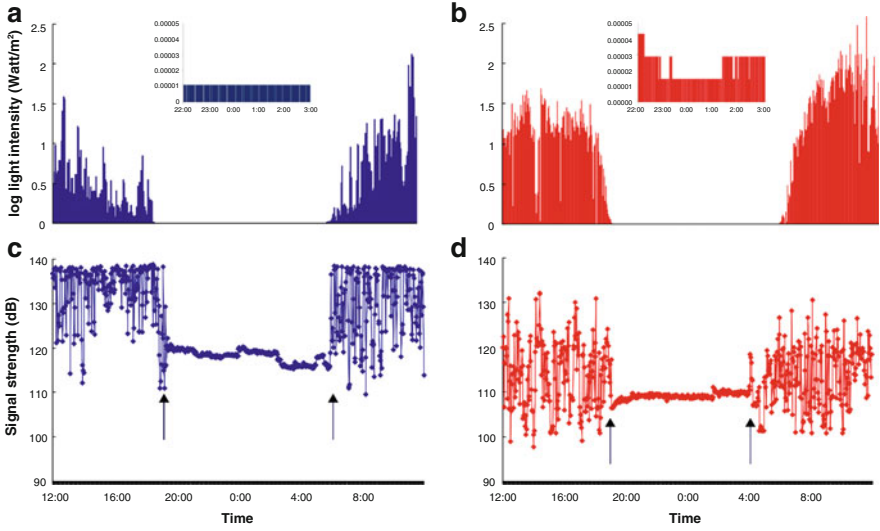
Fig. 13.9 Plots of raw light intensity and activity data. Data from one complete day are shown for one rural (**a**, **c**) and one urban bird from the business district (**b**, **d**). Light intensity data (**a**, **b**) was recorded by light loggers mounted on individual birds. Inlays show data used for the analyses, from 10 pm to 3 am. Activity data (**c**, **d**) was collected by automated telemetry stations (ARU, www.sparrowsystems.biz). ARU recorded the signal strength of radio-transmitters attached to individual birds. Switches between activity states (active/nonactive) were inferred by analysis of the change in signal strength between consecutive data points and are indicated by *arrows* in the graph. Light data is recorded on a 2 min basis, activity data on a minute basis
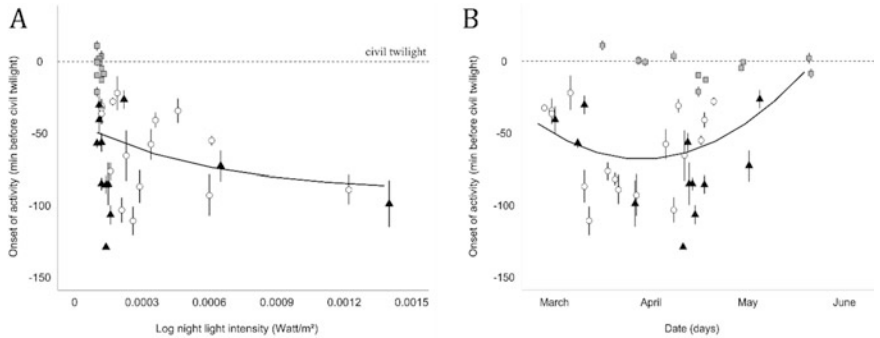
Fig. 13.10 Relationship between onset of activity and light at night (**a**) as well as season (**b**). *Symbols* (*grey squares* = rural; *white circles* = city parks; *black triangles* = business district) represent the mean for each individual. *Error bars* indicate s.e.m. *Black line* indicates a significant relationship between activity and light at night for the two urban sites pooled together. No significant relationship between the two explanatory variables and activity was found for the rural birds. The *horizontal dotted lines* represent the civil twilight, to which the onset of activity was standardized in order to control for seasonal changes in photoperiod

light-polluted areas were also prone to end their daily activity later than animals in darker areas. Among the other environmental variables considered, the only one found to be having a clear and significant effect was date (Dominoni et al. 2014). Indeed, birds started their activity earlier during the early spring (end of March and April), the time at which in our study sites male blackbirds have higher testosterone levels and females start to lay eggs. This result is in line with previous studies that have found that male dawn activity is stronger during the early breeding season, when males establish their territories and compete for access to females (Kunc et al. 2005). A recent work has confirmed that the effect of light pollution on dawn song in several songbird species is stronger in early spring (Da Silva et al. 2015).

13.4.4 Experimental Demonstration of the Effects of Light Pollution on Daily and Seasonal Cycles of Birds

All studies conducted in the wild, even the experimental approaches that have been used in recent studies, suffer from the potential confounding factor of any non-measured environmental variable that can bias the results. Thus, in order to really demonstrate an effect of light at night on any biological process, captive studies are needed. I therefore took advantage of the fact that, through the use of light loggers, I had collected individual-based recordings of exposure to light intensity in urban and rural areas to set up realistic simulations of night-time urban and rural light intensity in captivity. In the winter of 2010/2011, I exposed 40 wild-caught male European blackbirds of mixed origin (20 from the rural forest and 20 from the business district/urban parks) to two different light treatments. Birds were equally divided into the two treatments based on their origin. They were exposed to the same natural variation in local photoperiod, but with different light intensity at night. The control group was exposed to 0.0001 lux at night, a light intensity very close to complete darkness mimicking a forest-like environment. The experimental group was exposed to 0.3 lux at night, a light intensity within the median night-time values recorded on male blackbirds in the city of Munich using light loggers (Fig. 13.5). The main aim of this experiment was to analyse the effect of the light at night treatment on the daily activity patterns and reproductive physiology of blackbirds, in order to experimental test the hypotheses originated from field studies. Birds were housed in individual cages in two rooms corresponding to the two different light treatments. Locomotor activity of blackbird was recorded around the clock using infrared sensors mounted on top of each cage. From January to July, I recorded monthly the singing activity of birds and the size of their gonads and collected a blood sample to analyse plasma concentration of testosterone. In addition, from May on I checked weekly the intensity of primary and body feathers moult to assess the onset of the moulting period for each bird.

The results clearly indicate that birds exposed to light at night advanced the onset of both their reproductive physiology (gonadal size and testosterone) and
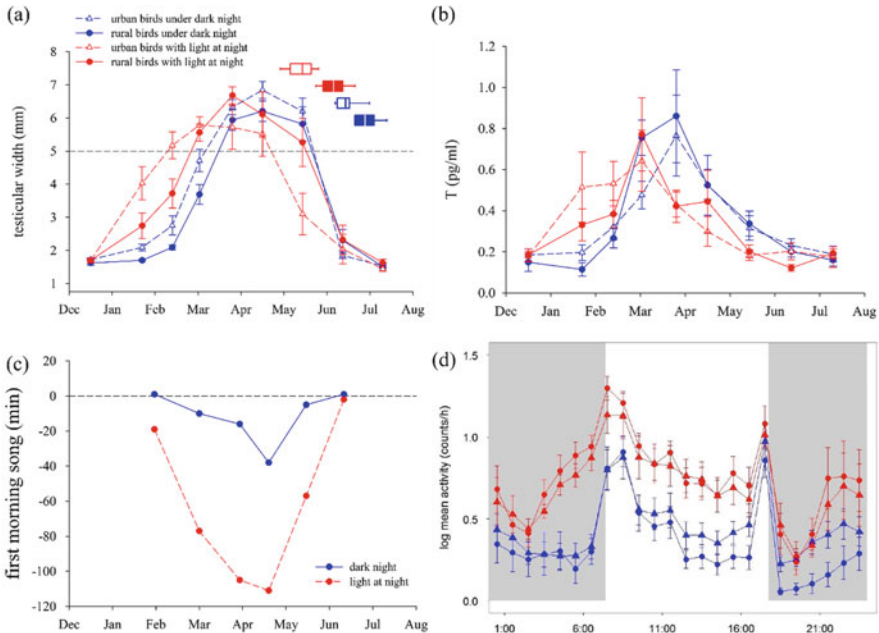
Fig. 13.11 Experimental demonstration of the effects of light at night on daily and seasonal timing in European blackbirds. Male blackbirds of either urban (*triangles*) or rural (*circles*) origin were exposed to either dark nights (*blue symbols*) or light at night of 0.3 lux (*red symbols*). In all graphs, *symbols* represent means and *bars* s.e.m. (**a**) Variation in testicular width during the reproductive phase. *Horizontal line* at 5 mm represents the size at which testes were considered to produce fertile sperm (half of the maximal size). *Horizontal box plots* represent average onset of moult in the four different treatment groups. (**b**) Variation in plasma concentration of testosterone from blood collected on the same week that testes' size was measured. (**c**) Onset of the first morning song in each treatment group. (**d**) Locomotor activity was recorded with infrared sensors attached on top of each individual cage. *Grey areas* indicate lights off and *white area* indicates lights on

their moult (Fig. 13.11a, b) (Dominoni et al. 2013b). The effect size ranged between 2 and 4 weeks of early onset, a difference comparable to what found in the wild, where urban birds were shown to reach reproductive readiness approximately 19 days before their forest conspecifics (Partecke et al. 2005). This difference is interesting because it is exactly what found in the analysis of day-length exposure that I have shown earlier in this chapter (Fig. 13.8a) and in a recent manuscript (Dominoni and Partecke 2015). Thus, it appears that light pollution can explain most of the variation in the timing of reproductive physiology between urban and rural blackbirds. Similarly, the analyses of both locomotor activity and singing behaviour both indicate that birds exposed to light at night advanced their morning activity significantly compared to birds exposed to dark nights, and also this effect size closely mirrors the difference found between urban and forest blackbirds

(Fig. 13.11c, d). Indeed, blackbirds under the light at night treatment started their activity considerably earlier, up to 2 h before dawn, than birds under dark nights, regardless of their origin (Dominoni et al. 2013c). In addition, as previously shown from field data (Fig. 13.10b), this difference appeared to be much more marked during the peak of the reproductive growth (Dominoni et al. 2013b), during the second half of March and the month of April (Fig. 13.11c). Taken all together, the results of this captive experiment clearly indicate that increasing the level of light at night to which birds are exposed to in the laboratory produces drastic changes in the reproductive physiology as well as in the timing of daily activity that confirms much of the variation in these processes found in birds breeding in urban habitats.

13.5   Conclusion and Future Perspectives

The study of the ecological effects of light pollution is a growing field of research. During the last decade, we have seen an increasing number of studies investigating the responses of individual organisms, populations and communities to the presence of anthropogenic night light. Besides evident effects of light pollution on immediate mortality, such as collision against lit towers at night (Longcore et al. 2013), one of the best examples of how light pollution can affect wild organisms is the change in the daily and seasonal biology observed in several species. Such changes have been shown by both correlational and experimental studies in the wild and controlled experiments in captivity, which I reviewed in this chapter. Although some other environmental cues have likely the potential to impact the same timing processes (McNamara et al. 1987; McNamara and Houston 2008; Saggese et al. 2011; Dominoni et al. 2015), too, light pollution has consistently been shown to play a major role. Individual-based measurements of light exposure at night obtained using light loggers have confirmed such findings and revealed that light pollution can potentially alter the perception of day length, with important consequences for the way that organisms interpret the lightscape and therefore time their daily and seasonal activities. So what's next?

An unresolved outstanding question in light pollution research is whether the observed changes in behaviour and physiology of individual animals come with fitness consequences. For instance, reproductive success of male songbirds that are able to sing earlier in the morning under light pollution seems to be enhanced due to increasing extra-pair paternity (Kempenaers et al. 2010). However, singing at night might come also with costs related to increased predation risk under poor visibility or decrease thermoregulatory capacity which could lead to higher energy expenditure. In addition, lack of synchronization between internal and external timing can also come with detrimental consequences, as extensive work in human shift workers has testified (Kantermann et al. 2010). Regardless of these specific examples, many studies have shown that the ecological effects of light pollution can be widespread and cause at the very least an increased in immediate mortality (Rich and Longcore 2006). Therefore, although it is imperative that future research will

examine the different ways through which light pollution may affect fitness, we should already be discussing way for mitigating light pollution (Gaston et al. 2012). Besides the physical design of streetlamps, recent work has also stressed the necessity to include the wavelength of light as an important variable in light pollution research. As presented, short to mid-wavelengths of light seem to be impacting organismal responses the most, with long wavelengths in the red spectrum having minimal effects (van Geffen et al. 2014; De Jong et al. 2015; Spoelstra et al. 2015). However, more evidence-based knowledge is needed if we want to inform policy-makers about the best way to design artificial lights and implement new policies that look at keeping the impact of light pollution minimal as a priority for environmental planning.

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Chapter 14
Human Initiation of Synurbic Populations of Waterfowl, Raptors, Pigeons and Cage Birds

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Abstract A common generalization is that wild birds somehow manage to colonize urban areas without human support, which is often true. This paper focuses on a different and probable, though not rare, course of events, when some urban bird populations emerge with immediate human support, by intentional introductions or escape from captivity. This alternate mechanism may be responsible for settling the very first colonizers directly into a strongly urbanized habitat. Such "pioneers" might later be followed by "surplus individuals" moving into cities from the neighbouring natural populations. Eventually, birds of local origin may constitute a prevailing part of the locally developed synurbic population, thus, overshadowing the early genetic contribution of the very first pioneers. Yet the latter individuals might be important as initiators of the colonization and geographical expansion of this process.

Keywords Urban habitat • Synurbic birds • Human introductions • Settling escapees

14.1 Introduction

To avoid terminological confusion, in this chapter, "urbanization" is understood to be a complex process of environmental changes converting a rural area or small human settlement into an urban one, while adaptation of wildlife to truly urban conditions is called "synurbization", following the definition by Luniak (2004).

How several wild birds have managed to breed close to crowds of humans remains an intriguing question. Recent research suggests that this is often achieved independently of human will and usually by (a) a gradual behavioural adjustment, learning/habituation, usually under pressure of an overpopulation in peri-urban

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habitats or of harsh winter conditions, and (b) by a gradual conditioning to human presence when some natural habitats become surrounded by urban development. This is a valid hypothesis and is a frequent reflection of most situations. Yet in the seminal book on avian ecology in urban environments (Marzluff et al. 2001), there is also some remark on the role of bird introductions. It comes as no surprise that American authors have pointed this out having introduced alien species (e.g. house sparrow, *Passer domesticus*; rock/feral pigeon, *Columba livia*; starling, *Sturnus vulgaris*) that form the bulk of avifauna in the New World cities. In Europe we often forget that some of our birds also are of alien origin (Central Asian, Middle Eastern, Mediterranean), or they are native birds which might had passed through a captivity stage. Therefore, though the phrase "species X has colonized the city..." has become colloquial, already early speculations (Sokołowski 1973) recognized two other possible ways expediting the process: (a) through spontaneous taming of wild ducks when fed at urban winter sites, and/or (b) through man-induced urban introductions, unintentional (through Zoos) escapes or intentional releases of captive birds (see Sol et al. 2016). In Central Europe the first option may be more likely with the winter climate amelioration; a recent estimate (for the years 2007–2009) shows that of all individuals wintering in Poland, at least 20 % of mallards, *Anas platyrhynchos*, were staying on waters surrounded by urban land; similarly c. 17 % of all mute swans, *Cygnus olor*; and 8–19 % of wintering coots, *Fulica atra* (Meissner et al. 2012).

The second option may also be important, at least locally. We still do not know how and how frequently a new urban behaviour was appearing (see Miranda 2016) and then why some urban populations expanded across the species range. Sometimes even crossing the former breeding range boundary and turning into a geographical expansion of the species (e.g. the past spreads of the house sparrow; rock/feral pigeon; serin, *Serinus serinus*; black redstart, *Phoenicurus ochruros*; or recently collared dove, *Streptopelia decaocto*).

Two issues should be reconsidered (a) whether and to what degree a start of some urban bird populations had resulted from a human support and (b) what is the mechanism(s) for the subsequent expansion of a successful urban population of a species.

14.2   Human Contribution to the Development of Tame Bird Populations

The possibility of human contribution, intentional or unwilling, to the origin of some tame bird populations, even if evident, often remains underestimated. The firm evidence for a man-supported origin of feral, tame and later synurbic populations can be found among waterfowl (Sokołowski 1973; Montier 1977; Blagosklonov and Avilova 2002). Keeping pinioned and non-pinioned swans and ducks began well before two famous breeding centres were established: the Russian

(now Ukrainian) centre for restoration of the steppe species at Askania-Nova (since 1883) and the British centre managed by the Wildfowl and Wetlands Trust at Slimbridge (since 1946). Both contain large numbers of wild birds, including many that could fly. Not unlike was in other parts of our continent, with its present not necessarily positive side effect of such action—a "biological contamination" of the European avifauna with exotic species (Cramp and Simmons 1977– 1983; Kelcey and Rheinwald 2005). According to Christensen (1997), at least 63 non-European species have been found breeding in the 14 North-West European countries (including the British Isles) as a result of escapes from captivity or introductions. The same is in Japan, where in Tokyo and its neighbourhood, 71 feral bird species were reported for the period of 1961–1981, 20 of them breeding in the wild (Narasue and Obama 1982 citation after Luniak 2004).

The early keeping of "ornamental waterfowl", chiefly flightless mute swans, was originally restricted to the countryside. Only during the nineteenth century, after demolishing city walls and subsequent city growth, several waterbodies have been incorporated into urban agglomerations creating good conditions for waterfowl. A recent list of breeding waterfowl from 16 European cities, from Lisbon to St. Petersburg (Kelcey and Rheinwald 2005), shows that mallards breed in all of them, more than half of cities contain breeding mute swans; tufted ducks, *Aythya fuligula*; and garganeys, *Anas querquedula*. Approximately 33–50 % of cities harbour breeding pochards, *Aythya ferina*; shovelers, *Anas clypeata*; gadwalls, *A. strepera*; and teals, *A. crecca*, and a few cities also have goldeneyes, *Bucephala clangula*, and greylag geese, *Anser anser*. Additionally, there exist breeding populations of exotic species such as *Aix galericulata*, *A. sponsa*, *Branta canadensis*, *Alopochen aegyptiacus*, *Anser cygnoides*, *Tadorna ferruginea* and *Cygnus atratus* (Christensen 1997).

Most of these reports, however, lack an estimate of the degree of synurbization of such populations: whether those birds bred only in suburban zones or formed inner-city (synurbic) populations. There is also a shortage of information how they were started.

14.3 Field Data According to Several Groups of Birds

14.3.1 Settling Wild Ducks into Inner-City Parks

The earliest reports come from London, where, since the mid-nineteenth century, tufted ducks were repeatedly introduced into the inner city. In 1913, in St. James' Park, there were several flightable females, which by 1929 were rearing up to 100 ducklings a year (Montier 1977). Around 1940 also pinioned and non-pinioned pochards were released into inner London parks. In other parts of the continent, it was similar. In Poland, apart from feral mute swans, the earliest record (1915) of some mallard females rearing young in a park in the very centre of

Poznań was preceded by a few years lasting stays of wild mallards on a pool in the municipal zoo (Sokołowski 1973). Before World War II, in Wrocław, the first tame mallards were also reported from the zoo located on the bank of the Oder River. After the destruction of their initial populations in both cities during the war, a repeated colonization in Wrocław has been speeded up in June 1960 by the release into the Botanical Gardens of a female mallard with ducklings reared in the zoo and settling there a hybrid of wild mallard with domestic duck (Sokołowski 1973). In nearby Legnica town, urban mallards appeared in 1973, possibly independently of people. The inner-city park of Legnica, with a pond and an island, has later become the site of regular breeding of several duck species (Tomiałojć 2007). During the years 2003–2004, there were up to 9–10 female mallards with ducklings, all fed by the public. The presence in the Legnica park of tufted ducks, the species nesting elsewhere only on the peripheries of Polish cities, was monitored since the very beginning. The first female with young in the park pond (in July 1996) originated from a few tufted duck ducklings brought there a year before by anglers from the fish-breeding lakes in the countryside. By 2003–2004 seven tame females bred in the pond, rearing 35 and 50 ducklings, respectively, and in July 2005 eleven tame females with young were regularly fed by the public.

The presence of breeding mallards and tufted ducks in Legnica and Wrocław soon attracted other species, such as sporadically breeding females of the goosander, *Mergus merganser*, and mute swans and nonbreeding stationary specimens of the Wigeon *Anas penelope* (Tomiałojć 2007). In the park of Poznań Zoo, breeding mallards attracted another species as well: in 1993 in a nesting box, a mixed clutch of mallard and goldeneye, *Bucephala clangula*, was found, with a mallard female later seen with its own young and two Goldeneye ducklings. During 1999–2000 one and two adult Goldeneye females bred there (Ptaszyk 2003).

The East European examples of extensive settling of wild ducks into urban parks are those from Moscow and Riga (Latvia). Around 1958, mallards breeding at first only at the Moscow Zoo pond (up to 200 females) have been replaced into other parks. During 1953–1961 Moscow Zoo personnel brought Goldeneye eggs for a purposeful introduction of reared in captivity young into urban waterbodies. Intentional was also the release of flightless ducklings of several species into urban parks of Riga (Blagosklonov 1981; Blagosklonov and Avilova 2002; Avilova et al. 2007).

Of similar origin were some urban "exotic" waterfowl, also half tamed during their stay in zoological gardens before escaping from captivity. For example, for some time on city-centre buildings, small populations of the ruddy shelduck, *Tadorna ferruginea*, were breeding: up to 29 pairs in Moscow and one–two pairs in Wrocław (Blagosklonov and Avilova 2002; Tomiałojć and Stawarczyk 2003).

14.3.2 Human Help in Establishing Urban Raptors

Briefly, it can be mentioned that human help could be involved in the colonization of urban areas by some diurnal birds of prey, Falconiformes and Accipitriformes. It

is highly probable that some past and recent cases of urban breeding of the peregrine, *Falco peregrinus*; kestrel, *F. tinnunculus*; hobby, *Falco subbuteo*; as well as the goshawk, *Accipiter gentilis*, and sparrowhawk, *A. nisus*, were in some cases preceded by keeping these species in captivity for falconry purposes and subsequent escapes of tame individuals, which could pair with the wild ones wintering in or around the cities. Recently, in several Polish and European cities, captive bred peregrine falcons have intentionally been settled, and they started to breed successfully (Sielicki and Sielicki 2006). There was a pronounced difference in their individual level of shyness, e.g. a female settled as a fledgling taken from captivity, and when being paired with a wild male for over 10 years and breeding in the centre of Warsaw, consistently showed an alertness and shyness typical of the wild individuals. By contrast, a pair staying in the Warsaw district Ruda (each year attempting nesting on the balcony of an inhabited flat) showed reduced shyness. The male of this pair has been reared in the falconry centre at the Warsaw airport (M. Luniak, in litt.).

Other two examples of a very quick synurbization of the raptors were those of the goshawk and sparrowhawk. In the Cologne/Köln area, the number of nesting goshawk pairs suddenly increased from three in 1989 to 14 in 1992 (Würfels 1994). Their tameness was remarkable; sometimes settling to breed 30 m from buildings or in frequented public parks. The same was with the sparrowhawks in Prague, where in 1980, even c. 90 breeding pairs were found, some close to the city centre (Peske 1990). Before this, in several Central European cities, wintering of wild sparrowhawks was known to be regular, but in the Czech Republic, the captive females of this species were additionally used for developing falconer skills (personal inf. from Czech falconers). Yet, in Łódź (Central Poland), where falconer practice was not known (Z. Wojciechowski in litt.), an increase of the sparrowhawk population happened as well, during 2000–2010 to reach 34 breeding pairs, some within the truly urban zone (Janiszewski et al. 2012). Increase proceeded here from the peripheries into the city centre, apparently without human help. In three cities, including the East Polish Lublin (Biaduń 2006), breeding sparrowhawks showed remarkably low shyness, presumably acquired during wintering in towns, but maybe also strengthened by unknown human support. It remains intriguing why tame urban sparrowhawk populations have been started in just those three cities, while not in dozens of neighbouring ones. Here, the telemetry technique may be helpful, as it documents how far, even well into other countries, some hand-reared raptors may disperse. Such distant movements may obscure disclosing ties between captive origins of a bird and elsewhere observed colonization of urban areas.

14.3.3 Human Help in Establishing Urban Pigeons and Doves

Several species from the family Columbidae were the subject of many attempts to domesticate them or to turn into cage birds. Most such attempts have been forgotten as unsuccessful or remain unknown as perhaps preceding in time a scientific report. One species, however, the rock/feral pigeon, may serve as an example not only of a millennia long process of domestication, breeding and exchanging these birds between distant human settlements. Not only has it been introduced into North America but was exchanged even between European cities: feral pigeons have purposefully been introduced into the second largest Polish city, Łódź, in the 1950s, when some hundreds of specimens were brought there from Warsaw and Cracow (Janiszewski et al. 2009). Numerous past attempts of taming and captive breeding are known (e.g. Brehm 1831) and of releases or escapes of other columbids, chiefly those which recently form strong urban populations, such as the collared dove; palm dove, *Streptopelia senegalensis*; and wood pigeon, *Columba palumbus*. Concerning the last species, I personally heard from pigeon breeders about two recent attempts to "domesticate" young wood pigeons taken out of wild nests in Poland. Attempts were classified as "unsuccessful", because captive reared, even tame, individuals always showed a strong migratory restlessness during autumn migration. They disappeared when released, which does not necessarily mean that they could not breed in human settlements the following season, becoming "pioneers" of urban breeding.

14.3.4 Introductions of Cage Birds into European Cities

14.3.4.1 Parrots and Exotic Passerines

Human contribution to the creation of urban populations of birds from other systematic groups is best exemplified by parrots. Recently in South and West Europe, mainly in greater cities, breeding populations of several species thrive: the ring-necked parakeet, *Psittacula krameri*; Alexandrine parakeet, *P. eupatria*; monk parakeet, *Myiopsitta monachus*; budgerigar, *Melopsittacus undulatus*; yellow-crowned Amazon, *Amazona ochrocephala*; blue-fronted Amazon, *A. estiva*; and yellow-collared lovebird *Agapornis personatus* (Christensen 1997; Hagemeijer and Blair 1997; Murgui 2000; Kelcey and Rheinwald 2005). In other European cities, including Moscow or Valencia, breed or used to breed small populations of exotic passerines: common myna, *Acridotheres tristis*, crested myna, *A. cristatellus*, and blue-glossy starling, *Lamprotornis chalybaeus*. As parrots and mynas originate from other continents, it is certain that their urban populations descend from cage birds.

14.3.4.2   Native Passerines

In contrast to "exotics", the native birds originating from captivity can easily be overlooked among wild conspecifics. Most ornithologists and birdwatchers tend to forget how widespread keeping cage birds was (until the middle of the twentieth century), a custom later replaced by radio. As late as the 1960s, there were a few active cage bird keepers or breeders in Warsaw (Luniak et al. 2001) while in Voronezh even to the present day (Numerov et al. 2013). Captive birds could increase chances for initiation of urban populations in two ways. First, unintentional, through attracting wild birds to caged birds in zoological gardens, where the former could adjust to the close presence of people. Such was the well-monitored case of an initiation of a synurbic hooded crow, *Corvus cornix*, population in Wrocław. Now this city is distinctive, owing to its very high breeding densities of this species, up to 0.5–1 pairs/ha in the city-centre districts and downtown parks (Tomiałojć 2005). The first tame crow pairs since c. 1960 were formed by individuals escaped from the local zoo and mating there with wild individuals, which used to forage in or at the enclosures for big mammals and, thus, had to stay close to crowds of people (after zoo-specialist, J. Danecki, pers. inf.). Recently an initial urban population of this species has also been monitored at the Łódź Zoo (Janiszewski et al. 2009).

The second way was through the release of tame songbirds during springtime (at Easter)—once a widespread and centuries-long tradition in Europe. However, before being released or escaped, some cage songbirds used to be the object of bird trade and transport even to distant markets, partly for an exchange of different song dialects (Taczanowski 1882; Pax 1925; Stastny et al. in: Kelcey and Rheinwald 2005). Such birds often were "mercifully" released, a.o. into an urban habitat, like c. 300 finches purchased and released at Easter 2012 in the centre of Voronezh (Numerov et al. 2013). The oldest written hint about a pair of released captive European blackbirds, *Turdus merula*, comes from 1781 in Orleans (France). Possibly that pair had constructed its nest in the same home yard while the male with song "expressed his gratitude" to its owner (Defay 1785 after Heyder 1969). Though this is not necessarily had to be the very beginning of the blackbird urban population in Europe, as not much later (1803), the reports appeared on urban blackbirds in distant towns (Leipzig, Dresden) of Central Germany (CL Brehm, after Rutschke 1980) or from Rome c. in 1828 (Cignini and Zapparoli in: Kelcey and Rheinwald 2005), yet such indeed could be the very beginning too. Also known are some purposeful replacements of urban birds between cities, chiefly blackbirds and song thrushes, *T. philomelos*, e.g. in 1906, six tame (urban?) blackbirds have been replaced to Posen/Poznań cemetery (Hammling and Schulz 1911) most probably from Thüringen (see Fig. 14.1). Precise information about their origin comes from a hint in old German literature. Remarkably, an increase of urban blackbirds in Poznań had been started exactly in 1907 (Hammling and Schulz 1911). Owing to the once widespread trade of cage birds (mostly from Thüringen and the Harz Mts in Central Germany, once known as two strongholds of the trade
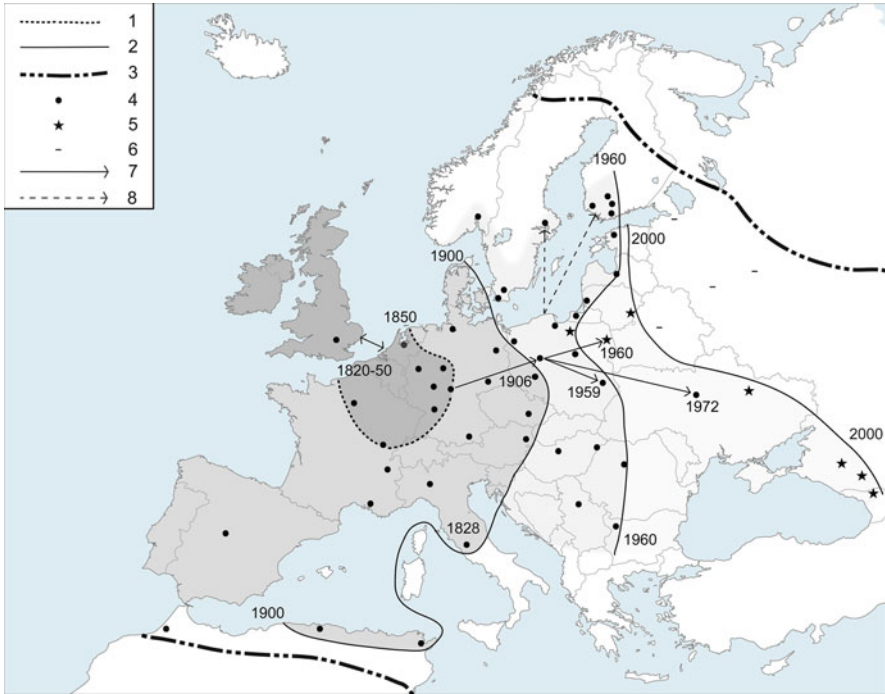
Fig. 14.1 Historical stages of the range expansion of urban blackbirds by 1850, 1900, 1950 and 2000. *Dots*—main cities with well-established synurbic populations, *stars*—cities with a few pairs in larger parks or in peripheries. *Arrows* show the range and direction of (known or suspected) replacements of urban birds. Compiled after Heyder (1955), Tomiałojć (1985), Luniak and Mulsow (1988) and updated according to recent literature and correspondence

of "Stubenvögel", see Berlepsch 1900), it was highly possible that, during the first half of the twentieth century, some other German blackbirds could have been replaced to Danzig/Gdańsk or Königsberg/Kaliningrad, cities then populated by Germans, and perhaps even to Helsinki and Stockholm. Such a guess can be deduced from the unexpected early emergence of those north-easternmost urban populations (Tomiałojć 1985).

Later relocations of captive bred blackbirds were continued as controlled experiments. During the 1950s some urban individuals have been replaced from Poznań to Lublin and Białystok in Eastern Poland, with full success in Lublin (Graczyk 1959). In July 1972 not less than 103 young urban blackbirds from Poznań, reared in captivity, have been released into the park of Kiev Zoo, Ukraine, again with success (Grachik et al. 1975). Synurbic blackbird population in Kiev continued to breed and increase throughout the 1980s and after 2000 (Kostiushin 1983, N. Atamas, in litt.).

14.4 Discussion

14.4.1 Synanthropy as Preadaptation of Birds to Breeding in Cities

Ancient data indicate that some bird species (house sparrow, swallow) were breeding close to humans several thousand years ago, either in caves or in tents/huts of ancient nomads (Schnurre 1921; Gladkov 1958; Bezzel 1982; Bocheński et al. 2012). With the change from nomadic to agricultural lifestyle, permanent villages appeared across most of Southern Asia and Europe. With them, or somewhat later, synanthropic birds had to spread geographically, either because of the abundant food supply of human habitats or owing to safety from predators. A few species (*Passer domesticus*, *Hirundo rustica*, *Tyto alba*, *Athene noctua*, *Ciconia ciconia*) turned into obligatory man followers, while others showed a preference for human neighbourhoods (*Apus apus*, *Corvus monedula*, *Delichon urbica*, *Milvus migrans parasiticus*). After a denser network of villages and towns was established, this group together with domestic pigeons (*Columba livia dom.*) expanded from the Middle East/Mediterranean Basin refuge into Western and Central Europe. Such a sequence of events can only be inferred, however, because the earliest written notices about "breeding close to humans" (e.g. concerning starling, house sparrow and other birds, mentioned by Gesner 1669, citation after Moller 2014 or by Cygański 1584 and Rzączyński 1721 citations after Bocheński et al. 2012) fail to differentiate between breeding in villages or within an urban habitat. Archaeological sources (e.g. Yalden and Albarella 2009; Bocheński et al. 2012) are useless here as well, as there is no indication whether bone remains were of birds breeding, wintering or were brought into towns from outside. Nevertheless, it can be safely assumed, that for millennia, long periods of living of some synanthropic birds in rural areas helped to colonize urban habitats, either still in their native lands or in Europe.

14.4.2 Origin and Character of the Very First Urban Colonizers

According to Carrete and Tella (2011), urban colonizers do not appear to be the individuals from more tame species but rather tame individuals from species with a variable response regarding fear of people and in accepting urban conditions. This suggests that behavioural flexibility should be regarded as a specific trait encompassing variability among individuals (see Miranda 2016). Signs of such individual variability have been documented in experiments with forest versus urban blackbirds reared in captivity (Walasz 1990), as well as strikingly different levels of shyness were observed to occur among individuals constituting undoubtedly natural forest populations (e.g. one from the Białowieża Primaeval Forest,

where an incubating female blackbird refused to leave her nest even when touched by an observer, and another escaping from her nest located at a height of 15 m when an observer was still 50 m from the nesting tree—own obs.). A degree of shyness-tameness may be individually related to a general level of nervousness (Wilson et al. 1994). Yet apart of inborn individual low nervousness, such features may also be acquired or strengthened by early experience, unknown to us, either through post factum spontaneous habituation to the presence of people while staying in cities or—still earlier—when being born or reared in captivity. Therefore, establishing truly urban (synurbic) populations might proceed in several ways, including by human-supported, unintentional or by purposeful introductions.

Here it should be added that according to old studies, even small birds and their eggs used to serve as a source of protein to humans for centuries, chiefly during springtime food shortages. This factor could contribute to maintaining a high shyness in birds of older times, causing them to postpone in some regions settling to breed close to humans.

14.4.3 Mechanisms of Further Increase of an Initiated Urban Population

How development of the once initiated urban population proceeds further remains poorly understood. Theoretically two possibilities were considered: either it might be a mere replenishment of the first "pioneers" exclusively (an inbreeding), resulting in a whole synurbic population descending from them, or the development of local urban populations may incorporate additional colonizers from the nearest natural population. The synurbic population may also acquire a mixed genetic character, but with passing time, presumably with a prevalence of the local geno-type. Such a compromising scenario on a mixed origin of the individuals building up a population in a new city has once been formulated (Tomiałojć 1985), but in the newest papers (Evans et al. 2009, 2010), it has been omitted. Yet in accordance to the "mixed-origin" model:

(a) The first examples of low shyness and an ability to nest in the city-centre zone could be brought into the city by the "pioneers" originating either from captiv-ity, from synurbic populations of other cities, or by wild birds which have lost shyness (due to habituation) while staying at the municipal zoological gardens or by wild birds settled to breed in the "remnants" of wild habitat patches surrounded by an urban sprawl.

(b) Later, the song of first colonizers established in urban areas might become a stimulus attracting later arriving dispersers or migrants (females and young males) to settle in the vicinity of earlier established (older) males. Here, a "conspecific attraction" may take place, when younger males follow experi-enced ones in selecting the habitat for breeding (Svärdson 1949; Smith and Peacock 1990; Fuller 2012). This has been described on the example of several

thrushes and *Phylloscopus* warblers (Morozov 2001/2002; Grendelmeier et al. 2013), as well as confirmed experimentally for titmice (Mönkönen et al. 1990). Moreover, attraction and imitation of urban "pioneers" does not need to be restricted to conspecifics, because strong data indicate the importance of "heterospecific attraction" as well (Morozov 2001/2002). Examples of both types of attraction by earlier urbanized individuals and species were incidentally observed for long among captive-bred waterfowl (Sokołowski 1973; Ptaszyk 2003; Avilova et al. 2007). Similarly, an overt behaviour and high breeding densities of some urban populations were shown to attract additional conspecifics and several other species, and sometimes to build up the highest overall bird densities in Europe—>300 pairs/10 ha—as this was in a decade-long monitored breeding bird assemblage of the Legnica Central Park, or in a park of Dijon, France (Tomiałojć 1980, 1998, 2007). According to this line of reasoning, urban zoological gardens can be seen as multispecies animal colonies with such their attributes as, as very high breeding densities, high level of noise, overt behaviour of settled individuals indicating safety of nesting and the absence of main predators. The strength of intraspecific and interspecific attraction of zoos may even attract the colonies of grey herons, *Ardea cinerea*, as in Vienna or Wrocław.

However, even if a newly established population in some new city was initiated by tame or captive-bred individuals, or by birds from other cities, after decades of "attraction" of wild birds from the neighbouring areas, this may terminate with a situation when local synurbic populations will be getting more and more similar to the local non-urban ones.

The mixed-origin model helps to explain an apparent contradiction between two phenomena: genetic similarity between local urban and rural populations developed owing to a gene flow between them ((Evans et al. 2009, 2010), and the fact that some synurbic populations show a clear geographical expansion, apparently because of the transfer of some birds from city to city. There is no inconsistency here, because transmission of the first carriers of low shyness and of the ability to breed in an urbanized habitat could be transmitted by a single or by few "pioneers", while later quantitative development of once initiated urban population may involve attracting individuals from neighbouring non-urban populations, chiefly when wintering in or visiting urban areas during migrations.

14.4.4 A Geographical Expansion of Some Synurbic Populations

At a geographical level, two theoretical possibilities have been considered: (a) "monophyletic" emergence of an urban population at first in just one city, with subsequent expansion of the modified population into other cities, or (b) emergence of several urban populations independently, in isolation from each

other, thus "polyphyletically" (Tomiałojć 1985). At first, the answer to this alternative was expected to be obtained from the knowledge whether urban populations from neighbouring cities remained genetically isolated or maintained contact with each other above the conspecific wild populations in between. Early observations have clarified this issue at least in the case of typical synurbic populations developed in the originally migratory species (Mallard, Woodpigeon, Blackbird) where an exchange of individuals between urban and neighbouring wild populations remains maintained (Tomiałojć 1980; Luniak and Mulsow 1988). Recent studies also confirmed that even between urban and neighbouring rural blackbird populations, a considerable genetic similarity occurs (Evans et al. 2009), and only a small genetic difference and a rather high gene flow have been found among Warsaw kestrels and those from two rural areas (Rutkowski et al. 2010). From this, a conclusion about "independent colonization of multiple urban centres" has been drawn (Evans et al. 2009), suggesting that (all?) blackbird urban populations descend from ancestors originating from nearest to particular town wild populations. Though this may be true in several cases, such a scenario conflicts with a well-documented phenomenon of geographic expansion of the Central European synurbic populations of just the blackbird and wood pigeon, as clearly progressing mainly into the NE and E (Pax 1925; Heyder 1955; Graczyk 1959; Tomiałojć 1985; Luniak and Mulsow 1988), i.e. mostly in accordance with the direction of their spring migration (Figs. 14.1 and 14.2).[1] At least in the wood pigeon case, this expansion suggests spontaneous replacements of some urban individuals from city to city. Subsequent development of urban bird populations presumably strengthened by conspecific and heterospecific attraction helps to better understand the geographical expansions of a "synurbization wave" within the species range.

In strictly resident species (as their Western and Central European populations are), a different pattern seems to emerge—the lack of a clear geographic expansion. Instead, a kind of a "polyphyletic", contemporaneous and independent, multiple origins of several urban populations in distant cities could be observed. The best example was that of the carrion/hooded crow synurbization, which after World War II followed a period of weaker persecution by game keepers and hunters causing a restoration of its strong rural populations. During the 1960s crow synurbization started fairly simultaneously in distant cities as London, Frankfurt, Hamburg,

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[1]In one respect the patterns of main expansion differ between two species. The urban blackbird populations expanded from the NW part of the centre of the continent in all directions, with the prevalence of NE settlement, while those of urban wood pigeons moved mostly to the east, across the European Lowlands, i.e. areas dominated by agricultural land. The latter ones clearly avoided colonizing the cities in sub-mountainous and mountainous regions, presumably because of the surrounding extensive forests. This agrees with an earlier finding that towns amidst farmland tended to hold several times higher wood pigeon densities than the neighbouring ones surrounded by forests (Tomiałojć 2005). Yet, in the past, the blackbird as well, at least between 1820 and 1850, was showing a delay with colonizing the towns amidst a mountainous and forested region (Heyder 1955).
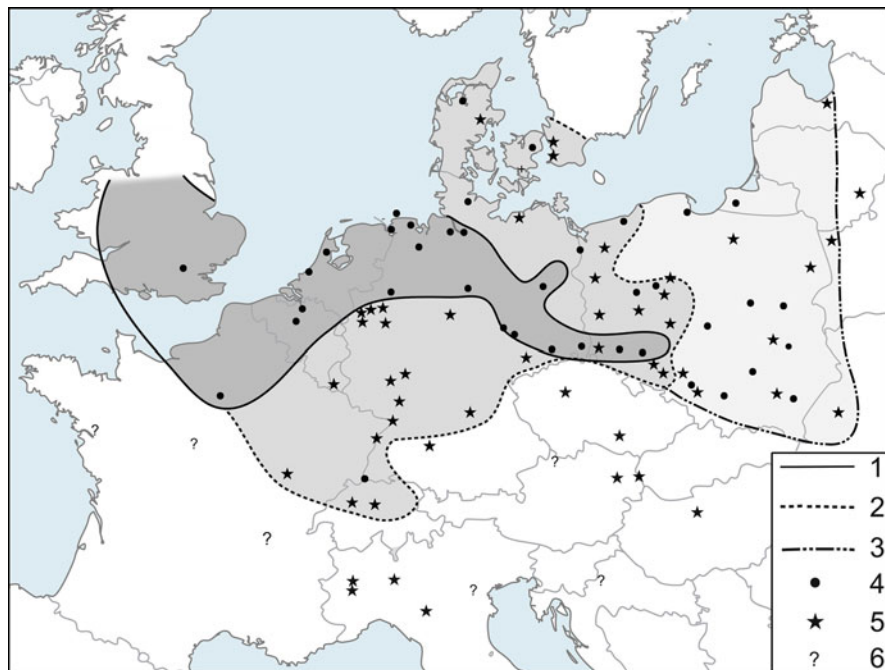
Fig. 14.2 Historical stages of the range expansion of urban wood pigeons by 1850, 1900, 1950 and 2000. *Dots*—main cities with well-established populations, *stars*—cities recently with a few pairs in the peripheries. The figure rounds up the more detailed map by Tomiałojć (1976) and updates it based on recent literature and correspondence

Berlin, Warszawa, Grodno, Moscow and, since the 1970s, also in Wrocław and Vien, while leaving free of crows, dozens of big cities in between (Glutz von Blotzheim and Bauer 1993; Tomiałojć 2005). At least four common features of early occupied cities can be pointed out: large size of urban agglomeration (a distinct isolation from rural populations), presence of a big river, the absence of main enemies (goshawk, peregrine falcon, pine marten) and the presence of large zoological garden, where wild crows had an opportunity to feed and adjust to the close presence of people. On the other hand, there are no clear signs of an individual exchange among several neighbouring cities with synurbic crows and those without them. It would be interesting to know if synurbic populations of other truly resident birds like the house sparrow, magpie, tree sparrow or feral pigeon exchange urban individuals among distant cities.

14.5 Summary

The first stage of adjustments to living close to humans—synanthropy—prepared some birds to later colonization of densely built and noisy cities. Subsequent "synurbization" of some species could be in several ways initiated or strengthened directly or indirectly by humans, more frequently than this can be inferred from the literature. Experiments of taming wild birds were often undertaken by laymen, thus, leaving no written traces. A few precise hints on tame or captive reared birds, sometimes replaced between distant sites, cities and regions, however, do exist. Moreover, during earlier centuries, thousands of cage birds kept in human homes were traded between cities, purposefully released or were escaping from captivity, while the waterfowl species were tamed or bred in waterfowl centres and in zoological gardens. As a result, European avifauna has been "contaminated" not only with exotic species escaped from captivity but presumably also filled up with secondarily tame individuals of several native species. Some of them could become the "pioneers" colonizing human settlements. Subsequent increase in abundance and adjustments of urban populations changing into truly synurbic ones probably resulted not only from mere reproduction but also due to attracting wild birds to urban habitats. This could proceed owing to "conspecific attraction" and/or "heterospecific attraction". As a consequence of such a "mixed origin" of tame and wild individuals, the later developed synurbic populations should now be dominated quantitatively by a local genotype, which overshadows the genetic contribution of a few "pioneers" from distant populations. And exactly this has recently been found to be the case (Evans et al. 2009). Such a finding does not prove, however, "an independent colonization of multiple urban centres"—because transmissions of small groups of individuals between distant cities have been documented and may be inferred from geographic expansions of urban populations of migrant species.

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Chapter 15
Bird Diversity Improves the Well-Being of City Residents

Marcus Hedblom, Igor Knez, and Bengt Gunnarsson

Abstract Humans are increasingly becoming urbanized. Because a number of bird species readily live in urban areas and birds are relatively easily observed, birds are becoming the largest everyday encounter with wild fauna people will have, globally. Despite, few studies have been made on how visual (or acoustic) bird encounter affects humans. The few existing studies show that birds provide humans with increased self-evaluated well-being when seeing and hearing them. These values provided by birds can be recognized as a cultural ecosystems service.

Here we review extant literature to consider why certain species fascinate humans more than others, and some can increase well-being and provide ecosystem services, while others offer disservices through unappealing characteristics. We particularly highlight indications of links between species diversity and well-being. Finally, we discuss possible reasons for variations in our responses to birds and birdsong associated with age, gender, childhood, contact with nature, and the biophilia theory.

If interaction with birds truly increases quality of life, then this value should be considered in the planning of sustainable cities. Both conservation and proper management of existing urban green areas are needed to increase possibilities to encounter many bird species.

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15.1   Introduction

Humans have become increasingly distanced from nature, both physically and emotionally, as the global population has shifted to urban areas. Although numerous animal species have adapted to urban life, birds are the wild fauna that people most commonly encounter, apart from substantially smaller taxa such as insects, in their everyday life (US Department of the Interior et al. 2011). Birds are active during daytime, easy to spot by sight or hear through birdsong, and have little fear of humans. Nevertheless, most previous research concerning urban bird fauna has focused on aspects related to their ecology, urban adaptations, and evolutionary processes, while the visual and acoustic effects of bird encounters on our well-being have generally received little attention. However, interest has emerged recently in birds' potential cultural values for humans, particularly in cities (Fuller et al. 2007; Bjerke and Østdahl 2004; Luck et al. 2011; Clucas and Marzluff 2014; Hedblom et al. 2014; Shwartz et al. 2014; Belaire et al. 2015).

It is not surprising that the potential cultural values of birds are being recognized in the urban environment. Bird density is higher in cities than other landscapes; hence there are higher frequencies of encounters between birds and urban residents (Marzluff 2001; McKinney 2002; Shochat 2004). Furthermore, bird sighting is easier in cities because birds have changed their behavior as they have adapted to urban environments, becoming less sensitive to humans (Jerzak 2001; Randler 2008 but see; Valcarcel and Fernández-Juricic 2009). Cities can also host a surprisingly high diversity of bird species (Lepczyk et al. 2016), especially in suburbs and natural remnants (Blair 2001; Hedblom and Söderström 2010). Additionally, humans can increase frequencies of interactions with birds by providing food and nest boxes (Lepczyk et al. 2012; Fuller et al. 2012).

The Millennium Ecosystem Assessment (MEA 2005) provides a potentially useful conceptual framework of cultural ecosystem services (consisting of spiritual, aesthetic, and cultural heritage and identity and inspirational, recreational, and educational values) for assessing birds' cultural values or immaterial services. Encounters between birds and humans can certainly have value in these respects, as several studies have shown that contact with nature reduces stress (Kaplan 1995; Grahn and Stigsdotter 2003; Hartig et al. 1991; Mitchell and Popham 2008; Tamosiunas et al. 2014; Alcock et al. 2014) and that certain habitats, such as woodland parks, have stronger stress-reducing effects than others, such as urban parks (Tyrväinen et al. 2014). Thus, as bird frequencies are strongly linked to urban greenery and wetlands, their sightings and sounds may be linked to the reported increases in well-being and/or reductions in stress associated with experience of nature.

The reasons why humans perceive birds in certain ways are complex. These perceptions seem to be influenced by cultural presentations in stories and film, as well as by individuals' gender, age, experiences of nature during childhood, and knowledge of ecology (Bjerke and Østdahl 2004; Cooper and Smith 2010; Shwartz et al. 2014; Belaire et al. 2015). Another explanation is offered by the biophilia

hypothesis that humans generally have a deep affiliation to other life forms (Wilson 1984). Moreover, it has been suggested that birdsongs and music share underlying biological mechanisms (Earp and Maney 2012). The perception of birdsong is also linked to human maturity, as older people seem to appreciate birdsongs more than younger people. Furthermore, gender seems to influence our perceptions of certain species (e.g., Bjerke and Østdahl 2004).

There also appear to be associations between knowledge of birds, our perceptions of them, and the attention paid to them. For instance, people who recognize more species also generally pay more attention to them, e.g., by providing food and nest boxes, and thus have more interaction with them. A further complication is that cities have limited urban green areas, so people who live close to them or have large gardens will have most contact with birds and nature generally on a daily basis. Thus, distances between people's residences and green spaces may be more important than knowledge of birds per se. Hence, the mechanisms involved in human appreciation of certain birds and birdsong are complex and far from well understood.

Here we review and discuss research on this transdisciplinary topic, most of which has focused on urban environments. We consider the few published studies on why some species affect humans more than others and apply results from a case study concerning birdsong combinations to address responses to perceiving multiple species. We then address findings regarding effects of age, gender, knowledge, and childhood memories on human perceptions of urban birds, mechanisms that may account for our perceptions of birds, and their links to the biophilia theory. Finally, we present reasons for taking these values into consideration for urban planning.

15.2   What Cultural Ecosystem Services Can Birds Offer?

The very meaning of an ecosystem services is to put a value on something that benefits humans, in our case the perception of urban birds. The MEA (2005) definition of cultural ecosystem services relates to words such as *appreciation*, *well-being*, *restorative perceptions*, *education*, *and spiritual enrichment* and differs from the interpretation of words used in the scientific literature of urban birds and cultural ecosystem services. Few studies explicitly use the framework of cultural ecosystem service to describe their frame of reference, although they do highlight topics raised by MEA (2005). This means that there are broader definitions of the cultural ecosystem service concept than the Millennium Ecosystem Assessment (2005) defines.

For example, it is difficult to allocate studies in urban areas using the term "spiritual values," although it is most likely that people experience specific environmental (i.e., biophysical and social) features as spiritual in the natural settings (Fredrickson and Anderson 1999), such as birds.

The concept of "inspiration" has been investigated by Plambech and Konijnendijk van den Bosch (2015), who mentioned birdsong as one of many natural factors that can inspire creative thinking. Measuring potentially relevant variables such as a bird's visual aesthetic appeal is far from straightforward (Belaire et al. 2015). Hence, many studies rely on self-evaluated estimations of effects of considered variables on people's well-being or other responses, but physiological variables such as saliva cortisol levels may provide more robust estimates of stress reductions and other important responses.

Ulrich et al. (1991) found that people exposed to natural settings (vaguely defined as areas free of people with trees, a light breeze, and birds) rather than various urban environments use lower levels of painkillers. Thus, even if a value of perceiving birds is obtained in some way, it must be interpreted in the context of pertinent background variables that relate to the ratings (e.g., which species is rated against which) or local cultures or similar. We begin by reviewing the existing literature concerning human perceptions of birds, especially those in cities.

15.2.1 Humans' Perceptions of Birds

The book *Birds and People* by Cocker and Tipling (2013) highlights cultural interactions between birds and people throughout history, providing insights into why humans appreciate certain birds and disapprove of others. Humans particularly seem to appreciate species that are visually spectacular and have distinguishing characteristics regarded as attractive. Prime examples are hummingbirds, which seem to be highly popular due to their extremely small sizes, bright colors, ability to hover, and ease of spotting (especially when a feeder is provided). Furthermore, as nectar feeders they do not adversely affect any vital human activities (such as farming or garden plants) or threaten to kill or injure other animals. General features of birds that promote popularity seem to include attractive plumage and a non-provocative character, according to Bjerke and Østdahl (2004). These authors also note that small species with nice songs are highly appreciated and seem to be associated with spring, summer, and organic growth (see also Ratcliffe 2015, p. 136), at least in temperate areas since spring and summer are not as well defined in the tropics.

However, various other factors also affect bird popularity, as not all birds with spectacular size are popular. For example, the marabou stork *Leptoptilos javanicus*, which breeds in urban areas, is rather spectacular but has, according to Cocker and Tipling (2013), a reputation for being one of the world's ugliest birds. Furthermore, not all birds that are easy to spot in the garden are popular, for example, the red-faced mousebird *Urocolius indicus* is poisoned, or even shot on sight, due to its inclination for the fruits and flowers of suburban gardens in southern Africa (Cocker and Tipling 2013).

Disservices of birds are surprisingly pronounced in the urban bird literature. Belaire et al. (2015) argue that people remember experiences with negatively

perceived bird species more clearly than experiences with positively perceived species. Accordingly, numerous studies highlight negative perceptions. Notably, Clergeau et al. (2001) found negative attitudes toward various bird species in French urban environments, for example, herring gull *Larus* spp., European starling *Sturnus vulgaris*, house sparrow *Passer domesticus*, and rock dove *Columba livia*. Similarly, Belaire et al. (2015) found that urban residents in the Chicago area not only had negative perceptions of the house sparrow, common grackle *Quiscalus quiscula*, and blue jay *Cyanocitta cristata* but also, surprisingly, mentioned no positive qualities of these birds. According to Belaire et al. (2015), these three species had negative associations due to not being "pleasant to the eye" or not having "spiritual values." Belaire et al. (2015) further argue that these negative experiences were not seen as a major problem, but rather were exaggerated and did not reflect the birds' real characteristics and/or people's true responses. Clergeau et al. (2001) reached a similar conclusion, as people interviewed in Paris had negative perceptions of some species, but 69–74 % of the interviewees found pleasure in the presence of birds.

Although numerous negative associations and experiences with birds are described in the literature, there *are* positive attitudes toward many bird species in urban areas. Some species are positively perceived in gardens, such as hummingbirds, robins, cardinals, and blue jays (Dawson et al. 1978), while other species, such as blackbirds, starlings, and ducks/geese, are positively perceived when not in the immediate garden (Brown et al. 1979). A study in Norway found that "small birds" and "ducks" were among the most highly rated urban animals (Bjerke and Østdahl 2004), indicating that species do not need to be visually vibrant to attract people. Furthermore, most birds are heard rather than seen, and natural sounds of the wind, water, and birdsongs are known to have restorative effects on humans (Ratcliffe et al. 2013). Additionally, natural sounds mostly have been compared with less attractive sounds from, e.g., noisy traffic (Viollon et al. 2002), and it is perhaps not very surprising that people prefer birdsong prior to traffic. However, most studies that highlight the positive influences of birdsongs mention only "twittering birds" or "birdsong" as the sound used, rather than a song of a specific species (e.g., Viollon et al. 2002; Annerstedt et al. 2013). This is somewhat surprising, since birdsongs vary greatly between species.

In the cited study by Ratcliffe et al. (2013), 20 British adults were played tape recordings of natural sounds, and birdsong was rated most frequently (by 35 % of the participants) as having the best potential for reducing human stress, followed by sounds of water (24 %), non-avian animals (18 %), elements (e.g., soft wind and rain 12 %), and other sounds such as interaction with nature and silence (11 %). Ratcliffe (2015) built on these findings in her doctoral thesis by proposing that certain birdsongs have higher "restorative perception," described as the potential to reduce stress, than others. Her respondents also ranked the songs of 50 common bird species from the UK and Australia according to their aesthetic value and self-perceived restorative potential. The Australian species were included to provide novel bird sounds to British respondents. Respondents were asked to listen to a birdsong and imagine how it would help them recover from certain stressful

scenarios, such as having an argument with a friend and feeling very stressed afterward. The results indicated that smooth or consonant sounds were considered more pleasant than rough sounds. However, she found no connection between either the pitch of a birdsong and its appeal to humans or the pitch and arousal. Pitch is defined as the perceived highness or lowness of a sound and is related to frequency (the number of sound waves per unit time). Thorpe (1961) found that low-frequency sounds were negatively associated with larger birds such as crows, jays, magpies, and owls, while high-pitched bird sounds were associated with positive values for humans. Similarly, Björk (1985) found that unpleasant sounds had low frequencies. Thus, low frequencies could be perceived as unpleasant because they are associated with large, potentially aggressive birds. On the other hand, high frequencies could have positive associations and may have higher restorative potential.

When qualitative aspects, such as *association* and *memories*, of the 50 bird species were ranked, the species with the highest scores were found to be abundant in urban areas, gardens, and even indoor environments (Ratcliffe 2015). For example, the three highest-ranked species, on a scale from 0 to 6, were dunnock (*Prunella modularis*; score 5.26), greenfinch (*Carduelis chloris*; score 5.23), and blackbird (*Turdus merula*; score 5.06), all of which are common in British gardens. In contrast, the three least appreciated were Australian raven (*Corvus coronoides*; score 1.65), red wattlebird (*Anthochaera carunculata*; score 1.50), and silver gull (*Chroicocephalus novaehollandiae*; score 1.50) (Ratcliffe 2015, p. 128). These results show that the perception of a species is strongly influenced by memories and associations of rather ordinary birds in the everyday surroundings.

15.2.2 Birds as Representatives of the Natural World in Urban Settings

There has been concern that residence in urban areas causes people to distance themselves from and lose an understanding of nature (Myer and Franz 2004; Miller 2005), particularly as a large and increasing fraction of the global population experiences childhood in urban areas with decreasing natural spaces. Hence, many people will have their first, and maybe only, interaction with nature in cities. Accordingly, several studies have shown that urban residents have limited knowledge about the birds that inhabit their cities (Dallimer et al. 2012; Shwartz et al. 2014).

A nationwide study in Denmark found that almost half of the respondents were motivated to visit parks and green spaces due to the presence of fauna and flora (Schipperijn et al. 2010). A similar survey in Paris noted that people visited the gardens to interact with nature (Shwartz et al. 2014). However, Miller (2005) argues that conservationists have failed to convey the importance, wonder, and relevance of biodiversity to the general public, tending to "preach" to those already engaged,

rather than reaching the unconverted and leaving the public with a feeling of helplessness about species extinction and habitat conservation. Miller (2005) further argues that if people could experience meaningful connections with nature close to where they work or live, then the connection between humans and the natural world would improve. This is consistent with suggestions by Belaire et al. (2015) that birds could connect urban residents, land managers, and environmental policymakers regarding the enhancement of ecosystem services. Similarly, Fuller et al. (2012) argue that feeding birds in public gardens could improve the engagement between humans and nature, leading to positive effects on quality of life. Efforts in this area could have large effects as, for example, 43 % of Arizona's population and 66 % of Michigan's population feed birds (Lepczyk et al. 2012). Furthermore, 200 million GBP (US $390 million) is spent annually in the UK and $3.5 billion in the USA (Fuller et al. 2012) on bird food. Clearly, feeding birds is a popular way for people to connect with nature. Birds *can* awaken an interest in the natural world and motivate people to learn how to appreciate it.

15.3 Perception of Bird Biodiversity

There is increasing evidence that a combination of bird species may be perceived more positively than the presence of a single species (e.g., Fuller et al. 2007; Luck et al. 2011; Hedblom et al. 2014). However, this conclusion is controversial as some studies have found that higher diversity increases well-being, while others identify perceived diversity to be more important than actual diversity (e.g., Dallimer et al. 2012; Belaire et al. 2015). We consider associations between diversity and perceptions in more detail in the following section, which begins by presenting findings from case studies of human responses to various birdsong combinations.

15.3.1 Case Study of Responses to Birdsong Diversity

In a preference experiment conducted in Sweden, 44 environmental science students were asked to rate various combinations of birdsongs (Fig. 15.1). The hypothesis was that species richness would be positively correlated with the ratings, based partly on results of a survey by Fuller et al. (2007) of perceptions of users of public urban green spaces in Sheffield, UK (including findings of a significant positive relation between bird species richness and psychological benefits, defined as *continuity with past and present*). The preference study was subsequently followed up in another study with fewer birdsong combinations but more participants (Hedblom et al. 2014).

Birdsongs were played for 45 s on loudspeakers in a lecture room, and then the participants were asked to rate their appeal on a scale of −7 to 7, with negative and positive numbers reflecting negative and positive associations, respectively. Songs
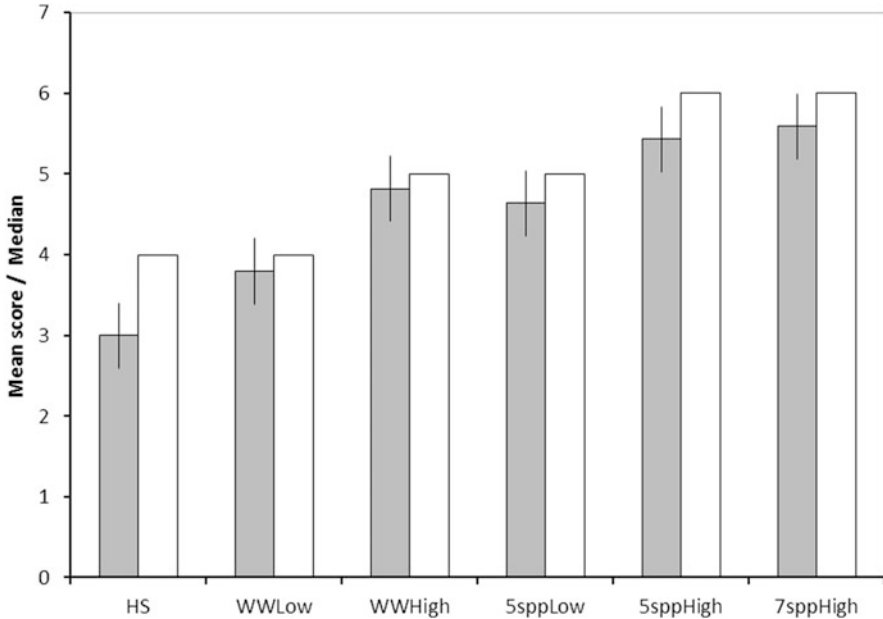
Fig. 15.1 Ratings of birdsongs of individual species and combinations of species with varying strophes. The *gray* and *white bars* indicate mean and median ratings, respectively. HS = house sparrow, WWLow = willow warbler with few (low abundance) strophes, WWHigh = willow warbler with many (high abundance) strophes; 5sspLow = five species with few (low abundance) strophes; 5sspHigh = the same five species with many (high abundance) strophes; and 7sspHigh = seven species with many (high abundance) strophes

could also be given a neutral score of 0. The effect of bird diversity was tested by playing songs of both individual species of birds and combination of species. The effect of bird abundance was tested by playing birdsongs with varying numbers of strophes (discrete birdsongs). For example, respondents were exposed to two willow warbler (*Phylloscopus trochilus*) sounds, one with 8 strophes and the other with 23 strophes. The combinations, played in random order, were house sparrow (33 strophes); willow warbler (8 strophes); willow warbler (23 strophes); five species, including chaffinch *Fringilla coelebs*, blue tit *Cyanistes caeruleus*, great tit *Parus major*, and European robin *Erithacus rubecula* (eight strophes); the same five species (16 strophes); and seven species (the previous five plus common blackbird and great spotted woodpecker *Dendrocopos major*, 26 strophes).

All of the species included in the study are common in suburban woodlands of southwestern Sweden (Hedblom and Söderström 2010; Heyman 2010), except the house sparrow, which mainly breeds in urban habitats such as hedges. A panel of three experienced field biologists reviewed the birdsong combinations before they were played to participants to ensure that they represented sounds that may be heard in a natural setting.

Table 15.1 Mean ratings for birdsong combinations and results of pair-wise comparisons of the ratings by a nonparametric Friedman two-way ANOVA test (overall results; chi-square = 68.423, df = 5, $P < 0.001$)

3.00	3.80	4.82	4.64	5.43	5.59	Mean score
HS	WWLow	WWHigh	5sppLow	5sppHigh	7sppHigh	
	1.000	**0.003**	**0.029**	**<0.001**	**<0.001**	HS
		0.055	0.34	**<0.001**	**<0.001**	WWLow
			1.000	1.000	0.214	WWHigh
				0.271	**0.031**	5ssLow
					1.000	5sppHigh
						7sppHigh

For meanings of abbreviations, see the legend of Fig. 15.1
Bold values indicate significance of $P < 0.05$

As hypothesized, both density and diversity of species were positively correlated to the songs' ratings (Fig. 15.1). The house sparrow song was rated significantly lower than all of the others (Table 15.1), while the combination including songs of seven species was most highly rated and significantly more highly rated than songs of the house sparrow, willow warbler (low abundance), and five species (low abundance). The score of the second most highly rated combination (five species, high abundance) differed significantly from scores for the house sparrow and willow warbler (low abundance) songs, but not from the willow warbler (high abundance) song. Interestingly, there was little difference between ratings for the birdsong with contributions from seven species and the willow warbler song with large numbers of strophes. This suggests that not only the *number of species* but also *bird abundance* affected the respondents' ratings of sounds, i.e., the respondents rated songs of multiple birds highly, irrespective of the number of species. In another study (Hedblom et al. 2014), three birdsong combinations, all with high abundance, in combination with photos of three different urban settings, were used. The ratings of the urban settings increased when birds were singing and were highest when multiple species were singing.

15.3.2 What Affects Perceptions of Diversity?

The results described above did not clearly demonstrate whether the appeal of multiple birds' songs was based more on bird diversity or abundance. Ratcliffe (2015) dissected the soundscape of birds into "intensity (dB) or loudness," "pitch or frequency," "roughness versus smoothness," and "aesthetic properties," but did not consider abundance, measured as the number of strophes per unit time, as a potential factor in birdsong perception. Diversity was briefly discussed as being linked to positive environmental perception, but her research concentrated more on how complex bird sounds are perceived as "more pleasant" and "more fascinating" than simple ones (Ratcliffe 2015, p. 115).

The perception of diversity is clearly a complex phenomenon, and various studies have provided conflicting indications of influential factors' effects, but deviations between actual and perceived diversity could be related to the visibility of organisms. For example, the previously cited survey of users of public green spaces in Sheffield, UK, found that their perceived biodiversity of plants was strongly correlated with actual plant biodiversity, whereas perceived and actual biodiversity differed for more "cryptic" birds (Fuller et al. 2007). Shwartz et al. (2014) also found that participants in the previously mentioned study in Paris, France, preferred flower diversity to that of birds or trees

An important issue that has not yet been addressed is the relationship (if any) between species diversity and human well-being. Dallimer et al. (2012) did not find a consistent positive relationship between well-being of human visitors of urban green spaces and actual species richness. On the contrary, they found that as plant species richness increased, well-being tended to decrease and concluded that people in urban environments have a limited capacity to accurately gauge the diversity of natural environments. Thus, well-being may be positively related to perceptions of species richness rather than actual richness. Results of an intervention in the previously cited study by Shwartz et al. (2014) support this hypothesis. The bird diversity in Parisian public gardens was actively increased by adding nest boxes, and the actual bird diversity increased by 26 %, with an average of 3.2 new species per garden. Visitors, who were not aware of the experiment, were questioned about their biodiversity perception and sensitivity to biodiversity before and after the increase. The results showed that there was no correlation between perceived and actual diversity. The visitors claimed that biodiversity was linked to their perception of well-being, but they did not notice that the biodiversity of birds had increased during the experiment. In accordance with Dallimer et al. (2012), Shwartz et al. (2014) concluded that city dwellers generally have poor knowledge of birds and cannot distinguish species. Similarly, results of a study in Rennes, France, showed that people in urban areas, where bird abundance is high and diversity is low, rarely perceive birds (Clergeau et al. 2001). On the other hand, a clear majority of people living in suburbs, where abundance is lower but diversity is higher, do perceive them.

Humans use all five senses when perceiving biodiversity. However, Viollon et al. (2002) argue that visual and acoustic stimuli are interdependent. Accordingly, in a study by Benfield et al. (2010) in which participants were played various sounds while viewing scenes of national parks, anthropogenic sounds, such as air or ground traffic, seemed to disrupt the experience, but the natural sounds of birds and foliage rustling in the wind had no negative effects on perceptions of the landscapes. In addition, three of the song combinations from the abovementioned case study (Sect. 15.3.1) were used in another experiment, which involved showing photos of urban settings (pictures of multifamily housing units surrounded by varying amounts of greenery) with or without birdsongs (Hedblom et al. 2014). The results showed that all of the urban settings were rated more highly when birdsongs were heard, even if it was only the chattering of house sparrows. Ratings were further increased by increases in species richness, indicating that diversity of birdsongs enhances people's appreciations of urban landscapes. Arguably, perception also

depends on attention and interest, i.e., people with a keen interest in, and knowledge of, birds will spot them more often.

To summarize, an increase in the diversity of birds, both seen and heard, seems to increase self-reported well-being and ratings of urban settings. However, these conclusions are tentative because they are based on results of only a few studies. Furthermore, an increase in the diversity of even a rather species-poor environment does not necessarily increase its attractiveness or the well-being of people present in it. Additional studies are also needed to determine whether humans are more appreciative of songs by numerous birds or a high diversity of birds. Thus, differentiation of perceived and actual bird biodiversity seems to be more complex than previously thought. It is possible that there is a limit to the number of species that people can perceive and that this limit is lowest for people who live in cities due to a lack of taxonomic knowledge.

Background variables could also account for some of the variation in the perception of diversity (see Sect. 15.4). On the other hand, some of the deviations in findings regarding perceptions of biodiversity could be due to flaws in experimental design (as indicated by Shwartz et al. 2014), such as basing studies on self-reported measures of well-being, as argued by Hough (2014). Hough (2014) further argues that the direct relationship between actual biodiversity and health presented in literature needs further research. However, there are now several lines of evidence indicating a relationship between contact with nature and human health (Hartig et al. 2014).

15.4   Specific Characteristics Affect How Humans Perceive Birds

Demographic factors, including gender, age, knowledge, and education, as well as where a person grew up (e.g., in a rural or urban environment), have demonstrated links to individuals' connection to nature (see, e.g., Dawson et al. 1978; Bjerke and Østdahl 2004; Shwartz et al. 2014; Belaire et al. 2015). The relationships between demographic factors and connection to urban birds have been less intensively studied. However, distances to and the availability of urban natural green areas (or waters) seem to be important factors in the perception of birds, and they are also strongly related to socioeconomic factors.

15.4.1   Age Affects Perceptions of Birds

Generally, older people have more positive perceptions of urban birds than younger age groups (e.g., Shwartz et al. 2014; Belaire et al. 2015) and are willing to spend more money on feeding birds (Clucas et al. 2014). Bjerke and Østdahl (2004)

confirmed that older Norwegians more highly rated "small birds," "seagulls," and "magpies." However, ratings for "birds of prey" declined with respondents' age. Shwartz et al. (2014) also found that older men in France tended to give higher, and more realistic, estimates of true bird biodiversity than younger men. Very few studies have addressed the relation between children and birds but (Bjerke and Østdahl 2004) found that Norwegian children's favorite bird species were swans.

15.4.2 Gender as a Factor of Bird Perception

Previous research has shown that gender affects people's views of green spaces and their opinions about spaces' ideal purposes (Cohen et al. 2007; Kaczynski et al. 2009; Schipperijn et al. 2010; Tyrväinen et al. 2007). The differences between genders are also reflected in the perception of birds. In Norwegian cities, Bjerke and Østdahl (2004) found that women had significantly higher preferences for seagulls, magpies, and crows than men, who preferred birds of prey. Furthermore, women tended to rate popular taxa (such as small birds) higher than men and less popular taxa (rats, mosquitoes, and mice) lower than men. Cooper and Smith (2010) found that men and women also had different objectives for bird-related recreation. Women were motivated by altruistic factors, such as helping birds, teaching children, or assisting scientific endeavors. Men, on the other hand, were more focused on activities linked to achievements, such as bird watching. Women were also more likely to get involved in activities related to nest boxes and bird feeding (Cooper and Smith 2010). Gender-related differences have also been seen in younger age groups, as Zhang et al. (2014) found that 9–10-year-old girls in China showed more willingness to conserve species than boys of the same age. This is consistent with indications that gender may operate as a "critical filter," through which personal goals and aspirations are managed (Fivush et al. 2012), and that women are more concerned about future generations and environmental issues than men (Jackson 1993; Knez et al. 2013). Emotional differences based on gender have been detected across several cultures, indicating that women are generally more emotionally intense and expressive than men (Timmers et al. 2003). Additionally, environmental psychology research has shown that differences in age and gender affect how we perceive environmental stimuli, such as light (Knez and Kers 2000), which is perceived both consciously and unconsciously in the brain (Knez 2014a).

A Danish study (Schipperijn et al. 2010) also suggested that the motivation for visiting urban green areas could be influenced by age *and* gender. In the study, people over 65 reported stress reduction as the most important reason to visit an urban green area. Younger people reported their main reason to be enjoying the weather and getting fresh air, followed by stress reduction. In addition, the study revealed a clear gender bias in the stress comparison, whereas 71 % of young women found stress reduction most important, compared to 52 % of the young men (Schipperijn et al. 2010).

15.4.3 Experiences of Nature and Education Affect Perception of Birds

Experiences with wildlife in early years have been argued to increase the understanding of nature later in life (e.g., Thompson et al. 2008; Zhang et al. 2014). This viewpoint was confirmed to some extent by Shwartz et al. (2014) as respondents who had spent a large part of their childhood in green environments scored higher on a measure of bird biodiversity perception than those who had spent their childhood further away from nature. Another study showed that growing up in a village in Tanzania created strong connections to birds and their songs (Sanga 2006). However, the relation between early nature experiences and a connection to the environment was found to be weak among Chinese respondents surveyed by Zhang et al. (2014), possibly due to children in both rural and urban areas lacking opportunities to interact with nature. Nevertheless, most (62 %) of the urban Chinese parents wished that their children could experience green spaces elsewhere than in urban areas. In Sweden, Giusti et al. (2014) found that children who were exposed to nature in preschools were more empathetic and concerned for nonhuman life forms, and more cognitively aware of human-nature interdependence, than children who had received minimal exposure.

15.4.4 Distance to Urban Greenery Affects the Perception of Birds

Several studies have shown that distances between people's homes and urban green areas influence their knowledge of nature. Notably, Clergeau et al. (2001) found that sociological differences along the urban-rural gradient in Paris seemed to affect people's perception of birds. Few residents of central urban areas, with the least greenery, fed birds, read about birds, and knew when birds arrived in spring or even about their annual cycles. In contrast, attitudes of people in suburbs with more greenery were closer to those of rural residents, and they often responded that watching birds was a source of personal pleasure. Interestingly, 11 bird species were identified in the central urban area, 19 in the adjoining suburbs, 11 in distant suburbs, and 23 in the rural sector (Clergeau et al. 2001). Thus, access to greenery seems more important than a high diversity of birds for sparking a person's interest in birds and their ecology.

Wealth seems to be another factor affecting bird perception, as wealthier neighborhoods typically have more greenery and better access to natural areas than poor neighborhoods (Melles 2005; Hough 2014; Sander and Zhao 2015). In Chicago, Davis et al. (2012) showed that low- to mid-income Hispanic residents lived further away from both open spaces and lakes, in areas with less tree canopy cover and bird biodiversity than residents with higher incomes. There was also a significant difference between wealthy and poor neighborhoods in the distance from Lake

Michigan. However, areas largely populated by low-income African Americans did not significantly differ from higher-income areas in terms of proximity to open space, tree canopy cover, or bird biodiversity. It might not always be clear what the cause is and what is the effect since it also might be that people with large interest in, e.g., bird watching, tend to settle in greener areas or manage gardens in a way that attract birds and increase bird abundance.

Clucas et al. (2014) noted that the demographic variable of income did not affect the money spent on feeding birds or its frequency in either Berlin or Seattle, but there were differences between the cities, as residents of Berlin in high income brackets spent more money on bird food, and participated in more bird-related activities, than corresponding residents of Seattle.

Demographic factors (age, income, etc.), urban green cover, and bird species richness all have complex interactive effects (Luck et al. 2011). Luck et al. (2011) showed that an increase in species richness improved residents' satisfaction with where they live. However, the strongest factors associated with well-being were greenery cover and the level of urbanization (Luck et al. 2011). This indicates that the relative proportion of green spaces in urban development may be more valuable for residents' well-being than, e.g., bird species richness.

15.4.5   Mechanisms Behind the Perception of Birds

Other important questions, which we can only currently speculate about, regard the mechanisms responsible for our perceptions of birds generally, specifically urban birds. Similarities in neural pathways involved in vocal learning in humans and birds may be involved (Bolhuis et al. 2010) and/or the similarity of birdsongs to music and/or evolutionary processes that have shaped our perceptions of the natural world (Earp and Maney 2012).

The ways humans learn to speak and birds learn to sing are surprisingly similar (Bolhuis et al. 2010). The neural pathways involved are far more similar than previously thought, and birds and humans even share a protein that is relevant for speech (Bolhuis et al. 2010). There is also an increasing evidence of parallel evolution of human language and birdsong (Balter 2010; Earp and Maney 2012), suggesting that convergence may have facilitated human perception, and appreciation, of avian vocal information. However, it is more likely that birdsongs inspired humans to sing (Sanga 2006), and some researchers have suggested that the first humans used songs rather than speech to communicate (Wallin et al. 2000). Several evolutionary psychologists have argued that humans "are emotionally moved by music" (Johns-Laird and Oatley 2010, p. 104). Thus, if we hypothesize that music is in some sense similar to birdsongs, then birdsong, as a form of music, may be an emotional stimulus. In this manner, we could connect research focusing on birdsongs to the field of emotional psychology, which has shown that our emotional responses increase with age (Magai 2001) and that emotions can be related to physical places, such as urban green spaces (Knez 2006, 2014b).

Human responses to birdsongs are not always positive, but can also be negative. These negative experiences may consist of heightened awareness of potential danger and an uncomfortable feeling. Ratcliffe (2015) recalled a respondent who associated a magpie (*Pica pica*) call as non-restorative due to its aggressive character. The respondent said, "... it's probably being aggressive to something else, and therefore that's a stressful sound...." Such responses raise intriguing questions about the validity of the interpretations of birds' calls and the mechanisms involved. Marler (2000) highlighted interesting examples of monkeys reacting differently to two negative stimuli. When monkeys heard an eagle call, they searched the sky and ran into bushes, whereas a leopard call caused the monkeys to leap into the tree canopy (where leopards cannot reach them). It is possible that an ancestor of modern humans may have linked certain bird alarm calls to impending danger. In accordance with this hypothesis, Krause (one of the world's best known recorders of natural sounds) describes pygmies in Africa relating certain sounds, including bird sounds, to food and potential danger (Krause 2014, p. 104). Furthermore, the absence of sound in an environment may also indicate danger. Björk et al. (2008) noted that quietness and serenity are desirable characteristics of natural environments, but total silence, or excessive suppression of natural sound, induces discomfort. Similarly, Kjellgren and Buhrkall (2010) found that if people were presented with visual stimuli of nature without sound, in videos, they missed the "smells and sounds" of nature and described it as being "too quiet." Thus, humans can react to various bird sounds in different ways and can also experience certain emotions when there is an absence of natural sounds. It is possible that our ancestors used bird sounds, such as the alarm calls of eagles, as indicators of potential threats, and for this reason, we perceive alarm calls as unpleasant sounds. On the other hand, the birdsongs of a certain habitat may indicate that there are no major threats present, and as they convey safety, we have positive perceptions of these sounds.

Another factor that may be highly relevant is "biophilia," defined as "love of life or living systems," in conjunction with a hypothesis by Wilson (1984) that humans have an intrinsic affiliation to other life forms, possibly as a result of our shared biological evolution. The hypothesis is supported by the altruistic responses adult mammals often show toward baby mammals of other species, which increase the survival rate of all mammals. Biophilia could explain why interactions between humans and certain bird species in urban settings evoke positive feelings. The mechanisms behind our positive perception of birdsongs are complex and seem to be influenced by our evolutionary history, but further research is needed to elucidate the processes involved.

15.5   Discussion

Overall, it seems that birds do provide humans with services of nonmonetary value, such as increased well-being and stress reduction. However, some species are valued more than others, depending on how we perceive them, as shown, for instance, by Ratcliffe (2015). The variations in perceptions of different species are not surprising, because characteristics such as the vibrancy of plumage also vary widely among species. Part of the perception and appreciation of birds, and their songs, may be due to a shared human fascination with nature. However, other factors that influence perception are based on demographic factors, such as gender and age. It has been predicted that 66 % of the human population will live in cities by 2050 (UN 2014). Thus, most children in the future will have their first encounter, and memory, of nature in an urban environment. Children in poorer neighborhoods will be less likely to encounter birds during childhood, partly because there will be less green spaces near their homes than in wealthier neighborhoods. This limited interaction with nature may cause the children to show less engagement with, understanding of, and empathy for nature as adults. Hence, future generations may be less willing to conserve nature (Melles 2005), and as a result of expected reductions in urban greenery, they will have fewer possibilities to enjoy the aesthetic values provided by urban birds.

Extant literature shows that not only visual encounters with birds in urban areas but also exposure to birdsongs can create positive memories and potentially reduce stress. The positive response is stronger when many species are heard. However, it is becoming increasingly difficult to hear birdsongs without background urban noises, even early in the morning or in remote suburbs. Payne (2013) observed that rural soundscapes had higher restorative potential than those of urban parks and other urban settings. However, it has been noticed that urban birds have raised the pitches of their songs, presumably through adaptive responses that allow them to compete acoustically with the high levels of urban background noise (Halfwerk et al. 2011). This evolution of birdsongs in urban environments raises intriguing research questions, such as whether the changes in pitch will affect humans' perceptions of species.

Knowledge of people's perceptions of birds may be highly valuable for managing bird populations in manners that improve our well-being. For example, urban forests could be managed to have a lower density of trees, allowing people to move through the area more freely, yet maintaining the same amount of bird species (Heyman et al. 2016). Moreover, certain species have negative perceptions but are still popular as part of the species richness of natural areas. For example, there have been many complaints about Canada geese *Branta canadensis* in both the USA and Sweden (Coluccy et al. 2001), but only 9 % of respondent to a survey in the USA agreed with the statement that there should be fewer geese in an area.

Research that has focused on the cultural services that birds can offer seems to be rooted in urban ecology. This is interesting, since it has been argued that urban ecology merely applies other theories to urban habitats. This highly

transdisciplinary field that integrates human psychology and ecology has been dominated mainly by social scientists (see also Keniger et al. 2013). However, ecologists now have the opportunity to make major contributions through investigation of bird species' characteristics, combinations, and behaviors linked to human perceptions.

The planning and management of urban green areas is a highly complex process. Birds are constantly losing potential habitats in cities, even with strong conservation efforts. Infrastructure and housing are the primary concerns in city planning, so the conservation of urban nature and birds receives less attention. However, functional green spaces may attract more interest as results continue to show that interactions with birds improve the health of city residents. Although the research area of cultural ecosystem services provided by birds is rather new, it may provide interesting insights into the environments where most of the human population lives, our cities.

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Part V
Urban Bird Habitats: Conservation and Management

Chapter 16
Grassland to Urban Forest in 150 Years: Avifaunal Response in an African Metropolis

Craig T. Symes, Kathryn Roller, Caroline Howes, Geoffrey Lockwood, and Berndt J. van Rensburg

Abstract Avian communities in urban environments of continental Africa are generally poorly understood. Gauteng, one of South Africa's nine provinces and the second largest mega-urban region in sub-Saharan Africa, includes the conurbation of Johannesburg and Pretoria. Rapid urbanisation in the province began in the 1880s after the discovery of gold and is, by northern hemisphere standards, a recent urbanisation event; extrapolating patterns of urban ecology from Europe and North America may therefore not be entirely appropriate. The urban transformation and establishment of an anthropogenically modified to natural vegetation gradient, the extension of woodiness (through bush encroachment and fire exclusion) from the savanna biome into grassland, and the 'greening' of suburbia with an increase in exotic trees and open water, have resulted in a transformed bird community. This tolerant subset of the local avifauna (both native and alien species), derived from species losses (e.g. grassland-specific species) and gains (species responding to more wooded habitats, e.g. dominated by cavity nesters, frugivores, obligate water-associated species, and cliff nesters), is remarkably diverse and is probably driven and supported by an increase in habitat heterogeneity. An assessment of the bird community at fine- to broad-scale highlights (1) the modifying effect of anthropogenic transformation and the establishment of an urban-resilient bird community brought about by this change, (2) the value of landscape heterogeneity (species composition and structural diversity) in supporting a species-rich bird community,

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and (3) the value of urban and suburban green spaces as refugia for avian species impacted by urban transformation.

Keywords Diversity • Urban gradient • Temporal change • Green spaces • Native invasives • Gauteng • Africa

16.1   Introduction

Human transformation of natural environments is occurring at a scale never before experienced on the planet (Ellis 2011; Sushinsky et al. 2013; Goudie 2013). Towns and cities are the world's fastest growing land-use type, driving extinctions around the world. This is a consequence of both the rate at which the global human population is growing, and the fact that 85 % of this growth is happening in urban areas (Cohen 2003). The study of these transformed landscapes, of urban ecology, is a rapidly growing field, and over the past four decades, there has been progress in understanding how to minimise the impact of urban development on biodiversity (Geddes 1915; Bolund and Hunhammar 1999; Tratalos et al. 2007; Evans et al. 2009; McDonnell and Hahs 2009; Gaston 2010; Shochat et al. 2010; Sushinsky et al. 2013). Important in the context of a rapidly growing human population and associated anthropogenic changes to the natural environment are the responses of different plant and animal species to this change (Luck 2007; Grimm et al. 2008; McKinney 2008; Evans et al. 2009). In particular, where there is intensive urbanisation and homogenisation of the environment, there may be a variable response by species, from some that become extirpated to those that thrive (either native or introduced) (Beissinger and Osborne 1982; Olden et al. 2004; Evans et al. 2006; Devictor et al. 2008; Chamberlain et al. 2009; Shanahan et al. 2014). Because birds respond to changes in the environment, each species found in an urban area will be associated with habitats that are favourable to their survival and reproduction after urbanisation has occurred (Hansen and Urban 1992; Blair 1996, 2004; McKinney 2006; Evans et al. 2011). Thus, they are effective environmental indicators because they are sensitive to changes in habitat structure and composition (Savard et al. 2000; Bino et al. 2008). Indeed, species can be classed according to their reaction to urbanisation: (1) urban avoiders that favour natural vegetation and are mostly native species; (2) suburban adapters, both alien and native species that are common in moderately urbanised areas; and (3) urban exploiters that dominate the community of highly urbanised areas and usually comprise a small number of alien species (McKinney and Lockwood 1999; Kark et al. 2007; van Rensburg et al. 2009).

   In South Africa, the biological impacts of transformation have been complex and have resulted in both positive and negative changes in avifaunal diversity and abundance, as well as the shift in composition of bird communities (van Rensburg et al. 2009). Birds are thus an important study tool to further our still basic understanding on the complex and ever-increasing impacts of man on the

environment (Gibbons et al. 1996; Catterall 2009) and provide a mechanism to explore the responses of organisms to urban effects (Chace and Walsh 2006).

16.1.1   Urbanisation in Sub-Saharan Africa

Cities in sub-Saharan Africa (SSA) are urbanising faster than those of any other continent, and during 2015–2050, populations in 28 African countries are projected to more than double (United Nations, Department of Economic and Social Affairs, Population Division 2015). The combination of a high rate of natural increase of the existing human population in urban areas and the migration of individuals from rural to urban areas have led to rapid urbanisation (Evans et al. 2006). Within SSA, southern Africa is the most urbanised region, where 48 % of the population lives in urban areas. Although urbanisation is often associated with economic development and poverty reduction, many African cities are experiencing increasing environmental, political, and social strains directly due to urbanisation (Davis and Henderson 2003; Barrios et al. 2006). Additionally, African cities are some of the most vulnerable to climate change, a phenomenon that is intricately linked to increased urbanisation and anthropogenic modification of the environment (Downing et al. 1997; Barrios et al. 2006). These environmental impacts of urbanisation include changes in ecosystem structure and function, which have consequent impacts on ecosystem services, the very services which allow mankind to sustain life on the planet, as well as a comfortable standard of living.

16.1.2   Urbanisation in South Africa and Gauteng

South Africa has a population of over 52 million people (Statistics South Africa 2014) of which more than 55 % reside in urban areas (Kok and Collinson 2006; UN-Habitat 2014). The country contains four urban agglomerations of more than three million inhabitants—more than any other southern African city (UN-Habitat 2014). These include Cape Town, Durban, Johannesburg, and Pretoria. The latter two agglomerations are located within the landlocked province of Gauteng, which is the second largest mega-urban region in sub-Saharan Africa. The province, with one quarter of the country's population in only 1.5 % of the country's land area, generates over 35 % of the country's GDP (Statistics South Africa 2014). In the last 10 years, Gauteng's population has grown by almost 25 %, and by 2020 it is estimated to become an urban region of 20 million people (Statistics South Africa 2014). Between 2001 and 2011, almost 1.5 million people migrated to Gauteng from within and outside of South Africa (Statistics South Africa 2014). With human growth figures like this, it is easy to understand why and how the natural environment has changed.

The rate and extent at which urban areas in the province have been established and at which they continue to develop and merge is driving rapid avian species turnover and thus attracting attention from ecologists (Dean 2000; van Rensburg et al. 2002, 2009; Cilliers et al. 2009). Studies in urban ecology, a rapidly emerging field of science, are beginning to document the interactions between avifauna and their changing urban habitats in this region (van Rensburg et al. 2002, 2009; Hugo and van Rensburg 2009). These differ from northern hemisphere examples for various reasons, including (1) the extent of the areas over which the change is occurring (large extent), (2) the time span of the change (relatively recent), and (3) the type of transformation (grassland to forest, as opposed to deforestation) (Shanahan et al. 2014).

16.1.3   Study Objectives

The primary objective of this chapter was to explore the spatial and temporal responses of bird species within the province of Gauteng in light of the relatively recent, rapid, and widespread urbanisation in the region. By assessing the bird community in the province at a broad-, medium-, and fine-scale, we attempt to present a holistic interpretation of the current avian community and associated responses to these transformations in space and time. The complex effects of multiple factors across time and space, for a diverse bird community in two dominant biomes, have not been explored in detail; however, a presentation of the current state of avifauna in the region are an important synthesis in attempting to understand some of these changes.

16.2   Methods

16.2.1   Study Area

Gauteng is situated at the interface of the country's two largest biome types: savanna and grassland (Mucina and Rutherford 2006; Fig. 16.1). Annual average precipitation is 600–700 mm per annum, with most falling during summer months (October/November to February/March) (van Wilgen et al. 2008; Dyson 2009). Winter months (April/May to August/September) are dry and little to no rainfall occurs; frost is common (Dyson 2009; South African Weather Service 2013/2014). Savanna dominates the northern third of the province, with a gradual decrease of woody elements into grassland at generally higher altitude in the south (Mucina and Rutherford 2006; Fig. 16.1). Accordingly, the central and southern regions of the province, often referred to as the Highveld, are chiefly comprised of grassland. Together with rapid urbanisation and land transformation, there has been a
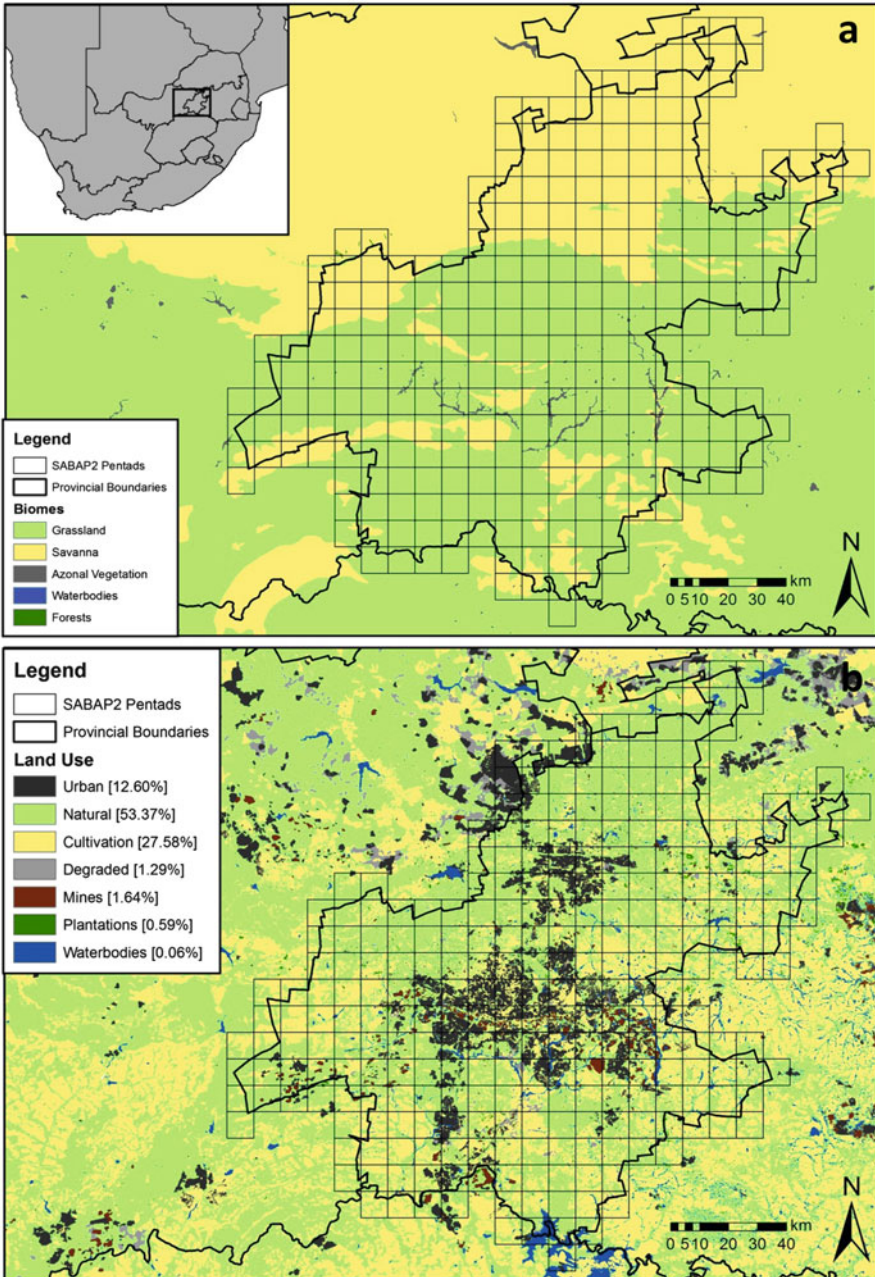
Fig. 16.1 (**a**) Biome types in South Africa's Gauteng province (and surrounding provinces) indicating savanna dominant in north and grassland dominant in south (South African National Biodiversity Institute 2012), (**b**) Land-use types for Gauteng and surrounding areas (percentage areas are indicated in legend and refer to Gauteng only) (South African National Biodiversity Institute 2009). Pentad boundaries (5′ × 5′ grid; $n = 287$) are overlaid only for those that include Gauteng province. The two primary developed urbanised areas of Gauteng can be identified as the dark grey shaded cores; Pretoria in the north of the province and the greater Johannesburg region in the south
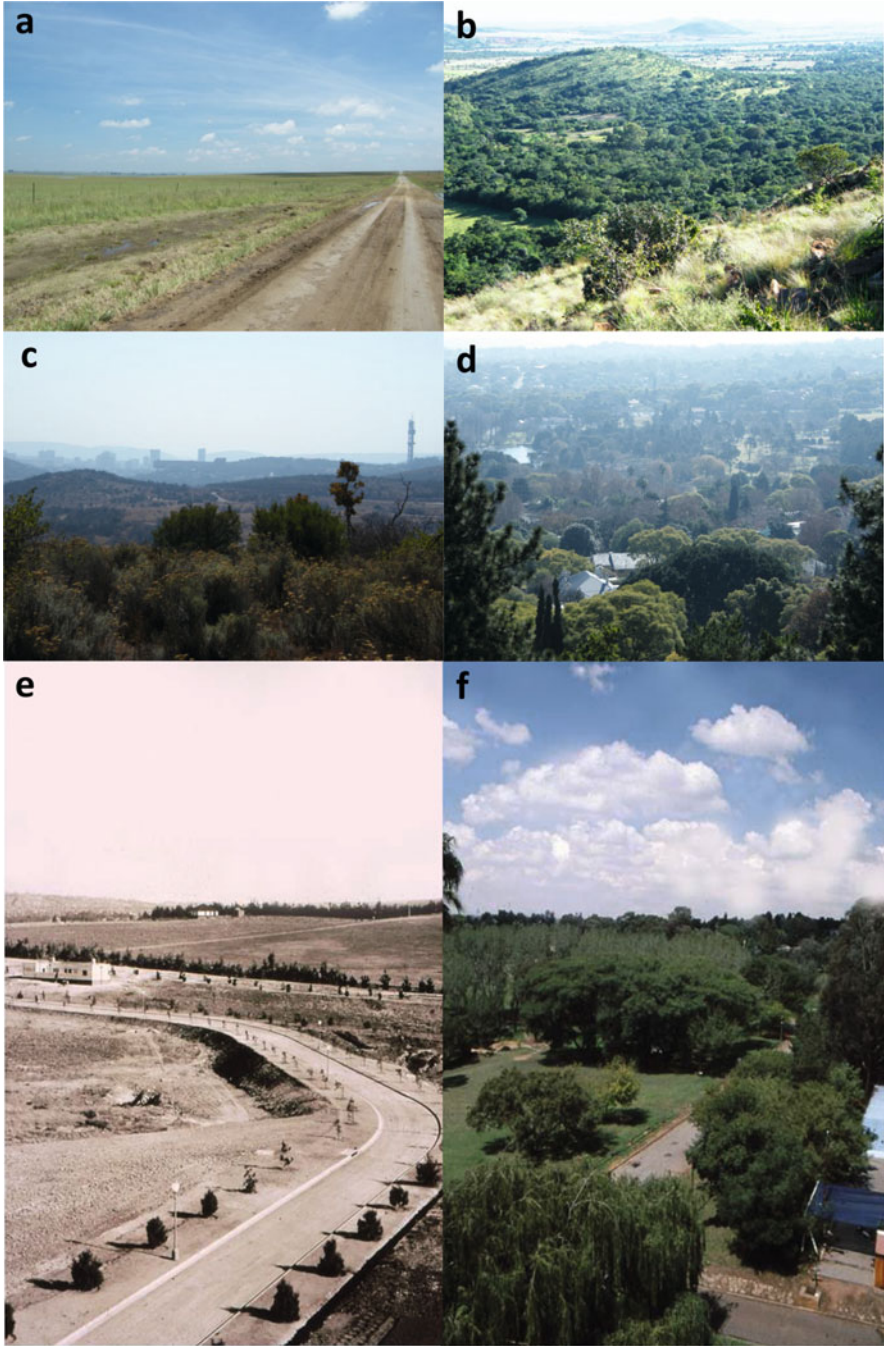
Fig. 16.2 (**a**) Open grasslands southeast of Johannesburg (Devon area), (**b**) Savanna biome northeast of Pretoria, viewed north from north slope of the Magaliesberg mountain range, (**c**) Pretoria viewed north from Groenkloof Nature Reserve, (**d**) forested northern suburbs of Johannesburg, viewed northwest from Westcliff ridge. Access road to Delta Park Environmental Education Centre, view southeast in, (**e**) 1934, and (**f**) 2004 (70 years later); (Photograph credits: **a–d**, C. Symes; **e–f**; G. Lockwood)

widespread introduction of woody plant species brought about by (1) bush encroachment as a result of changed fire regimes (Bond et al. 2003; Conedera et al. 2009) and (2) the planting of trees, both exotic, e.g. Syringa *Melia azedarach*, *Quercus* spp., *Eucalyptus* spp., *Plantanus* sp., conifers, *Cedrus* spp., *Jacaranda mimosifolia* sp., *Phoenix canariensis* and *Celtis* spp., and indigenous, e.g. *Celtis africana* and *Searsia* spp. for aesthetic purposes, e.g. along road verges, parks, and gardens (Trollope 1980; Ward 2005; Mucina and Rutherford 2006; O'Connor et al. 2014; Figs. 16.1 and 16.2). This floral change has consequently brought about a response by bird species that can either, tolerate, adapt to, or exploit this new environment (Erz 1966; Tarboton 1968; Siegfried 1968; Winterbottom 1971; Sirami et al. 2009; Sirami and Monadjem 2012).

Pretoria, the administrative capital of South Africa and located c. 55 km north-northeast of Johannesburg, was established in 1855 as the capital of the Boer Republic and played a key role in the Second Anglo-Boer War (1899–1902). Johannesburg, the third most populous city in sub-Saharan Africa (UN-Habitat 2014) and the 35th most populous urban agglomeration in the world (UN-Habitat 2014), developed independently to Pretoria, after the discovery of gold in 1884, on the Witwatersrand ridge (Beavon 2004). Johannesburg is the self-proclaimed 'largest man-made urban forest' in the world. Through the process of urbanisation, Johannesburg and Pretoria have merged to form a multicentric megapolitan urban system (Geyer et al. 2012). The current layout is the result of a tumultuous, yet short history of *apartheid* policies, first implemented as law in the 1950s, that imposed restrictions on where people lived, and many communities (predominantly non-White) were forced to relocate to the urban fringe (Beavon 2004). This created a spatial pattern of variable wealth that despite the abolishment of these laws in 1994 persists today. The fall of *apartheid*, rapid population growth for the last two decades, and the perception that cities hold greater economic and employment opportunities have stimulated further expansion of the conurbation of Johannesburg and Pretoria in recent decades (Njoh 2003; Geyer et al. 2012).

16.2.2 Broad Scale: South African Bird Atlas Data and Citizen Scientists

First, we engage in a broad-scale analysis of Southern African Bird Atlas Project (SABAP2, initiated 2007) data over the full extent of Gauteng province. SABAP2 uses the contributions of both experts and citizen scientists to document the spatial distribution and relative abundance of bird species across seasons (Harrison et al. 2008; Robertson et al. 2010). Bird species lists ('cards'), compiled from visually and aurally detected species, are submitted by individuals on the SABAP website <http://sabap2.adu.org.za> according to the demarcated 'pentad' (c. 8.3 × 9.2 km area in Gauteng) in which each species was recorded (one quarter degree grid cell is divided into nine 5′ by 5′ pentads) and certain criteria related to the

period of sampling (see Harebottle et al. 2007 for details of sampling protocol). Because of the high population density and relative abundance of amateur ornithologists and birders in the region, the province of Gauteng is well surveyed compared to more remote pentads in the subregion (Harrison and Underhill 1997). Bird abundances are not reported (but rather presence) so we utilised a reporting rate (the proportion of cards reported for a particular pentad for each species) as an index of abundance (Buckland et al. 2008; Harrison et al. 2008). These data were extracted from the SABAP2 database for 287 pentads (all data up to 12 April 2015) to give a species list, with reporting rate (abundance index) for each pentad utilising both 'Full Protocol' and *ad hoc* submission cards (these each require a minimum sampling period of 2 h and <2 h, respectively) (see Harebottle et al. 2007).

Although a committee screens submission records, especially out of range species, we 'cleaned' the raw data for unacceptable species and repeats. For example, we excluded species such as unknown, unidentified duck, domestic duck, greylag goose *Anser anser*, and African red-eyed–dark-capped Bulbul *Pycnonotus* spp. hybrids). We retained species where single accounts exist but emphasise that their presence needs to be accepted amidst speculation, e.g. olive thrush *Turdus olivaceus*, which is out of range and may be confused with juvenile Karoo thrush *T. smithi* (Wilson et al. 2009) and Streaky-breasted Flufftail *Sarothrura boehmi*.

To understand these bird communities at the pentad level across the province, we sourced environmental vegetation (South African National Biodiversity Institute 2012; Fig. 16.1a) and land-use data (South African National Biodiversity Institute 2009; Fig. 16.1b), providing a perspective on the ecological preferences of some of Gauteng's most prominent native and alien bird species and the associations these species have with particular characteristics of change. For each pentad we summarised the proportion of land identified as (1) natural, (2) transformed land (including urban, cultivated, degraded, mines, and plantations, Fig. 16.1b), or (3) water (rivers, dams, and water impoundments). Furthermore, we derived a measure of habitat heterogeneity (land-use heterogeneity index) for each pentad using the method employed by Laiolo (2005).

For all alien species and species with SABAP2 reporting rates of >10 % for Gauteng ($n = 358$ species), we assessed each species using (1) visual assessments of their distributions and reporting rates in the broad-scale SABAP2 data and their associations with land use across the province, (2) interpretations of each species occurrence at the medium and fine scale, and (3) the authors' ornithological knowledge and understandings of the life histories, to allocate each to a disturbance response category (with particular reference to Gauteng province) as follows: (1) *disturbance sensitive* (urban and suburban avoiders; native species whose abundance drops or whose presence is lost due to a decrease in preferred natural environments (grassland and savanna)); (2) *suburban adapters* (native and alien generalists which have persisted in the region and extended their ranges across the gradient of urbanisation, often due to the increased woodiness and landscape heterogeneity, as well as increased open water and food availability that accompany

this transformation); (3) *urban adapters* (native and alien species which have benefitted from the availability of heavily modified urban environments); and (4) *uncategorised* (species that occurred in low abundance and for which an interpretation was not clear). We investigated the relationship between bird diversity for each of these disturbance response categories, in each pentad, with the proportions of different land-use types (viz. biome, transformed, water, land-use heterogeneity index) in each pentad using a Spearman's correlation. In addition, for each of these disturbance response categories, we defined species as (1) cavity (primary and secondary) or open nesting species, (2) frugivore (determined where fruit is an obligate or important part of the diet) or non-frugivore species, (3) water associated (not obligate, but a strong association with water bodies and/or drainage lines with water present) or not, (4) grassland-specific species or not and (5) cliff-nesting species (obligate and facultative with a strong association) or not (Hockey et al. 2005). Classification of species into a single category is not mutually exclusive, and the interpretation provides an understanding of how certain categories respond to a gradient of disturbance across a broad spatial area.

16.2.3   Medium Scale: Delta Park and an Intensely Sampled Pentad

Delta Park (26°07′30″S, 28°00′33″E; altitude c. 1545–1630 m a.s.l.), approximately 10 kilometres north of the city centre, is one of Johannesburg's largest urban green spaces (104 hectares). The park has lost much of its native grassland vegetation to manicured lawns, exotic woody plant species, man-made surfaces, and artificially controlled water sources. In 1975, a 10-hectare, fenced-off bird sanctuary was established within the park's boundaries as one of the first in the province. Additionally, the heterogeneous nature of the parks remaining landscape provides an array of niches for birds to utilise (Evans et al. 2011). It has, in fact, become well known for hosting vagrant bird species over the past few decades (GL pers. obs.).

Bird species present in the park, detected visually or audibly by GL, were recorded during (1) survey walks around the park that varied between early morning full circuits of the park (mostly on weekends, plus some very early in midsummer before work hours); alternating early morning surveys of either the south-western, or north-eastern river end of the park, and afternoon/evening surveys including either part of, or the whole park; attempts were made to survey the entire park on foot at least twice, but preferably three times, on foot every week; full survey walks took approximately 2 h each and (2) early morning watches that took place from the tower on the Education Centre and allowed better monitoring for raptors and some other species than was typically the case with the survey walks; these did however miss small passerines with localised distributions in the park; these sessions were typically at least 1 h each morning and 5 h a week, but also included incidental observations in the afternoon/evenings. For each month, the

number of days a species was detected as a proportion of days observed was used as a measure of abundance for that species each month. Thus, the analysis of species sightings data collected within Delta Park during a 12-year period (2002–2013) is used to understand the bird community within a 'green space' within a single pentad (2605_2800) and any possible changes in this limited time period.

Within this analysis we extracted all bird species observed for Pentad 2605_2800 (with sampling following the protocol referred to in the broad-scale analysis), a region that incorporates a number of middle- to upper-income suburbs of Johannesburg's northern suburbs region, e.g. Houghton, Parkview and Greenside. Within the pentad are found a number of green spaces, including public parks with large open water bodies, i.e. Delta Park, Emmarentia Dam and park, and Zoo Lake; golf courses, i.e. Parkview Golf Course, Houghton Golf Club, Killarney Country Club, Wanderers Golf Club; and parks, i.e. James and Ethel Gray Park (no water bodies), Johannesburg Zoo (northern section, and continuous with Zoo Lake).

16.2.4   Fine Scale: A Spatial Perspective of Johannesburg's Urban Avifauna

A fine-scale analysis of the bird community across an urban gradient in Johannesburg was conducted during autumn when most birds had finished breeding and many migrants were still present (May to June 2011), to define the fine-scale relationship between the level of urbanisation and community composition, diversity, and abundance. The study delineated four distinct environmental 'zones' along the urban gradient, namely, (1) urban, (2) suburban, (3) urban green, and (4) natural. Urban zones were defined as highly urbanised areas consisting mainly of high-density residential and commercial (high-rise) buildings, roads, and other paved surfaces (Braamfontein suburb); suburban zones low- to moderate-density housing, yards and tar roads (suburbs of Greenside and Saxonwold); urban green zones (including parks and golf courses) as managed landscapes consisting of planted or managed native or non-native species (Emmarentia dam and park, Killarney Golf Course, and Zoo Lake); and natural zones as fragments of remaining natural vegetation that have been protected from human development in the form of reserves or undeveloped spaces (Melville Koppies) (Grobler et al. 2006).

A total of 105 ten-minute point counts of avifauna were conducted at seven sites (given above) across each of the zones (15 point counts per site). Each site was sampled on different days during three time periods; morning (0600h–1000h), midday (1000h–1400h), and afternoon (1600h–1800h), to account for different patterns of bird activity in a diurnal period. All birds seen and heard at each study point, within a 65-metre radius (defined *post hoc*, as a cut-off distance suitable for maximising species detection across all species and environmental zones), were identified and recorded. In addition, seven environmental variables relating to the

structure and composition of the landscape as well as the level of disturbance were measured on site within each sampling area. These included (1) percentage grass cover (estimated lawn and natural grass cover), (2) percentage artificial surface area (estimated, including paving, road, and building cover), (3) number of trees (counted, where trees are defined as woody vegetation over two metres in height), (4) tree height and diameter at breast height of the five largest trees (measured to the nearest centimetre), (5) proportion of the five largest trees that were native (trees identified and counted), (6) the percentage canopy cover (estimated), and (7) greenness, measured as the Normalised Difference Vegetation Index (NDVI) obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite photographs, which acts as a proxy for primary productivity (Seto et al. 2004; Pettorelli et al. 2005). The results of the avifaunal survey were thus combined with the analysis of local environmental variables to gain insight into the ecological responses of the city's bird species to changes in their local environmental composition and structure.

To understand which environmental factors contributed to the *a priori* defined environmental zones we used principal components analysis. To compare the vegetation structure and bird species composition of each point across the four zones, we used non-metric multidimensional scaling Bray-Curtis analysis of similarity (ANOSIM). These comparisons were made using the Community Analysis Package (CAP) (Seaby et al. 2004).

For all of the above analyses, birds were classified as native or exotic. A native or indigenous bird species was defined as one that occurs in an area irrespective of human interference and an exotic or alien bird species as one that did not occur in the area before introduction by humans, including species indigenous to South Africa but not the area of study, e.g. aviculture escapees.

16.3 Results

16.3.1 Broad Scale: South African Bird Atlas Data and Citizen Scientists

A total of 521 species, of 77 families, were recorded in 287 pentads (Fig. 16.3a). An average of 73.4 ± 146.6 cards (range of full protocol cards submitted per pentad = 8–1043), was submitted per pentad. The number of species was positively correlated with the number of bird lists submitted per pentad (Spearman's R, $p < 0.001$). A large proportion (34.5 %) of all species were recorded in <10 % of pentads (Fig. 16.4). Twelve species (2.3 %) were recorded in all pentads, including helmeted guineafowl *Numida meleagris*, laughing dove *Streptopelia senegalensis*, Cape turtle dove *Streptopelia capicola*, red-eyed dove *Streptopelia semitorquata*, crowned lapwing *Vanellus coronatus*, cattle egret *Bubulcus ibis*, Hadeda Ibis *Bostrychia hagedash*, barn swallow *Hirundo rustica*, greater striped swallow
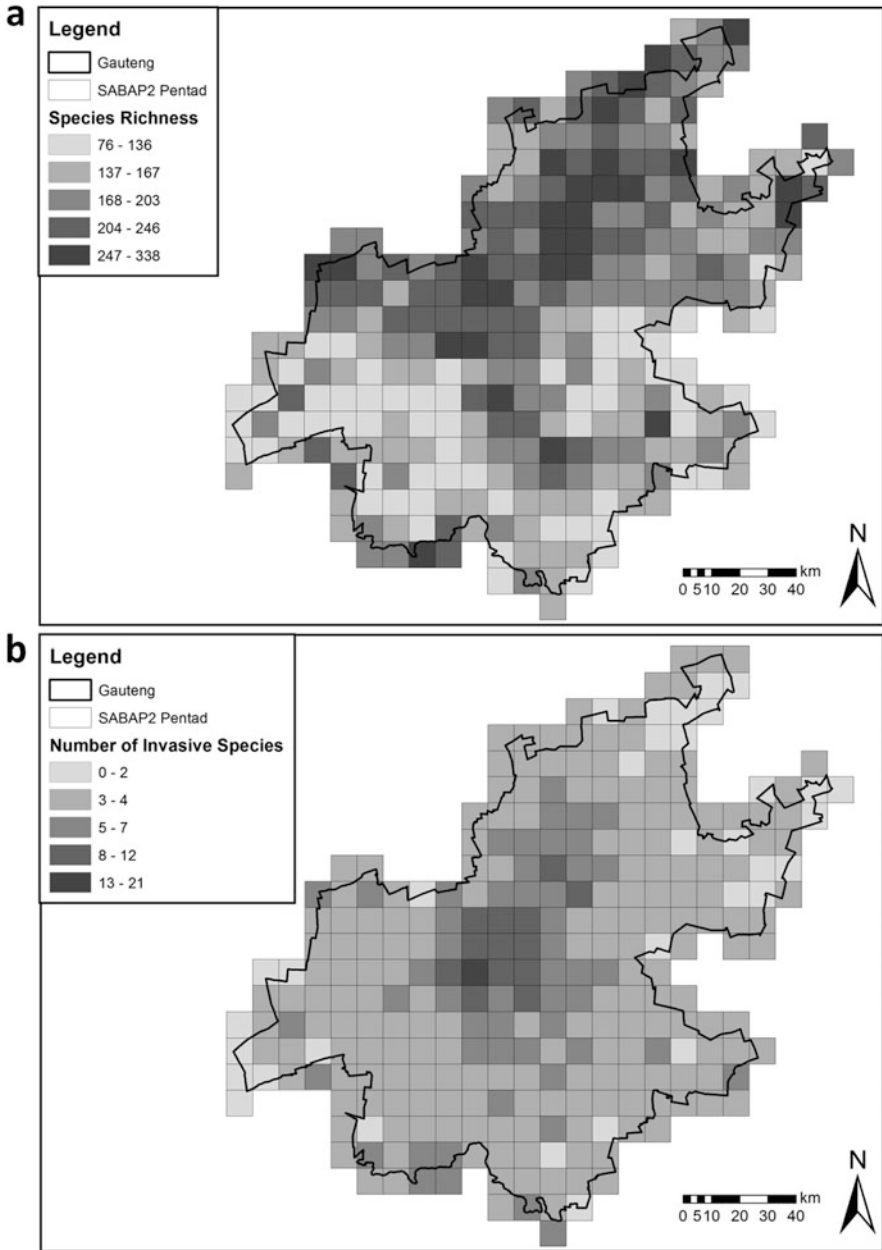
Fig. 16.3 (**a**) Complete avian species richness, and (**b**) Alien avian species richness, across Gauteng, as determined by SABAP2 data at the pentad ($5' \times 5'$ grids) level of sampling
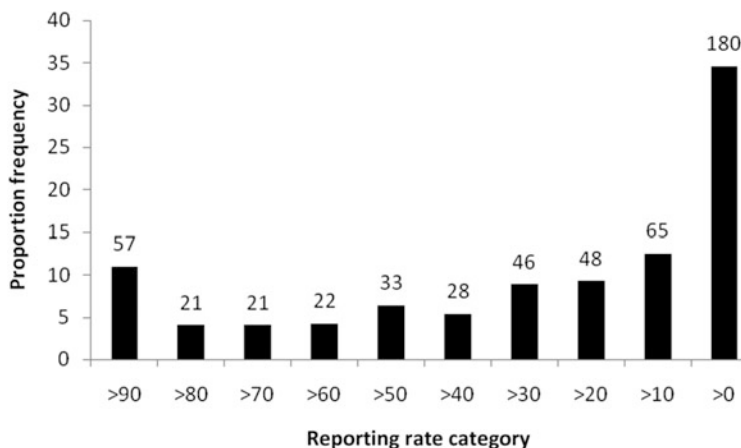
Fig. 16.4 Proportion of all species recorded in Gauteng for SABAP2 for different reporting rate categories. >90 indicates >90–100 %, >80 % indicates >80–90 %, etc. Number of species indicated above each bar

H. cucullata, Cape glossy starling *Lamprotornis nitens*, southern masked-weaver *Ploceus velatus*, and pin-tailed whydah *Vidua macroura*.

We categorised each pentad as being either mostly savanna ($n = 84$) or grassland ($n = 181$) (>60 % of each biome), or mixed ($n = 22$; <60 % of each biome), and found a mean number of species ($\pm$SD) per pentad of 205.7 ± 46.9, 163.5 ± 42.7, and 187.2 ± 46.8, respectively, for each habitat type. The grassland biome had significantly fewer species than savanna and mixed (Kruskal-Wallace, $K = 47.848$, df $= 2$, $p < 0.0001$). There was an inverse relationship between the number of species per pentad and percentage grassland (Spearman's R, $p < 0.001$) and percentage transformed land (Spearman's R, $p < 0.001$) and a positive relationship between the number of species per pentad and percentage savanna (Spearman's R, $p < 0.001$).

We identified 26 exotic species from six families, with Anatidae (12 species and mallard hybrid) and Psittacidae (8 species) most represented (Fig. 16.3b; Appendix 1). Three of these species were recorded in >50 % of pentads: common myna *Acridotheres tristis* (99.7 %), house sparrow *Passer domesticus* (94.1 %), and rock dove *Columba livia* (90.2 %), with mallard *Anas platyrhynchos* and common peacock *Pavo cristatus* in 31.4 and 13.2 % of pentads, respectively. Rose-ringed parakeet *Psittacula krameri* was recorded in 11.5 % of pentads and common starling *Sturnus vulgaris* in 5.2 % of pentads. All other exotic species ($n = 19$) were recorded on <2.5 % of pentads. Whilst comparisons of abundance indices between our different scales of analysis may not be appropriate because of different sampling and analysis procedures, the results demonstrate the variable detection of exotic species across the province (Table 16.1; Appendix 1). There was a positive relationship of the number of invasive species in each pentad with the proportion of transformed land and the land-use heterogeneity index (Spearman's R, $p < 0.01$),

Table 16.1 Summary statistics for different scales of sampling, indicating species richness, species with >50 % reporting rate, and number of exotic species

Scale of sampling	Total species	Species >50 % recording	Exotic species
Gauteng SABAP2 data	521	155 (29.8)	26 (5.0)
Delta Park Pentad (2605_2800)	230	48 (20.9)	12 (5.2)
Delta Park	209	69 (33.0)	8 (3.8)
Fine scale	54	11 (20.4)	5 (9.3)

Values in parentheses indicate percentages. Fine-scale proportions are the percentage of point counts in which the species was present

but no relationship with the proportion of grassland, the proportion savanna, or the proportion water in each pentad (Spearman's R, $p > 0.01$).

The number of disturbance-sensitive species in each pentad was inversely correlated with land-use heterogeneity, the proportion of transformed habitat, and the proportion of grassland, yet positively correlated with the proportion of savanna (Spearman's R, $p < 0.05$). There was no correlation with the proportion of water (Spearman's R, $p > 0.05$). The number of suburban adapter species in each pentad was inversely correlated with the proportion of grassland and positively correlated with the proportion savanna (Spearman's R, $p < 0.05$); there was no correlation with water, land-use heterogeneity, and transformed habitat (Spearman's R, $p > 0.05$). The number of urban adapter species in each pentad was positively correlated with land-use heterogeneity and transformed land (Spearman's R, $p < 0.05$); there was no correlation with water, grassland, and savanna. For the uncategorised species, there was an inverse correlation with land-use heterogeneity, transformed land, and grassland (Spearman's R, $p < 0.05$), a positive correlation with savanna (Spearman's R, $p > 0.05$), and no correlation with water (see Fig. 16.5).

The number of cavity-nesting species in each pentad was negatively correlated with the proportion of water, the land-use heterogeneity index, the proportion of transformed land, the proportion of grassland (Spearman's R, $p < 0.05$), and positively correlated with the proportion of savanna in each pentad (Spearman's R, $p < 0.05$). The same pattern was observed for the frugivorous guild, and the inverse pattern with waterbirds. The number of grassland bird species in each pentad was inversely correlated with the proportion of transformed land Spearman's R, $p < 0.05$; for all other land-use proportions, there were no correlations. For cliff-nesting species, there was a negative correlation with transformed land and grassland and a positive correlation with savanna (Spearman's R, $p < 0.05$); there was no correlation with water and land-use heterogeneity (Spearman's R, $p > 0.05$) (see Fig. 16.6).
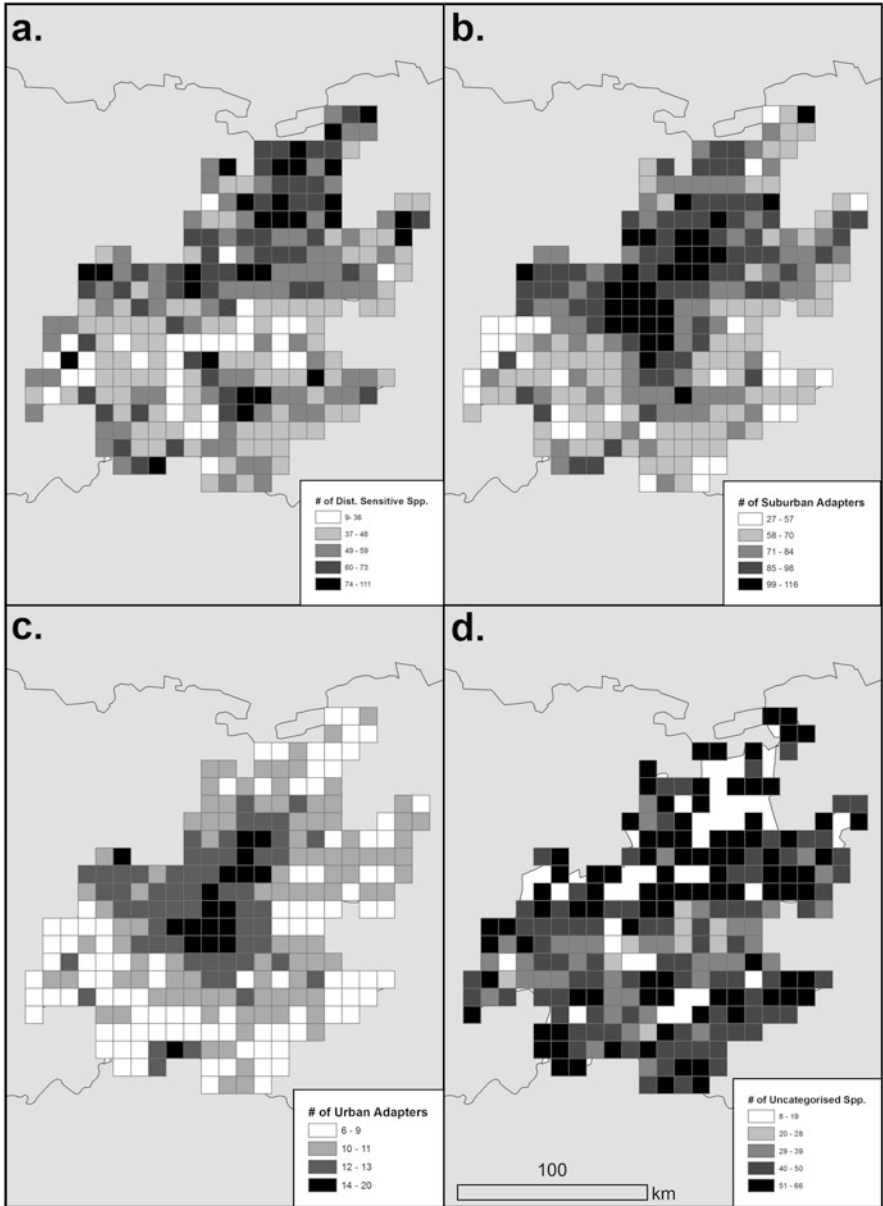
Fig. 16.5 Species richness at pentad scale across Gauteng for different disturbance response categories of birds. (**a**) Disturbance sensitive, (**b**) Suburban adapters, (**c**) Urban adapters, (**d**) Uncategorised. Numbers of each species (and proportions) for each disturbance response category are given in Appendix 2
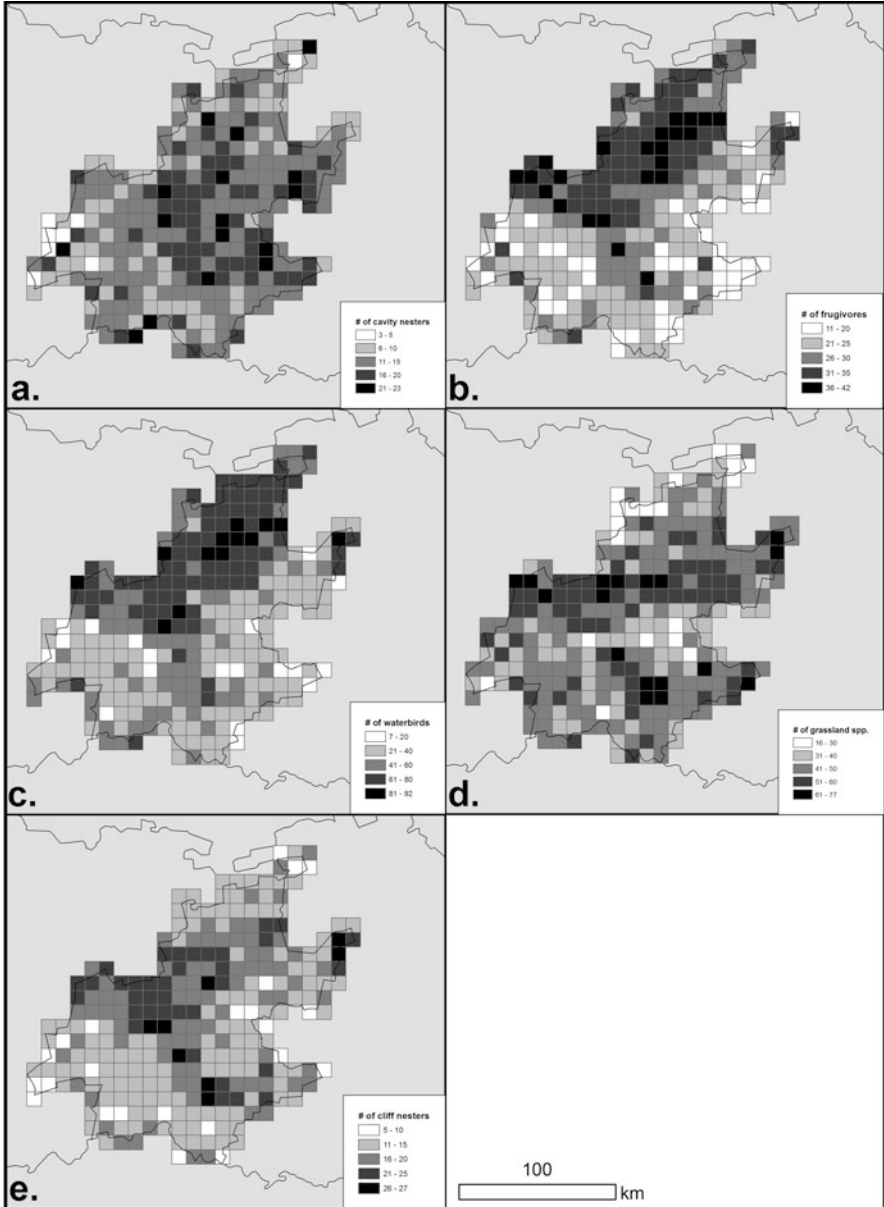
Fig. 16.6 Species richness at pentad scale across Gauteng for different behavioural guilds, (**a**) Cavity (primary and secondary) nesting species, (**b**) Frugivorous species, (**c**) Water associated, (**d**) Grassland specific species, (**e**) Cliff-nesting species (Hockey et al. 2005). Numbers of each species (and proportions) for each behavioural guild are given in Appendix 2

16.3.2 Medium Scale: Delta Park and Associated Pentad

16.3.2.1 Delta Park

A total of 209 species were recorded in Delta Park, and of these, 20 (9.6 %) were not recorded for SABAP2 for pentad 2605_2800, the pentad in which Delta Park occurs. The total species count for each year was relatively consistent and ranged from 118 (2008) to 141 (2013) and for each month from 107 (June) to 158 (December) (Fig. 16.7). A decrease in species richness is observable for the austral winter months (June to August) in which migrants are mostly absent.

Whilst the time period of 12 years may not detect temporal changes in all species, it does provide a unique opportunity to monitor species population changes over the period of observation at Delta Park (Fig. 16.7). Although many species do not present apparent changes, there are those that are obvious; increases are apparent in four raptor species (black sparrowhawk *Accipiter melanoleucus*, black-shouldered kite *Elanus caeruleus*, African harrier-hawk *Polyboroides typus*, and long-crested eagle *Lophaetus occipitalis*), two seedeaters (yellow-fronted canary *Serinus mozambicus* and thick-billed weaver *Amblyospiza albifrons*), an aerial insectivore (rock martin *Hirundo fuligula*), and a resident insectivore (African stonechat *Saxicola torquatus*), and apparent decreases are evident in two insectivores (Cape weaver *Ploceus capensis* and black-chested prinia *Prinia flavicans*), a nocturnal raptor (barn owl *Tyto alba*), and an aquatic piscivore (pied kingfisher *Ceryle rudis*) (see Fig. 16.8).

16.3.2.2 Delta Park Pentad

For Pentad 2605_2800, 230 species were recorded, of which 41 (17.8 %) were not recorded at Delta Park. Overall, the total number of species recorded for Pentad 2605_2800 was 250 species, 48.0 % of all species recorded for Gauteng.
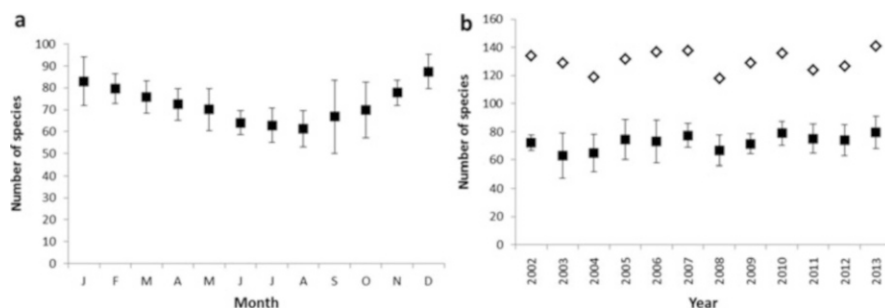
Fig. 16.7 (**a**) Monthly variation in mean number of species observed each month (±SD) at Delta Park for 2001–2013, and (**b**) Mean number of species observed each year (±SD) (open diamond indicates total species count for respective year), at Delta Park for 2001–2013
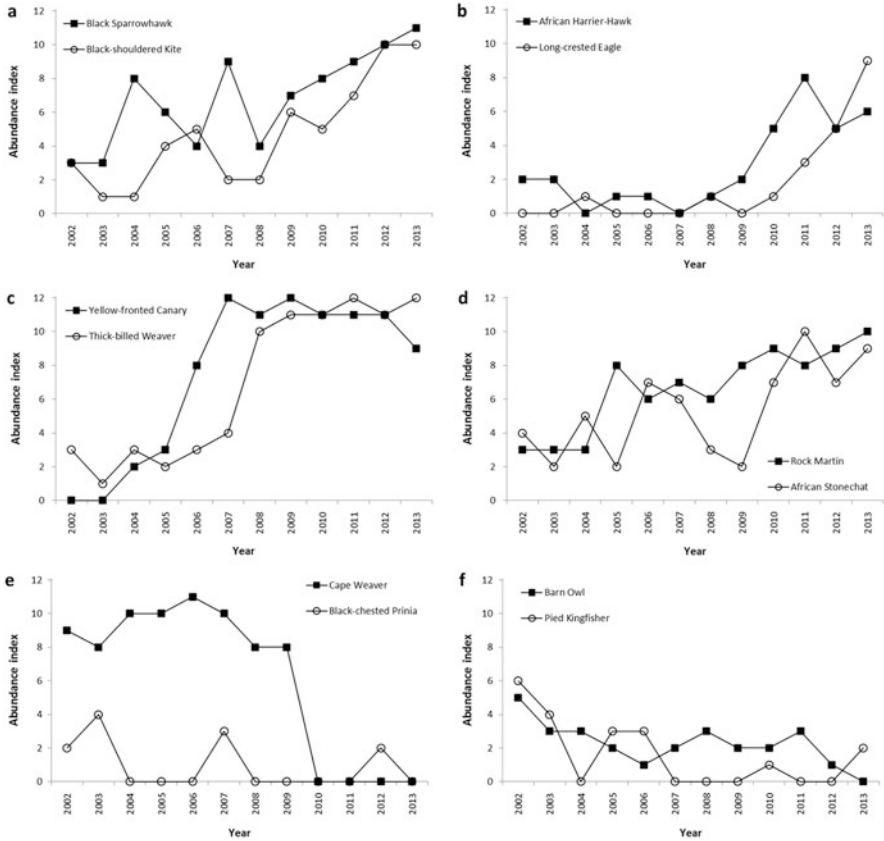
Fig. 16.8 Changes for select species showing apparent increases, (**a**) Black sparrowhawk *Accipiter melanoleucus* and black-shouldered kite *Elanus caeruleus*, (**b**) African harrier-hawk *Polyboroides typus*, and long-crested eagle *Lophaetus occipitalis*, (**c**) yellow-fronted canary *Serinus mozambicus* and thick-billed weaver *Amblyospiza albifrons*, (**d**) rock martin *Hirundo fuligula* and African stonechat *Saxicola torquatus*, and apparent decreases, (**e**) Cape weaver *Ploceus capensis* and black-chested prinia *Prinia flavicans*, (**f**) barn owl *Tyto alba* and pied kingfisher *Ceryle rudis*. Abundance indices for each year are the number of months in each year that each species was recorded

16.3.3 Fine Scale: A Spatial Perspective of Johannesburg's Urban Avifauna

A total of 54 bird species (3845 individuals) were identified during the sampling period within the prescribed sampling area, with seven (13.0 %) species common to all seven sites (Table 16.1). Overall total species richness was highest in the urban green zone (34 species) and lowest in the urban zone (12 species). However, species richness per point was highest (17.2 ± 2.6 species per point) in the natural zone and lowest in the urban zone (3.6 ± 1.3). The urban green zone had higher species

richness (16.2 ± 4.4) than the suburban zone (15.3 ± 2.1). Native species richness was higher in the natural zone (15.6 ± 4.1) than the suburban (14.0 ± 2.6), urban green (13.0 ± 4.7), and urban zone. Alien species richness was higher (2.3 ± 0.9) in the urban zone than the suburban (1.6 ± 0.8), urban green (2.1 ± 1.0), and natural zone (0.8 ± 0.8). In addition, total abundance was highest in the urban green zone (128.5 ± 68.9 individuals per point; includes three sampling sessions), followed by the urban zone (107.6 ± 62.1) and lowest in the natural zone (76.4 ± 13.0). Exotic species abundance was highest in the urban zone and lowest in the natural zone. Native species abundance was highest in the urban green zone and lowest in the urban zone.

16.3.3.1 Environmental Analysis

Each of the four zones had a distinct vegetation community, which reinforces the presence of the different zones that were *a priori* selected (Fig. 16.9). Certain environmental variables are strongly associated with particular zones, like percentage artificial surface areas with the urban zone; percentage native trees and average variation in greenness with the natural zone; percentage tree cover and percentage artificial surface area with the suburban zone; and average greenness, percentage grass, number of trees, average tree diameter at breast height and average tree height with the urban green zone (Fig. 16.9).

16.3.3.2 Bird Community Analysis

Each of the bird communities recorded at each of the zones were significantly different, with the community of the urban zone least similar to the other three zones (Fig. 16.10). The communities of the urban green and suburban zones were more similar and have some overlap. The urban green zone had substantial variation between each sample point.

There were found to be no species unique to the urban zone. However, the suburban zone was found to have two unique species; the Cape wagtail *Motacilla capensis* and the fiscal flycatcher *Sigelus silens*. The urban green zone had the most unique species (18) including seven water bird species, as well as other birds that make use of reeds and other vegetation frequently located in close proximity to water. Four unique species were observed in the natural zone, including red-winged starling *Onychognathus morio*, cardinal woodpecker *Dendropicos fuscescens*, neddicky *Cisticola fulvicapilla*, and Cape longclaw *Macronyx capensis* (the latter two being grassland species). These four species associated typically with natural habitats are most likely a result of limited sampling effort and that for a broader understanding of the avian community for the region, a more comprehensive sampling and detailed synthesis is required (Table 16.1).
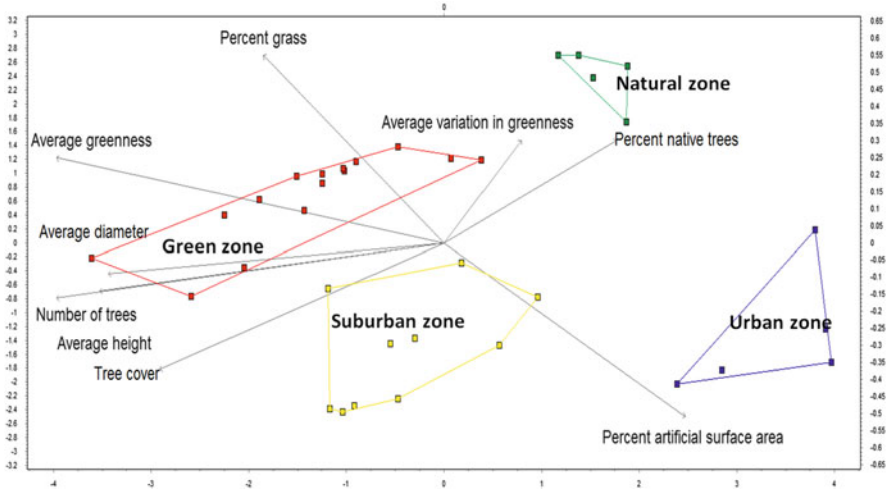
Fig. 16.9 Principal component analysis plot of the environmental data, which demonstrate the relationships between different variables and the distinctive nature of each zone. Environmental variables aligning with each zone are those that contribute most to defining the uniqueness of that zone
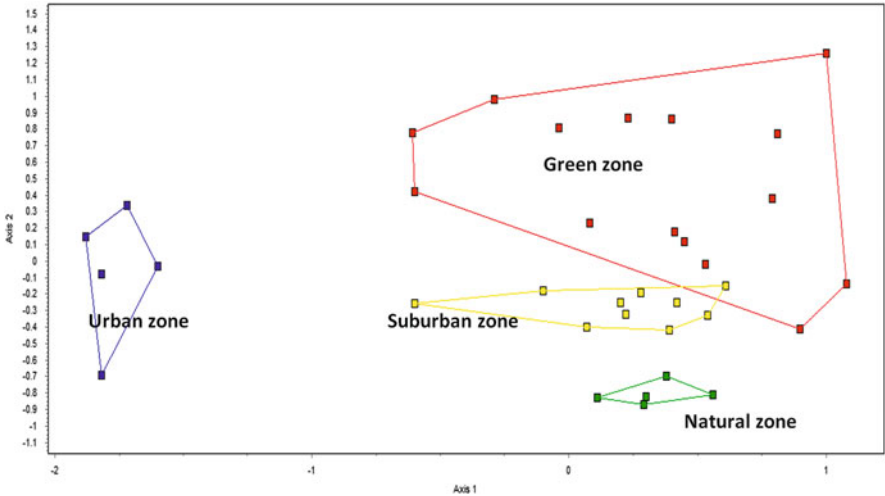
Fig. 16.10 Bray-Curtis non-metric multidimensional scaling plot of the four zones based on bird species richness and abundance data, demonstrating the distinct nature of the bird communities at each point in the four zones. All zones were significantly different at a significance level of 0.05 using analysis of similarity (ANOSIM) (Community Analysis Package, Seaby et al. 2004)

16.4 Discussion

The changes in the bird community that we see today in Gauteng are primarily a result of, and a response to, anthropogenic transformation of the Gauteng landscape during the past century (Markus 1964; Tarboton 1968; Siegfried 1968; Winterbottom 1971; Bunning 1977). Since the discovery of gold in the 1880s, the most obvious changes have been (1) broad-scale land transformation changes brought about by urbanisation, industrialisation, and agriculture and mining; (2) increase indigenous woodiness brought about by a southern extension of the savanna biome south into grassland of the south of the province because of fire control; (3) increased exotic woodiness (afforestation) brought about by planting of trees in urban and suburban environments and the invasion of exotic plant species; and (4) increase water availability through the impoundment of water and the creation of dams. These broad changes and urban transformation have thus resulted in the establishment of an anthropogenically modified to natural vegetation gradient, where change has been both varied and multidirectional at the species population and community level. In an environment, mainly in the south of the province, that was depauperate of trees, there is now a greater woody component (much of it exotic), where large trees provide substrates for cavity-nesting species and fruit attracts a greater proportion of fruit eating species. The impoundments of drainage lines and rivers provide habitats for wetland and water-associated species, and buildings, from crevices in houses to high-rise buildings that replicate cliff environments, provide a novel niche for a cohort of species that utilise these niches (Evans et al. 2011; Sullivan et al. 2015). The gradient of modified environments come together to define an urban ecosystem in which a greater degree of heterogeneity support a diverse bird community (Fontana et al. 2011). The transformation has led to both species losses and species gains, and this is likely to continue changing as humans continue to transform the landscape. Although this transformation is widespread, rapid, and recent, there are still currently suitable tracts of unmodified habitat that remain. These areas still sustain species that are sensitive to habitat modification and, in the current climate, meet important conservation objectives.

16.4.1 A Heterogeneous Landscape for Birds

Urban green spaces are important for avian diversity and at a fine-scale analysis held the highest abundance of species. At the pentad scale (c. 8.3×9.2 km), large enough to incorporate a wide range of urban green zones, species diversity is enhanced across a diverse landscape. Across the gradient there is a variable response by the bird community, and this is detected at both the fine scale and broad scale. At the fine scale, the urban green zone supported many unique species found in no other zone. In addition, urban green spaces are more often than not

associated with some form of water body as well as large sections of grass or lawns. The habitat heterogeneity provided by these environmental features makes these zones attractive, and important, areas for birds.

At the fine scale, the natural zone contained a lower abundance of native birds than the green and suburban areas. However, the natural area of the study was largely grassland, and extensive afforestation, like that which has occurred in Johannesburg, has been linked with lower grassland bird diversity (Allan et al. 1997). Additionally, the remnant of protected natural area itself may be too small to sustain large populations of native grassland birds, especially larger species like bustards that at a broad-scale analysis show a fall out in heavily human-modified areas in the province. Thus the use of a matrix of natural areas in sustaining native bird populations is equally important in maintaining habitat heterogeneity and associated bird diversity (Bailey et al. 2004; Fontana et al. 2011). As detected in the broad-scale analysis, outlying regions beyond the central development hubs of Johannesburg and Pretoria, relatively less modified habitats, continue to sustain species classified as disturbance sensitive. Indeed, a number of species' (recorded at sufficient reporting rates to warrant some interpretation) distributions at the broad scale demonstrate an absence (or reduced reporting rates) from the major urban centres. For different species the threshold at which species are excluded may vary, from total exclusion due to any form of anthropogenic effect to a gradual reduction in abundance (reporting rate) as environmental modification increases. These areas may indeed attract and sustain birds that cannot otherwise exist in a highly urbanised setting, where urban gardens, for example, may act as refugia (Florgård 2009; Pryke et al. 2011). These species could be termed 'suburban adapters', as they occur in areas that are moderately urbanised (van Rensburg et al. 2009). Some species may be classed as seasonal 'suburban adapters' whereby the urban environment becomes an attractive refuge during particular times of the year, e.g. sunbirds, Cape glossy starling, and Karoo thrush (Parker 2011, 2012, 2014; CTS *pers. obs.*). In addition, an incursion of species into suburbia during droughts might also promote urban diversity (GL *pers. obs.*). In the long term, these areas may therefore be useful to mitigate the negative effects of anthropogenic change and urbanisation on avian biodiversity (Fernández-Juricic et al. 2001; Sandström et al. 2006; van Rensburg et al. 2009).

The classification of birds into categories according to their response to urbanisation (viz. disturbance sensitive, suburban adapters, urban adapters, uncategorised) may be more useful for conservation (and management) purposes than categorising them using the traditional categorisation of indigenous or alien. Numerous indigenous species (defined by political international boundaries) have responded to urbanisation positively and in a biological context may be classed as 'invasive' or 'alien'. Therefore, these 'indigenous' (e.g. African olive pigeon *Columba arquatrix*, Hadeda Ibis, *Amblyospiza albifrons*) and 'alien' (e.g. rose-ringed parakeet, common myna, house sparrow) species can therefore exhibit invasiveness (van Rensburg et al. 2011), a response to fill a novel niche created by anthropogenic transformation (Markus 1964; Tarboton 1968; Macdonald et al. 1986; Oatley 2005; Kark et al. 2007; Duckworth

et al. 2012; Sullivan et al. 2015). Whilst urban areas have high artificial surface area, no lawn and few trees, making the loss of natural habitat difficult for many bird species to survive (Marzluff et al. 2001; Trammel et al. 2011), synanthropic species may still make use of the countless nesting sites in the tall and dense buildings as well as the food and waste provided by humans to sustain large populations in the urban zone, and it is here that a unique cohort of species (proportionately more exotics) exists. The bird species found here could be classified as urban and include indigenous, e.g. speckled pigeon *Columba guinea*, rock martin and exotic species, e.g. rock dove, house sparrow, that favour tall dense buildings and little vegetation cover (Kark et al. 2007; van Rensburg et al. 2009; Magudu and Downs 2015).

16.4.2 Introduced Invasive Species

The effects of alien invasive species on local avifauna, and in particular cavity-nesting species, have been well studied and conflicting evidence presented (Kark et al. 2007). Whilst the introduction of many species may remain benign, there are some that have major impacts on their recipient environments (Kumschick et al. 2015), and numerous studies exist demonstrating the effects of these invasive species on biodiversity. However, Koenig (2003) found no conclusive scientific evidence that alien invasive cavity-nesting species affect native cavity-nesting species. The arrival of an exotic species such as common myna or rose-ringed parakeet often evokes alarm in the well-intentioned public, but this concern remains widely unsubstantiated. In this respect we suggest that an alien invasive should be viewed no differently to a native species that has responded with range increases within the Johannesburg grassland regions due to the increased availability of food and nest sites from planted trees. Indeed, in Australia it is shown that common myna has little competitive impact on resource use by native bird species in modified urban environments (Lowe et al. 2011). Southern Gauteng's landscape is naturally dominated by the grassland biome—a biome devoid of trees and hence cavity-nesting species. In what was once largely grassland (particularly in the south of Gauteng), there would have been a quite different bird community, as is demonstrated in the current distributions of many grassland specialist species. Therefore, the current bird community is one existing (and responding) to an already modified man-made environment (Peacock et al. 2007). Attributing any exclusion of indigenous species is purely speculative; the loss of indigenous species is rather the result of habitat loss and modification. Thus, the patterns of species losses and gains are far more likely associated with the human modification of the landscape, as demonstrated by Hugo and van Rensburg (2008), than competitive exclusion.

Across the province only three exotic species occurred at a broad scale in more than 50 % of all pentads, common myna, house sparrow, and rock dove. There is apparent concern over the presence of rose-ringed parakeet, a more recent arrival with no records for the 1960s (Tarboton 1968), which was recorded in 11.1 % of

pentads (Symes 2014). The common myna was an early introduction but in recent years has spread its range across South Africa, with a rapid colonisation front extending from its introductory origins on the east coast (Peacock et al. 2007). In October 1962 a single individual seen at the Union Buildings in Pretoria may have signified the colonisation of Gauteng and Markus (1964) predicted, '...there seems to be no reason why this introduced alien could not establish itself more permanently in Pretoria in due course'. Tarboton (1968) reported that it was a common breeding resident of the Johannesburg northern suburbs, present (apparently introduced) since 1938. Indeed, this species has now spread beyond the borders of South Africa north, and, if any, together with mallard may be the regions single most invasive bird species.

Each of these two species, mallard and common myna, pose quite different threats. Whilst that of the myna relate to possible competitive exclusion, those of mallard (recorded in 30.9 % of pentads in Gauteng) relate to genetic hybridisation. Mallard is a threat globally to a number of duck species and has been recorded to hybridise with at least 50 other species (McCarthy 2006); in South Africa most importantly with yellow-billed duck *Anas undulata* (Zaloumis and Milstein 1975; Milstein 1979). Genetic conservation will require focus, and efforts will have to extend beyond species-level conservation. A large proportion (~46 %) of exotic species recorded for Gauteng are ducks, most likely escapees from aviculture; indeed this figure is likely higher if we assume the reporting of uncommon exotic species to be less prioritised in atlasing programmes. In a novel urban environment, the potential to survive and hybridise with indigenous ducks may thus be the greatest threat to native duck species.

Whilst there may be concern that the house sparrow may outcompete indigenous species, e.g. Cape and grey-headed sparrow, there is no evidence to suggest that this is the case. In Johannesburg, like Pietermaritzburg in southeast South Africa, it is a species of heavily transformed areas (Magudu and Downs 2015), much like in Britain (in its indigenous range) where it is, with common starling, more abundant in urban than rural areas (Evans et al. 2009). The common starling is a more recent invader, and the current abundance values for this species may represent a colonisation phase. Given its success elsewhere as an invasive species, it could quite likely become an additional successful exotic species across the country.

16.4.3 Conservation Mitigation

As a response to the threat of landscape modification through urbanisation, numerous conservation policies have been put in place to protect local biodiversity within the region of Gauteng. This includes a 'Ridge Policy' instituted by the Gauteng Department of Agriculture and Rural Development which, for example, prevents development at the Walter Sisulu National Botanical Gardens and thus assists in the conservation of the pair of Verreaux's eagles *Aquila verreauxii* nesting on the cliffs (Symes and Kruger 2012). Whilst this may protect unmodified habitats from

anthropogenic modification, the value of urban green spaces such as parks and golf courses should not be undermined (Jokimäki 1999). The ability of these spaces to act as refuges to bird species which would otherwise be displaced by urbanisation, as well as sites of significant food, water, and roosting sites for new arrivals, signifies that they play a comparable role in the preservation of biodiversity as those areas preserving pristine natural habitat.

Conservation in urban areas typically focuses on slowing down the loss of regional biotic uniqueness. However, there is also a necessity to conserve birds for aesthetic and cultural reasons, in conjunction with the main justification of protecting biodiversity and ecosystem balance (Bolund and Hunhammar 1999; Irvine et al. 2010). There is also an economic implication of urban wildlife conservation, e.g. the contribution of ecotourism towards human livelihoods, and the impact of a change in bird community assembly on agriculture. Whilst much of the transformation within the province is directed towards human indulgence, the spin-offs in creating a heterogeneous landscape in which a diversity of species can persist are equally beneficial. This in turn contributes to human health and well-being and the value of green spaces for the human condition (Kellert and Wilson 1993; Fuller et al. 2007).

Whilst this chapter has presented a broad view of avifauna in the greater Gauteng region and addressed some of the numerous factors responsible for these changes, it has also teased out some of the species-specific drivers responsible for these changes. However, more detailed research on, for example, the role of diet, thermal boundaries, and degrees of habitat specificity, would be required in understanding current ranges and expansions/contractions in relation to anthropogenic change. Species such as fork-tailed drongo *Dicrurus adsimilis* have failed to extend south into the suburbs of Johannesburg from a warm savanna environment, and its strict invertebrate diet may limit this expansion, whilst a northern expansion of African red-eyed bulbul *Pycnonotus nigricans* may have little to do with urbanisation but rather defined by thermal limits (Lloyd et al. 1997). In addition it is unclear why speckled mousebird *Colius striatus*, previously (1960s) an unrecorded species for the Highveld (grassland) (Tarboton 1968), is now a common species, whilst the closely related white-backed mousebird *C. colius*, recorded with greater frequency and breeding in suburban Johannesburg gardens (Tarboton 1968; Bunning 1977), is now confined to the extreme south of the province. Species accounts may provide insight into these changes across Gauteng during the short history of recent human occupation, and with more thorough analyses may assist in a more detailed understanding of how we manage and conserve this diversity.

16.4.4   Conclusion

Urbanisation has transformed the earth's surface and many of the birds that occur within urban areas are there as a result of this human modification (Møller 2009). The human-facilitated planting of trees and widespread irrigation in Johannesburg's

grassland biome have led to an increased abundance of certain indigenous bird species in urban and suburban areas, and a decreased abundance of these birds in seminatural areas. Without this anthropogenic influence, these native bird species would certainly not occur in the abundances that they do. Additionally, overall avifaunal diversity has been enhanced because the apparent heterogeneity introduced through human modification opens up new niches to suit certain species. However, the community assemblage of the province has changed and continues to experience turnover in space and time, mostly to the detriment of many grassland specialist species.

Development within one of Africa's largest economic hubs will continue to maintain pressure on undeveloped land in Gauteng for economic growth. However, there are suitable environments at the broader landscape level to support stable bird communities although a greater focus on the conservation of bird fauna in South African cities is required. This includes the incorporation of urban green spaces into urban and conservation planning. These sites act as refuges for birds that would otherwise become locally extinct, and thus offset some or all of the biodiversity loss that urbanisation and habitat modification would ultimately cause. Of particular importance is the conservation of species reliant on larger areas for their persistence, such as bustards in grasslands.

With ongoing population growth, urban expansion, and anthropogenic change, our focus can rarely be on rehabilitating or preserving a pristine landscape. Urbanisation creates an epicentre for invasions of non-native species (Marzluff 2001) and is much less reversible than other major land-use transformations such as logging, mining, and agriculture (Stein et al. 2000). In the current circumstance, we can utilise Gauteng's new woodland environment and its urban green spaces and afforested suburbia, to maintain a state of high biodiversity and provide proactive conservation strategies for a healthy environment in a novel urban ecosystem (Pautasso et al. 2011; Sanderson and Huron 2011).

Appendix 1

Relative abundance of exotic species recorded in Gauteng for, (1) Delta Park (proportion of months that the species was recorded), (2) Delta Park pentad (2605_2800) reporting rate, and (3) SABAP2 species reporting rate for Gauteng province

Species	Delta Park	Delta Park pentad	SABAP2
Phasianidae			
Common peacock *Pavo cristatus*	–	0.2	13.2
Anatidae			
Ruddy shelduck *Tadorna ferruginea*	–	–	2.4
Garganey *Anas querquedula*	–	0.1	0.7
Mallard *Anas platyrhynchos*	13.2	75.0	31.4
Mallard hybrid *Anas* hybrid	–	17.8	7.3
Blue-winged teal *Anas discors*	–	–	0.7
Ringed teal *Callonetta leucophrys*	–	–	0.3
Tufted duck *Aythya fuligula*	–	–	0.7
Muscovy duck *Cairina moschata*	–	6.4	1.7
Domestic goose *Anser anser*	–	14.1	11.8
Barnacle goose *Branta leucopsis*	–	–	0.7
Red-crested pochard *Netta rufina*	–	–	2.1
Carolina wood duck *Aix sponsa*	–	–	1.7
Mandarin duck *Aix galericulata*	0.7	1.3	1.7
Psittacidae[a]			
Meyer's parrot *Poicephalus meyeri*	–	–	1.0
Brown-headed parrot *Poicephalus cryptoxanthus*	–	–	0.3
Senegal parrot *Poicephalus senegalus*	–	–	0.3
Rosy-faced lovebird *Agapornis roseicollis*	2.8	2.2	2.4
Yellow-collared lovebird *Agapornis personatus*	–	–	0.3
Rose-ringed parakeet *Psittacula krameri*	94.4	67.1	11.5
Plum-headed parakeet *Psittacula cyanocephala*	–	–	0.3
Budgerigar *Melopsittacus undulatus*	–	–	0.3
Columbidae			
Rock dove *Columba livia*	99.3	94.0	90.2
Sturnidae			
Common starling *Sturnus vulgaris*	1.4	0.4	5.2
Common myna *Acridotheres tristis*	100.0	96.8	99.7
Passeridae			
House sparrow *Passer domesticus*	4.9	48.2	94.1
Total	8	13	26

[a]An additional 11 parrot species, at least, are recorded by Symes (2014) for Gauteng, although only rose-ringed parakeet and *Agapornis* spp. appear to breed successfully

Appendix 2

Bird community response in Gauteng for different groups of birds according to disturbance response categories. Percentages are given for comparative purposes with number of species given in parentheses for each group and category. Bold values highlight greatest proportion of species, and associated disturbance category, for different groups of birds. Only species with >10 % reporting rate for SABAP2 are considered

	Disturbance sensitive (137)	Suburban adapted (123)	Urban adapted (20)	Uncategorised (78)
Cavity nesters (28)	21	**35**	25	18
Open nesters (330)	**40**	34	4	22
Frugivore (48)	27	**40**	25	8
Non-frugivore (310)	**40**	34	3	24
Water associated (106)	26	**50**	2	22
Non-water associated (252)	**43**	28	7	22
Grassland (83)	**67**	13	0	19
Non-grassland (275)	30	**41**	7	23
Cliff nester (28)	25	18	**32**	25
Non-cliff nester (330)	**40**	35	5	22
All Birds (358)	38	35	6	22

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Chapter 17
Ecology and Conservation of Australian Urban and Exurban Avifauna

Grant Daniels and Jamie Kirkpatrick

Abstract We review the literature on the ecology and conservation of Australian urban birds and report the results of the first Australian study on the relationship between avifauna and habitat variation in exurbia, which is the low-density zone of development on the outer margins of a city. The Australian urban avifauna has synanthropes found widely elsewhere. It also has a large number of native species, some of which are globally threatened. The distribution of species in Australian urban areas relates better to their niche characteristics than their nativity or exoticness and better to very local variations in habitat type than to environmental variation at the landscape scale, which is often masked by the vegetation thickening associated with suburbanisation. In two exurban regions of Hobart, Tasmania, we sampled birds in unmodified wildland forest (native forests away from development), unmodified exurban forest (native forest on exurban properties), modified exurban forest (native forest on exurban properties and with the understorey removed), exurban gardens and exurban paddocks (cleared land). We tested the hypotheses that exurban habitats were different in bird species compositions from wildlands, that similarity in avifaunal assemblages within habitats increased with the degree of human interference and that, within dry open forests, the perforation (small clearances) and fragmentation associated with exurbanisation would be associated with populations of an aggressive small-bird-excluding edge species, the noisy miner *Manorina melanocephala*. The noisy miner occurred on old land clearance boundaries and not at all in recent forest perforations. In the absence of noisy miners, exurban bird species assemblages were organised by habitat, with the greatest internal consistency being within gardens. In both regions, paddocks had more heterogeneous bird assemblages than expected, and wildlands had identical species assemblages to unmodified exurban forests, but not to other habitat types. The mixture of habitats characteristic of exurbia may not necessarily be detrimental for avifaunal conservation as long as it includes substantial areas of undisturbed native vegetation, even though exurban development may be undesirable for other reasons. We conclude that it is the distinctiveness and high beta diversity of urban

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and exurban habitats that create opportunities for a wide variety of native and exotic bird species, that local manipulations and creations of urban and exurban habitat can substantially affect avifaunal conservation outcomes and that urban bird management should be a major component of many species recovery plans.

17.1 Introduction

17.1.1 General Introduction

The present paper is part of a global consideration of the ecology and conservation of urban avifauna. In some ways, the urban and exurban areas of Australia are but a reflection of those elsewhere in the 'New World'. At their heart are cities with high densities of concrete towers and canyons. These are ringed by extensive reaches of suburban plots, with uniform densities of houses and yards, the garden and street trees of which form urban forests and woodlands, which complement remnant patches of native vegetation captured within the urban matrix. Then, on the outer city boundaries, in the transition zone from developed to undeveloped land, occurs a heterogeneous urban zone known as the exurban fringe (which we define as low-density developments with 1–6 ha plots). In contrast to the similarities with global patterns of development, Australia has a highly endemic and distinctive biota, not least amongst its birds (Keast 1959) and forests, which are dominated by trees that let through relatively high levels of incident light and which grow rapidly on the typically nutrient-poor Australian soils (Kirkpatrick 1997). These sun-drenched forests contrast markedly with the dark, dense-crowned urban forests and woodlands created over two centuries by the European invaders of Australia (Kirkpatrick et al. 2011). Urban areas in Australia are different from native vegetation in ways that are as extreme as an Arizonan city (in the USA) is different from the surrounding desert. The extreme contrast is not at all like the gradual change in structure and floristics found with increasing urbanisation in the cities of New England (McDonnell and Pickett 1990).

We provide a brief review of knowledge of avifaunal ecology and conservation in the urban areas of Australia, focusing on determining any globally distinctive features, as well as the universal question of the relative importance of landscape and local in ecology and conservation. We then address a series of related specific questions in presenting the results of our local investigation of the effect of exurbanisation on bird ecology and conservation around Hobart, Tasmania (Fig. 17.1). Finally we return to discuss strategies for avifaunal conservation, both globally and locally, that are suggested by our work.

Fig. 17.1 Location of Hobart, Tasmania, and all other Australian cities mentioned in text

17.1.2   *Ecology and Conservation of the Australian Urban Avifauna*

Possibly because of guilt over the recent dispossession of indigenous peoples (Pascoe 2014), European Australians tend to be more fond of native species and less fond of exotic species than the surviving indigenes and people elsewhere in the world (Head and Muir 2004). Much of the earlier Australian literature on urban birds addressed the balance between native and exotic species, finding that exotic urban birds are associated with exotic vegetation and native urban birds are associated with native plant species (Green 1986; Green et al. 1989; Parsons et al. 2006). However, observations of the behaviour of individual birds in gardens have provided a more nuanced picture. Catterall et al. (1989) found that the native silvereye (*Zosterops lateralis*) and exotic birds in Brisbane do not select by plant origin or physiognomy, while, in Sydney, two Australian native plant genera were more attractive than two exotic genera to exotic and native birds combined, as well as native birds on their own (French et al. 2005). In Hobart suburbs, native birds are wide ranging in their plant species use, with Daniels and Kirkpatrick (2006) concluding that it is possible to have an excellent complement of native birds in a garden solely composed of exotic plants (for the role of exotic plants in urban bird conservation, see Gleditsch 2016). In contrast, the exotic birds in Hobart gardens

hardly stray from exotic plants (Daniels and Kirkpatrick 2006). In a landscape-scale analysis in Melbourne, Conole and Kirkpatrick (2011) note that both exotic and native bird species are both urban avoiders and urban adaptors, concluding that the origin of a bird is much less important in determining its urban distribution than its functional attributes. In fact, most of the urban adaptors were native species, not all of which were native to the Melbourne region before the European invasion. For example, the crested pigeon *Ocyphaps lophotes*, an urban exploiter, invaded the Melbourne region from the Mallee country of Victoria only in recent decades.

Conole and Kirkpatrick (2011, p. 18) found that species most likely to be urban adaptors in Melbourne were '(1) medium-bodied, cavity or canopy nesting, and (2) omnivorous, granivorous or nectarivorous'. In contrast, insectivorous species that nest close to the ground or on the ground tended to be in the urban avoider class in Melbourne (Conole and Kirkpatrick 2011), as elsewhere (Chace and Walsh 2006; Minor and Urban 2010).

One of the most important questions in urban bird ecology is the relative influence of landscape attributes and local habitat conditions on bird assemblages. Landscape explanations have been adopted without any more evidence than a general tendency of bird assemblages to relate to measurable indicators of urbanisation (e.g. Goddard et al. 2010). The fact that landscape patterns can be related to avifaunal patterns does not demonstrate that processes that operate at a landscape scale, such as limitation of range related to resource availability or limitation of range due to suitable habitat being outside dispersal range, pertain (but see Litteral and Shochat 2016). It may be that the gradients reflect the attenuation or increase of suitable habitats for individual species within urban land cover gradients. A species relying on fruit trees for sustenance would have difficulty in surviving in any central business district (CBD). Daniels and Kirkpatrick (2006) show that there is no difference in the ratio between floristic distance and avifaunal distance between front- and backyards on the same block and all pairs of front- and backyards, indicating that geographic distance is an unimportant component of an explanation for avifaunal differences in Hobart. It may well be that, if a garden with characteristics that suit a particular group of species is very remote from other such gardens, landscape effects will be evident. However, all garden types tend to be found in all suburbs in Australia, albeit at different frequencies (Kirkpatrick et al. 2007). Parsons et al. (2003) demonstrate a lack of influence of adjacent natural vegetation on the suburban avifauna of Sydney, contrasting with the distance effect found in young suburbs in Canberra (Munyenyembe et al. 2006). Bird species richness in remnants is affected by connectivity of native environments in Brisbane, and total bird abundance is affected by an interaction between remnant size and connectivity (Shanahan et al. 2011).

There is strong evidence that particular aspects of the urban environment can have a beneficial effect on some threatened species. These include extra and relatively constant available moisture, enhanced nutrient availability and high alpha and beta plant species diversity. During drought years, the endangered swift

parrot (*Lathamus discolor*) depends for its feeding on the flowering of large remnant individuals of Tasmanian blue gum (*Eucalyptus globulus* ssp. *globulus*) growing in well-watered suburban lots, making the steady depletion of such trees alarming (Allchin et al. 2013). The predatory grey goshawk (*Accipiter novaehollandiae*) frequents domestic chicken yards to hunt species attracted to the surplus grain, while the rare powerful owl (*Ninox strenua*) can be more easily observed in botanical gardens (where it hunts the possums supported by a profusion and diversity of vegetable resources) than in its natural forest habitat (Low 2002). In a similar manner, migratory waterbirds find sewerage farms and sewerage treatment ponds productive habitats. However, the potential to support populations of raptors and owls from the nutrient sink of the city can be moderated by the impact of poisons. For example, secondary poisoning from rats has become more common as rat poison has been made of more persistent chemicals, making many domestic chicken yards and public spaces death traps. Mortality through window strike can also mitigate the benefit of suburban resources, as in the case of the swift parrot (Allchin et al. 2013).

17.1.3 Ecology and Conservation of the Exurban Avifauna of Hobart

On the periphery of New World cities, there are often substantial areas in which land parcels that are too small for viable farming or forestry enterprises, and much larger than those typical of suburbia, are occupied by commuters, small business people or retirees (Brown et al. 2005)—this intermediate zone between the suburbs and the countryside is what we refer to as exurbia. It is characterised by building density <2.5/ha and residential human density 1–10/ha (Marzluff et al. 2001). Typical exurbia in Australia consists of 1–6 ha (3–20 acre) land parcels containing a house and outbuildings, with the grounds supporting some or all of gardens, waterbodies, native vegetation, seminatural vegetation, fields, orchards, crops, sports facilities and horse-training tracks. The process of exurbanisation fragments, perforates and disturbs native vegetation, as well as modifying land that was previously farmed. Consequently, exurbanisation can result in shifts in the distribution and abundance of bird species and communities (Nilon et al. 1995; Odell and Knight 2001; Merenlendera et al. 2009; Suarez-Rubio et al. 2011; Schlossberga et al. 2011). Studies of exurbanisation from a variety of ecoregions are vitally important in order to determine consistent implications for biota (Hansen et al. 2005), but exurbia remains critically understudied outside of the USA.

Exurbanisation has been found to result in a significant increase in edge habitat (Nilon et al. 1995) and can also result in an opening up of native understoreys. In both suburban and rural areas in eastern Australia, forests with open understoreys,

forest edges and small forest remnants are dominated by a medium-sized Australian native honeyeater, the noisy miner *Manorina melanocephala*, which consistently co-occurs with other edge species such as the Australian magpie *Gymnorhina tibicen*, the grey butcherbird *Cracticus torquatus* and rosella species of the *Platycercus* complex (Catterall 2004). The noisy miner aggressively excludes smaller birds (Dow 1977), can reduce nesting success in some species (Piper and Catterall 2004) and alters the composition of bird species communities even in non-urban habitats (Grey et al. 1997, 1998; MacDonald and Kirkpatrick 2003). Closed forests are too structurally complex for noisy miners to defend and are thus not typical habitat. In our case study, we therefore predicted that within a region dominated by dry open forest, the perforations and fragments characteristic of exurbia would have noisy miners and, consequently, an avifaunal assemblage distinct from wildland communities.

Miner-free eastern Australian suburbs can support a diverse assemblage of small woodland birds (Daniels and Kirkpatrick 2006; Conole and Kirkpatrick 2011), but these still mostly lack a number of species shown to be sensitive to habitat alteration and urbanisation, such as grey shrike-thrushes *Colluricincla harmonica*, grey fantails *Rhipidura albiscapa*, golden whistlers *Pachycephala pectoralis*, superb fairy-wrens *Malurus cyaneus*, striated pardalotes *Pardalotus striatus*, satin fly-catchers *Myiagra cyanoleuca*, yellow-throated honeyeaters *Lichenostomus flavicollis*, and the Tasmanian scrub wren *Sericornis humilis* (Green 1986; Wood 1996; Catterall et al. 1998). Because of the greater extent of native habitat in exurbia, in our case study, we predicted that an exurban region with unsuitably dense habitat for noisy miners would have sufficient undisturbed habitat to support such urban-sensitive species.

Urbanisation homogenises bird communities between sites within habitats, between habitats within regions and between habitats across regions (Chace and Walsh 2006). Levels of intersite similarity are typically higher in suburban habitats than in wildland or remnant habitats (Parsons et al. 2003; White et al. 2005). Intersite similarity has been found to be highest in streetscapes with exotic vegetation, lower in recently developed streets largely devoid of woody vegetation and lowest in streets with native vegetation (White et al. 2005). Regional similarities increase with the level of human influence (Blair 2001). Based on these patterns, within our case study, we predicted intersite similarity in exurbia to be highest in gardens, lower in paddocks and lowest in forests, which could be taken to represent a gradient of declining human interference.

Thus, in the first study to document variation in bird species assemblages related to exurbanisation in Australia, we test the hypotheses that (1) exurban habitats support bird species assemblages different in composition to those in wildlands; (2) within dry open forest, the perforations associated with exurbanisation are associated with the presence of noisy miners; and (3) exurban avian assemblages increase in similarity between sites within habitats the greater the human interference.

17.2   Methods

17.2.1   Study Areas

The study areas are spatially distinct areas of exurbia located on the periphery of the city of Hobart, Tasmania, Australia. The first area consists of the South Arm Peninsula ('South Arm'), and the second is an area south-southwest of the CBD (referred to as 'Kingborough'). South Arm (43°00′ S, 147°30′ E) receives between 300 and 600 mm of precipitation per annum, while Kingborough (42°55′ S, 147°13′ E) receives between 800 and 1100 mm. Natural vegetation in both the South Arm and Kingborough areas consists largely of forests dominated by *Eucalyptus* species. The Kingborough forests have dense understoreys dominated by a mixture of scleromorphic and broad-leaved small trees and tall shrubs, whereas the South Arm forests have more open understoreys dominated largely by scleromorphic shrubs.

South Arm has an area of 6090 ha, of which 1358.8 ha consists of exurban properties with a mean area of 2.51 ha. Around 40 % of South Arm maintains native forest cover, but close to 70 % of this forest area is occupied by exurban development. Of the non-urban land in South Arm, approximately 800 ha is forested wildland (native forests without development), while the remainder is mostly cleared land (paddocks). Less than 50 ha of the forest in South Arm is isolated by cleared land, but most of the wildlands are separated by patches of exurban properties, such that the two largest wildland patches are around 300 ha. In other words, although overall forest cover is high, the connectivity relies on exurban properties within the forest. In addition, because of the peninsula location, the region as a whole is separated from other more extensive wildlands (>400 ha) by suburbs and the sea.

Kingborough has an area of 4340.9 ha, of which 1449.3 ha consists of exurban properties with a mean property size of 4.16 ha. Around 66 % of Kingborough maintains native forest cover, with 55 % of this occupied by exurban development. In contrast to the isolated peninsula of South Arm, Kingborough is directly adjacent to extensive wildlands in excess of 1000 ha.

17.2.2   Site Selection

Within the two study areas, landowners residing on blocks between 2 and 6 hectares in size were approached through door knocking, and permission was sought to conduct field work on their property. There were very few refusals. While this could not be a random sample, because of refusals and absences of owners when requesting access, pre-knowledge of most conditions on the properties was lacking. One hundred and sixty-four sampling sites were located in South Arm ($n = 73$), Kingborough ($n = 71$) and forested wildlands ($n = 20$). Within exurbia, sites were

non-purposively distributed across the four most prominent habitats: exurban forest (defined as native forest on exurban properties—$n = 37$), modified forest (native forest on exurban properties and with the understorey removed—$n = 39$), gardens ($n = 33$), and paddocks (cleared land—$n = 35$). Plots were placed to avoid edges between habitats where possible.

Wildlands were natural forest vegetation in large remnants (>400 ha). These were located away from any urban influence and thus broadly represented the situation before forests were fragmented and perforated. Data collection within wildlands took place no less than 250 m from the forest edge and a minimum of 500 m from any dwelling. Exurban forest was unmodified native forest vegetation located on exurban properties. Modified forests were native forests on exurban properties that had between 25 and 100 % of their understorey vegetation modified structurally by clearance or ongoing suppression (slashing and/or stock grazing). Tree clearing was often evident, but not extensive, and often resulted in the broadening of the crowns of the remaining trees. Thus, canopy cover was comparable to that in corresponding wildland and exurban forests, but sometimes constituted fewer individual trees, which further contributed to the openness of the understorey. Paddocks were areas of cleared land on exurban properties and were largely devoid of woody vegetation (<5 % total cover). Paddocks had a dominant stratum <60 cm in height comprised predominately of grasses and herbs. Gardens were non-natural exurban sites created by the deliberate planting of ornamental and/or productive species of plants. Exurban gardens were generally located adjacent to a house. Bird survey sites within garden habitats often included an area of maintained lawn, but other garden plants covered >25 % of the survey area. Because exurbia was locally highly heterogeneous, wildland was the only habitat type in which data collection plots were always embedded within homogenous areas.

17.2.3   Field Observations

Birds were sampled in survey plots 625 m^2 in order to negate differences in detection probability between open and dense habitats. The small plots ensured that the vegetation within each site was visible and that it was easy to determine whether calls emanated from within the plot or from the outside. The location from which the observer conducted the survey remained constant within sites over time. The location maximised site visibility and minimised observer disturbance. In densely vegetated sites, the location tended to be within the survey plot (usual maximum horizontal distance between observer and plot boundary being 12.5 m), whereas in sparsely vegetated sites, the location was generally a short distance (20 m) away from the plot, preferably next to something that afforded the observer some level of cover. Plots were square or rectangular because these shapes better fitted the shapes of domestic gardens and paddocks than circles.

Between 8 June 2006 and 21 August 2008, a total of seven 20-min point count surveys were conducted in the plot at each site. Each site was surveyed four times during the morning period (dawn to 11 am), three times during the afternoon period (2:30 pm to dusk), twice during the southern hemisphere spring (September to November), twice during the summer months (December to February), once during the autumn (March to May) and twice during the winter (June to August). Bird surveys were not carried out in rain, or when wind was sufficient enough to be a potential hindrance to accurate identification. Birds flying over or through the site were not recorded, except for aerial insectivores, which were included if foraging within 5 m of canopy height or below.

17.2.4   Data Analysis

The data that we used for all analyses were the percentage of observation times at which a species was observed. Frequency was used, rather than mean count, to avoid the recognised problems of the latter measure in comparing the birds of heterogeneous vegetation types (for censusing bird in urban settings, see van Heezik and Seddon 2016). Site bird frequency data were ordinated using non-metric multidimensional scaling with the default options in DECODA (Minchin 2001). This technique produces the least distortions for data sets with large numbers of zeros (Minchin 1987).

The hypothesis that exurban avifaunal assemblages were different from those of wildlands was tested using Permanova (Anderson et al. 2008) with one factor containing the levels: wildland related to South Arm, wildland related to Kingborough, South Arm garden, Kingborough garden, South Arm paddock, Kingborough paddock, South Arm modified forest, Kingborough modified forest, South Arm exurban forest and Kingborough exurban forest. To test the hypothesis that the presence of noisy miners can homogenise assemblages, we used Permanova with one factor containing wildland related to South Arm, South Arm garden, South Arm paddock, South Arm modified forest and South Arm exurban forest, but with the latter four classes only containing data from sites from which noisy miners were observed.

To test the hypothesis that the perforations associated with exurbanisation favour the occurrence of the noisy miner, the association between edge type (recent perforations versus old edges) and the frequency of the noisy miner was tested using ANOVA. The classification of old edges and recent perforations was based on examination of aerial photos taken in 1965.

Pearson's chi-square was used to test if bird species varied significantly in their frequencies between habitats. Within each region, records from wildland sites and exurban forest sites were collated into an 'unmodified forest' class because of the lack of significant community difference in the Permanova analysis. Species were considered habitat specialists if they were significantly associated with the same habitat in each region and regional habitat specialists if they were significantly

associated with a certain habitat in one region only. Within individual exurban habitat types, differences in the frequencies of occurrence of species between sites in which noisy miners were recorded and sites in which noisy miners were not recorded were tested using ANOVA.

To test the hypothesis that exurban avian assemblages increase in similarity between sites the greater the human interference, Bray-Curtis similarity values were calculated for all pairs of sites within each exurban habitat and then the influence of the factors habitat and region, and their interaction, assessed using a general linear model with a logit link function.

17.3   Results

Sixty-one species were recorded from our exurban sites and 36 species from wildland sites. Excluding species that were recorded in less than ten surveys in total (for which there were insufficient data to make generalisations), not a single species was recorded exclusively in wildlands, while ten species were recorded in exurbia, but not in wildlands (Table 17.1). Six of these ten were natives: masked lapwing *Vanellus miles*, Tasmanian native hen *Tribonyx mortierii*, forest raven *Corvus tasmanicus*, Australian magpie, eastern rosella *Platycercus eximius* and the noisy miner (Table 17.1). The latter three are classic edge species and were recorded exclusively in South Arm (Table 17.1).

Within each region, gardens, paddocks and modified forest had bird communities that were distinct from those in the regionally associated wildlands, but exurban forests did not (Fig. 17.2). Thus, wildland bird assemblages can inhabit forested exurban habitats. Within South Arm, the bird species assemblages of modified forest and exurban forest did not significantly differ, while the assemblages within gardens and paddocks were distinct from those in all types of forest and each other (Fig. 17.2). In exurban Kingborough, all habitat types had different assemblages to each other, but the modified forests and wildland forests had identical assemblages to the South Arm wildland forests (Fig. 17.2).

Despite the presence of noisy miners, not all of the exurban habitats in South Arm supported bird assemblages distinct from the assemblage in the respective wildlands (Fig. 17.2). This is because noisy miners were not distributed uniformly across the South Arm region. Residential forest perforations did not create points of invasion for noisy miners, which were restricted to small forest remnants and habitats on the edge of land that had been cleared for agriculture earlier than 1965 (Fig. 17.3, mean frequency in recent perforations $= 0.00$; mean frequency in edges and remnants $= 32$, $F = 29$, $P < 0.001$). However, if only exurban sites in which miners were present are considered, then all individual South Arm exurban habitats had bird assemblages discrete from the wildlands assemblage, and paddock was the only exurban habitat type with a distinct avian assemblage (Fig. 17.4).

Overall, noisy miners were regional modified forest specialists (Table 17.1). Nine species, all small native insectivores, were unmodified forest specialists at

Table 17.1 Bird species recorded ten or more times in exurbia and/or wildlands, showing their percentage frequency in different habitats, including the collective unmodified forest habitat (wildlands and exurban unmodified forest combined)

Species[a]		Kingborough unmodified forests	Kingborough modified forest	Kingborough gardens	Kingborough paddocks	Kingborough P (df=3)[b]	South Arm unmodified forests	South Arm modified forest	South Arm gardens
Striated pardalote	*Pardalotus striatus*	9.36	7.14	2.52	0.00	0.002	13.37	11.43	7.14
Brown thornbill	*Acanthiza pusilla*	25.62	18.57	15.97	8.04	0.001	10.71	11.43	15.18
Satin flycatcher	*Myiagra cyanoleuca*	3.94	1.43	0.00	0.00	0.019	2.55	0.71	0.00
Strong-billed honeyeater	*Melithreptus validirostris*	7.39	5.00	4.20	0.00	0.020	0.51	0.00	0.00
Tasmanian scrubwren	*Sericornis humilis*	14.78	2.86	1.68	0.89	0.000	0.51	0.00	0.00
Tasmanian thornbill	*Acanthiza ewingii*	8.37	5.71	5.04	0.00	0.019	1.53	0.00	0.00
Golden whistler	*Pachycephala pectoralis*	4.43	7.14	2.52	0.00	0.025	3.06	5.71	0.00
Spotted pardalote	*Pardalotus punctatus*	5.42	9.29	4.20	0.89	0.027	12.24	14.29	7.14
Australian magpie	*Cracticus tibicen*	0.00	0.00	0.00	0.00	NS	0.51	5.71	7.14
Eastern rosella	*Platycercus eximius*	0.00	0.00	0.00	0.00	NS	1.53	5.71	5.36
Noisy miner	*Manorina melanocephala*	0.00	0.00	0.00	0.00	NS	10.20	21.43	17.86
Scarlet robin	*Petroica boodang*	3.45	15.00	14.29	8.04	0.001	10.71	15.00	5.36
Common blackbird*	*Turdus merula*	3.45	12.14	25.21	6.25	0.000	0.00	1.43	16.96

(continued)

Table 17.1 (continued)

Species[a]	Kingborough unmodified forests	Kingborough modified forest	Kingborough gardens	Kingborough paddocks	Kingborough P (df=3)[b]	South Arm unmodified forests	South Arm modified forest	South Arm gardens
Green rosella *Platycercus caledonicus*	4.93	7.14	9.24	0.89	0.036	5.61	8.57	11.61
House sparrow* *Passer domesticus*	0.00	1.43	23.53	8.04	0.000	0.51	2.14	29.46
New Holland honeyeater *Phylidonyris novaehollandiae*	14.78	20.71	47.90	10.71	0.000	12.76	13.57	18.75
Superb fairy-wren *Malurus cyaneus*	14.29	29.29	57.14	21.43	0.000	10.71	14.29	31.25
Welcome swallow *Hirundo neoxena*	0.99	7.14	15.13	8.04	0.000	3.06	7.14	13.39
Common greenfinch* *Carduelis chloris*	0.00	0.00	0.00	0.00	NS	0.00	0.71	3.57
Common starling* *Sturnus vulgaris*	1.48	2.14	5.04	2.68	NS	0.00	1.43	8.04
Crescent honeyeater *Phylidonyris pyrrhopterus*	14.29	10.71	15.13	0.00	0.000	3.57	5.00	4.46
Eastern spinebill *Acanthorhynchus tenuirostris*	11.33	4.29	12.61	0.89	0.001	3.57	4.29	2.68
Little wattlebird *Anthochaera chrysoptera*	0.99	2.14	3.36	0.00	NS	2.04	5.71	30.36
Silvereye *Zosterops lateralis*	8.37	11.43	15.97	1.79	0.001	5.10	3.57	5.36
Masked lapwing *Vanellus miles*	0.00	1.43	0.00	8.93	0.000	0.00	0.00	0.89
Yellow-rumped thornbill *Acanthizachrys orrhoa*	0.00	0.71	1.68	3.57	0.043	1.53	5.00	2.68

Tasmanian native-hen	*Tribonyx mortierii*	0.00	2.14	0.00	0.00	NS	0.00	0.00	4.46
Grey fantail	*Rhipidura albiscapa*	17.24	21.43	13.45	3.57	0.000	11.73	8.57	3.57
Black-headed honeyeater	*Melithreptus affinis*	10.84	11.43	5.88	0.89	0.005	12.76	9.29	3.57
Yellow-throated honeyeater	*Lichenostomus flavicollis*	14.29	19.29	11.76	3.57	0.003	28.06	13.57	8.93
European goldfinch*	*Carduelis carduelis*	0.00	6.43	8.40	1.79	0.000	0.00	3.57	1.79
Dusky robin	*Melanodryas vittate*	5.91	7.86	9.24	3.57	NS	4.59	2.86	0.89
Grey currawong	*Streptera versicolor*	2.46	2.86	0.84	0.00	NS	1.02	0.71	0.89
Grey shrike-thrush	*Colluricincla harmonica*	2.96	5.00	5.04	0.00	NS	1.53	1.43	0.00
Flame robin	*Petroica phoenicea*	2.46	1.43	0.84	1.79	NS	1.53	2.14	0.89
Forest raven	*Corvus tasmanicus*	0.49	2.14	0.84	0.00	NS	2.55	2.14	0.00
Shining bronze-cuckoo	*Chrysococcyx lucidus*	1.97	0.00	1.68	0.00	NS	2.04	1.43	0.89
Tree martin	*Petrochelidon nigricans*	3.94	1.43	0.84	0.89	NS	3.06	11.43	6.25
Yellow wattlebird	*Anthochaera paradoxa*	2.46	5.00	1.68	0.00	NS	1.53	0.71	0.00

(continued)

Table 17.1 (continued)

Species[a]		South Arm paddocks	South Arm P (df=3)[b]	Habitat specialisation[c]	Functional group[d]	Kingborough wildlands	Kingborough exurban forest[e]	South Arm wildlands	South Arm exurban forest[e]
Striated pardalote	*Pardalotus striatus*	0.75	0.001	F	I c S	10.00	9.02	15.71	11.90
Brown thornbill	*Acanthiza pusilla*	6.77	NS	r F	I d S	25.71	25.56	11.43	10.32
Satin flycatcher	*Myiagra cyanoleuca*	0.00	NS	r F	I b S	5.71	3.01	7.14	0.00[x]
Strong-billed honeyeater	*Melithreptus validirostris*	0.00	NS	r F	I b S	5.71	8.27	1.43	0.00
Tasmanian scrubwren	*Sericornis humilis*	0.00	NS	r F	I d S	14.29	15.04	1.43	0.00
Tasmanian thornbill	*Acanthiza ewingii*	0.00	NS	r F	I d S	8.57	8.27	2.86	0.79
Golden whistler	*Pachycephala pectoralis*	1.50	0.035	MF	I b S	4.29	4.51	4.29	2.38
Spotted pardalote	*Pardalotus punctatus*	0.75	0.000	MF	I c S	1.43	7.52	5.71	15.87[x]
Australian magpie	*Cracticus tibicen*	1.50	0.003	r MF	O b L	0.00	0.00	0.00	0.79
Eastern rosella	*Platycercus eximius*	0.00	0.009	r MF	G c M	0.00	0.00	0.00	2.38
Noisy miner	*Manorina melanocephala*	5.26	0.000	r MF	I b M	0.00	0.00	0.00	15.87[x]
Scarlet robin	*Petroica boodang*	8.27	NS	r MF	I b S	7.14	1.50[x]	12.86	9.52
Common blackbird*	*Turdus merula*	0.75	0.000	G	O b M	0.00	5.26	0.00	0.00
Green rosella	*Platycercus caledonicus*	0.00	0.001	G	G c M	4.29	5.26	10.00	3.17[x]

House sparrow*	Passer domesticus	5.26	0.000	G	G dc S	0.00	0.00	0.00	0.79
New Holland honeyeater	Phylidonyris novaehollandiae	1.50	0.000	G	N b S	10.00	17.29	15.71	11.11
Superb fairy-wren	Malurus cyaneus	13.53	0.000	G	I d S	10.00	16.54	12.86	9.52
Welcome swallow	Hirundo neoxena	12.78	0.002	G	I b S	0.00	1.50	2.86	3.17
Common greenfinch*	Carduelis chloris	2.26	0.048	r G	G c S	0.00	0.00	0.00	0.00
Common starling*	Sturnus vulgaris	3.76	0.000	r G	O c M	0.00	2.26	0.00	0.00
Crescent honeyeater	Phylidonyris pyrrhopterus	0.75	NS	r G	N b S	18.57	12.03	7.14	1.59[x]
Eastern spinebill	Acanthorhynchus tenuirostris	0.75	NS	r G	N b S	18.57	7.52[x]	7.14	1.59[x]
Little wattlebird	Anthochaera chrysoptera	3.01	0.000	r G	N b M	1.43	0.75	4.29	0.79
Silvereye	Zosterops lateralis	0.75	NS	r G	O b S	5.71	9.77	7.14	3.97
Masked lapwing	Vanellus miles	6.77	0.000	P	I g L	0.00	0.00	0.00	0.00
Yellow-rumped thornbill	Acanthiza chrysorrhoa	7.52	0.039	P	I d S	0.00	0.00	1.43	1.59
Tasmanian native-hen	Tribonyx mortierii	7.52	0.000	r P	GH g L	0.00	0.00	0.00	0.00
Grey fantail	Rhipidura albiscapa	4.51	0.027	r MF/r F	I b S	11.43	20.30	12.86	11.11
Black-headed honeyeater	Melithreptus affinis	0.00	0.000	r MF/r F	I b S	11.43	10.53	12.86	12.70
Yellow-throated honeyeater	Lichenostomus flavicollis	3.01	0.000	r MF/r F	I b S	12.86	15.04	17.14	34.13[x]
European goldfinch*	Carduelis carduelis	4.51	0.031	r G/r P	G b S	0.00	0.00	0.00	0.00

(continued)

Table 17.1 (continued)

Species[a]		South Arm paddocks	South Arm P (df=3)[b]	Habitat specialisation[c]	Functional group[d]	Kingborough wildlands	Kingborough exurban forest[e]	South Arm wildlands	South Arm exurban forest[e]
Dusky robin	*Melanodryas vittate*	2.26	NS	–	I b S	7.14	5.26	7.14	3.17
Grey currawong	*Streptera versicolor*	0.00	NS	–	O b L	2.86	2.26	1.43	0.79
Grey shrike-thrush	*Colluricincla harmonica*	0.00	NS	–	C b M	2.86	3.01	1.43	1.59
Flame robin	*Petroica phoenicea*	0.00	NS	–	I b S	2.86	2.26	4.29	0.00[x]
Forest raven	*Corvus tasmanicus*	0.00	NS	–	O b L	0.00	0.75	0.00	3.97
Shining bronze-cuckoo	*Chalcites lucidus*	0.00	NS	–	I p S	0.00	3.01	4.29	0.79
Tree martin	*Petrochelidon nigricans*	3.01	NS	–	I c S	8.57	1.50[x]	0.00	4.76
Yellow wattlebird	*Anthochaera paradoxa*	0.00	NS	–	N b M	0.00	3.76	2.86	0.79

[a]Asterisk denotes exotic species

[b]NS indicates no significant ($P > 0.05$) difference in a four-way comparison of unmodified forests, modified forests, gardens and paddocks

[c]F=collective unmodified forest; MF=modified forest; G=garden; P=paddock; r=regional specialist only

[d]C=carnivore; G=granivore; H=herbivore; I=insectivore; N=nectivore; O=omnivore; b=bowl/open cup/platform nester; c=cavity/chamber nester; d=dome nester; g=ground nester; p=parasitic nester; S=small body size (<50 g); M=medium body size (50–200 g); L=large body size (>200 g)

[e]An adjacent 'x' indicates a significant ($P < 0.05$) difference in a paired comparison with the corresponding wildlands
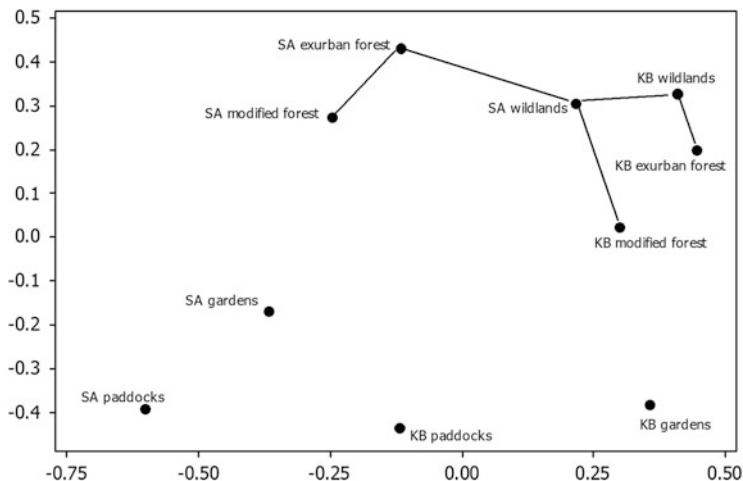
Fig. 17.2 Mean locations of bird assemblages by habitats and region in two-dimensional global non-metric multidimensional scaling ordination space (stress < 0.20). Habitats joined by lines do not statistically differ at $P > 0.05$ in the Permanova analysis. SA = South Arm, KB = Kingborough

least on a regional basis (Table 17.1). Within individual exurban habitats in South Arm, several species had a significant ($P < 0.010$) difference in their frequency of occurrence between sites in which noisy miners were recorded and sites in which noisy miners were not recorded (Table 17.2).

The general linear model for within habitat similarity showed strong effects for region ($F = 67$, $P = <0.001$), habitat ($F = 30$, $P = <0.001$) and their interaction ($F = 13$, $P = <0.001$), with a low r^2 (14 %). The bird assemblages of unmodified exurban forests were equally similar between sites in Kingborough and South Arm, while those in the other three habitats were much more similar between sites in Kingborough than in South Arm (Fig. 17.5). In South Arm, the bird assemblages of unmodified exurban forest, modified forest and gardens were more uniform than those of paddocks (Fig. 17.5). In Kingborough, gardens had the most uniform bird assemblages, followed by modified forest, unmodified exurban forest and then paddocks (Fig. 17.5).

17.4 Discussion

17.4.1 Differences Between Wildlands and Exurban Habitats

Previous studies have demonstrated that exurban areas can support avifaunal communities as diverse as wildlands (Bock et al. 2008) in which individual species of conservation concern prosper (Haskell et al. 2006), but our work is the first to demonstrate that, in the absence of or with only local dominance of edge species,
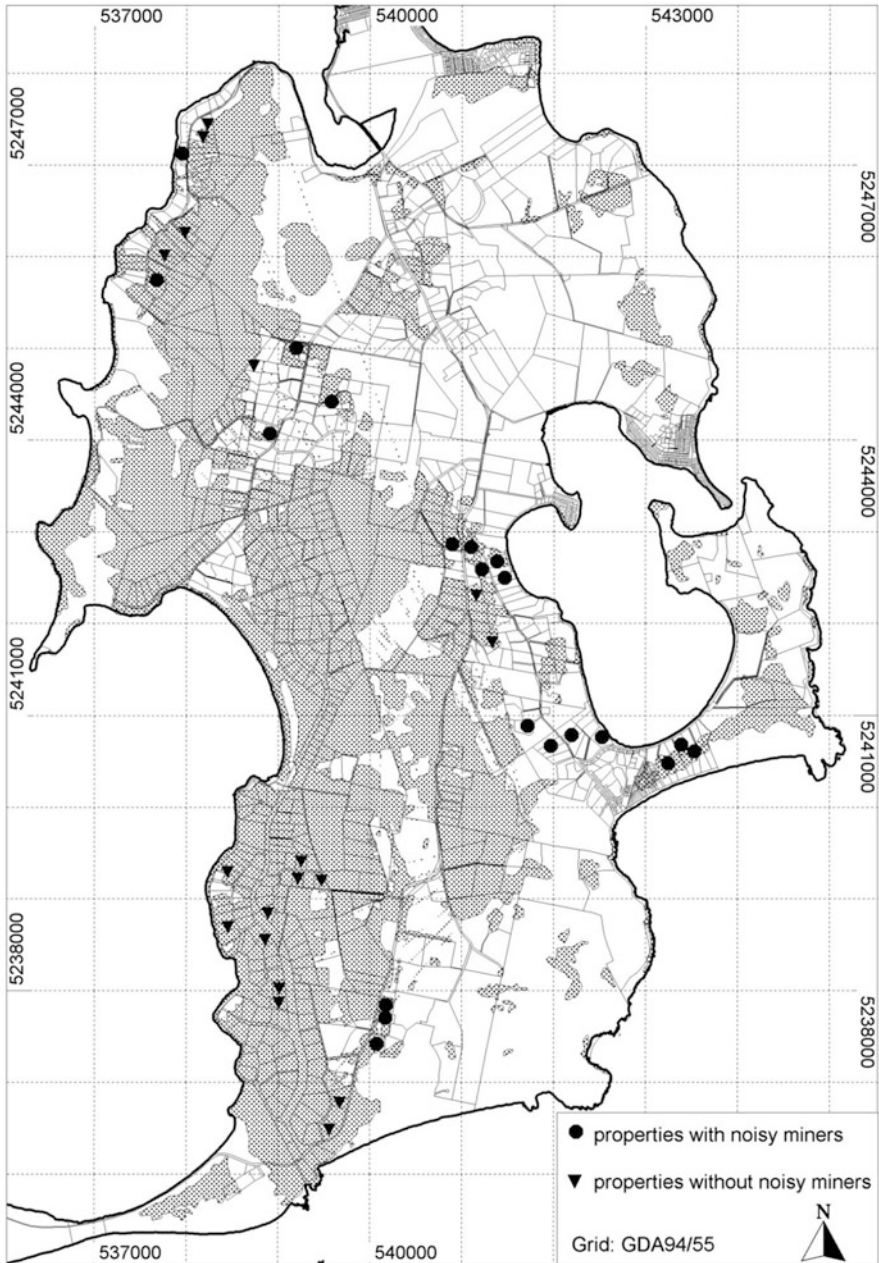
Fig. 17.3 The distribution of noisy miners at South Arm sites in relation to forest (*shaded*) and paddocks/cleared land (*non-shaded*). The *fine lines* indicate exurban property boundaries (cadastre)
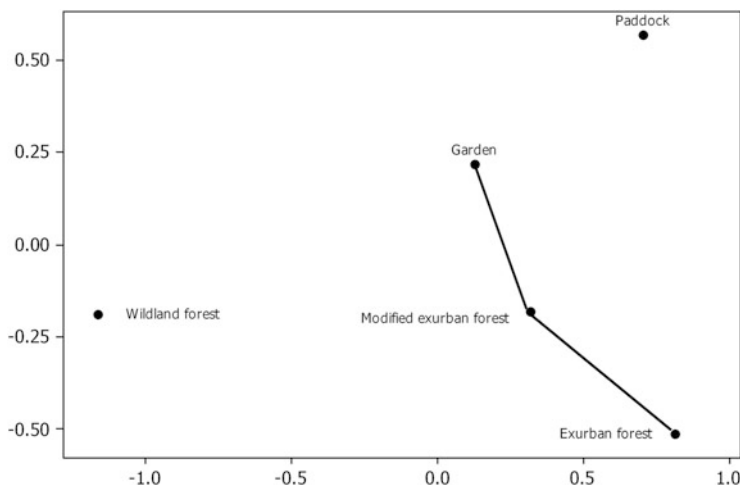
Fig. 17.4 Mean locations of bird assemblages within habitats (exurban habitats only include those sites in which noisy miners were recorded) in two-dimensional global non-metric multidimensional scaling ordination space (stress = 0.17). Habitats joined by lines do not statistically differ at $P > 0.05$ in the Permanova analysis

wildland bird species assemblages can survive in an exurban matrix. This has substantial implications for urban avifaunal conservation in that it suggests that typical urban effects on bird species communities can be ameliorated by maintaining forest continuity and integrity in the exurban matrix, even if the forest is perforated by houses and gardens. This outcome may partly relate to the survival of trees with hollows (cavities), as in the west of the USA (Blewett and Marzluff 2005).

If forest integrity could be maintained in suburban density developments, wildland bird assemblages might still suffer from density-associated stressors such as domestic mesopredators (Odell and Knight 2001) and disturbance from human activity (Schlesinger et al. 2008; Glennon and Kretser 2013). Indeed, previous studies of exurban avifaunas have documented the decline of individual species of songbird (Odell and Knight 2001), as well as total bird species richness (Bock et al. 2008; Pidgeon et al. 2014), with increasing housing density, and have recorded very different abundance responses to exurbanisation of different species (Whittaker and Marzluff 2009). However, given the invariable proximity of domestic gardens to houses and the distinct garden bird assemblages recorded in this study, future studies on the effects of housing distance and density in typically heterogeneous urban environments must take into account avifaunal responses to habitat change. The presence of certain edge species may also be influential. A previous American study found that one of the main differences between the avifaunas of exurban developments with clustered houses, and exurban developments with dispersed houses, was a greater number of nest predators and parasites

Table 17.2 Frequencies of occurrence of bird species with statistically different (ANOVA, $P < 0.10$) frequencies between sites in which noisy miners were recorded and sites in which noisy miners were not recorded, within individual South Arm exurban habitats

	Australian magpie	Black-headed honeyeater	Brown thornbill	Common starling	Crescent honeyeater	Eastern rosella	Eastern spinebill	Grey fantail	House sparrow	Musk lorikeet	New Holland honeyeater	Scarlet robin	Silvereye	Spotted pardalote	Striated pardalote	Superb fairy-wren	Tree martin	Yellow-throated honeyeater
Exurban forest without miners	0.00	16.33	13.27			0.00		14.29		0.00		12.24		20.41	14.29			43.88
Exurban forest with miners	3.57	0.00	0.00			10.71		0.00		7.14		0.00		0.00	3.57			0.00
F	4.15	3.30	6.19			10.18		4.15		12.44		3.76		6.58	3.20			14.26
P	0.06	0.09	0.02			0.01		0.06		0.00		0.07		0.02	0.09			0.00
Modified forest without miners	0.00				9.09	0.00	9.09		3.90	0.00	23.38	20.78	6.49			22.08	15.58	18.18
Modified forest with miners	12.70				0.00	12.70	0.00		0.00	4.76	1.59	4.76	0.00			6.35	4.76	6.35
F	4.73				7.94	7.92	4.22		3.04	4.95	4.03	4.93	3.89			5.16	4.69	4.24
P	0.04				0.01	0.01	0.55		0.10	0.04	0.06	0.04	0.06			0.04	0.04	0.54
Garden without miners					9.52				59.52		42.86	11.91						
Garden with miners					1.43				11.43		4.29	1.43						
F					3.98				10.93		13.62	4.92						
P					0.07				0.01		0.00	0.04						
Paddocks without miners				5.50												18.68		
Paddocks with miners				0.00												2.38		
F				3.36												3.29		
P				0.09												0.09		

Fig. 17.5 Means and 95 % confidence intervals for similarity between bird frequencies by region and habitat. Habitat EF = exurban unmodified forest, MF = modified forest, G = gardens, P = paddocks

where the housing was clustered (Nilon et al. 1995), although another study found no difference (Lenth et al. 2006).

Urbanisation results in the gradual decline and extirpation of specialists and the invasion of synanthropes (Sorace and Gustin 2010). However, not a single species can conclusively be considered to have been extirpated by the exurbanisation of the forests in our study areas. Three species were recorded exclusively in wildlands, the scrubtit *Acanthornis magna*, swift parrot *Lathamus discolor* and the blue-winged parrot *Neophema chrysostoma*, but each of these were individually recorded in less than three surveys in total, making generalisations on their distribution difficult. Indeed, the blue-winged parrot was seen breeding in South Arm but not within a sampling area. In addition, South Arm is known to have critical habitat for the migratory swift parrot (Munks et al. 2004).

In contrast, a number of species, for which there were sufficient data to make generalisations (recorded in ≥10 surveys), were recorded only in exurban sites. Most of these were classic edge species or exotics, but native species restricted to exurbia included an endemic corvid and two grassland birds. Grassland species are typically less adaptable to urban environments than forest species (Croci et al. 2008). In a previous study, the urban sensitivity of grassland species was expressed in dramatically contrasting bird species communities across a grassland-urban interface (Sodhi 1992). Exurbanisation has been shown to vary in its impact on grassland birds from relatively little (Bock et al. 2008) to a decline in the number of ground and shrub nesters (Maestas et al. 2003). Within our study area, the

Australasian pipit *Anthus novaeseelandiae* and the Eurasian skylark *Alauda arvensis* are two ground-nesting grassland species that can be observed in non-urban paddocks in the vicinity of exurban properties, but were not recorded in any of our exurban plots. Grassland species can be particularly vulnerable to reductions in habitat area (Vickery et al. 1994) or isolation within a forest matrix (Soderstrom and Part 2000); however, the exurban paddock estate we studied is extensive and interconnected (Fig. 17.3). Thus, these species may avoid exurban properties due to nest disturbance or predation. Two of the paddock specialists in our study area, the Tasmanian native hen and the masked lapwing, are also ground nesters. However, both of these species are known to rear multiple broods per annum, and high fecundity can enable bird species to persist despite urban stressors (Reale and Blair 2005).

17.4.2   The Effects of Exurbanisation on Noisy Miners and Small Bird Diversity

In contrast to forest clearances created for picnic areas (Piper and Catterall 2006), small patches of forest clearance (perforations) for exurban housing do not appear to create additional habitat for noisy miners. Perforation size and the complexity of the vegetation that remains, or, as in the case of gardens, is added, probably plays a substantial role in determining the likelihood of noisy miner invasion. Where miners did occur in our study area, which was on old clearance boundaries, their presence was associated with bird communities distinct from wildland communities. The distinctiveness related to low frequencies of occurrence of numerous species previously observed to be infrequent in miner-occupied suburbs (Sewell and Catterall 1998; Parsons et al. 2003) and rural forests and woodlands (MacDonald and Kirkpatrick 2003). In contrast to a previously studied suburban region comprised of parks and gardens (Parsons et al. 2003), miners did not homogenise exurban bird communities irrespective of habitat. This suggests that their level of interspecific aggression is proportional to local habitat quality, which is supported by observations of disproportionately high numbers of attacks on species that compete with them for food resources (Maron 2009).

17.4.3   Does Within-Habitat Similarity of Bird Assemblages Reflect the Degree of Disturbance?

Levels of similarity between sites within habitats did not follow the pattern we predicted in our hypotheses, which was based on the pattern of similarity found within habitats in suburban Melbourne that were structurally similar to our sample

of exurban habitats (White et al. 2005). In particular, paddocks homogenised exurban avifauna less than expected. The division of cleared land into many exurban parcels appears to have resulted in a greater diversity of habitat conditions than would have resulted from commercial agricultural use or maintained suburban lawns. The primary paddock condition that varies, both temporally and spatially, appears to be grass height, which can have significant impacts on bird species (Whittingham et al. 2006). The similarity of bird assemblages in gardens, modified forest and unmodified exurban forest in Kingborough had the sequence predicted in our hypotheses, but did not in South Arm. The results for South Arm are probably a result of noisy miners on species composition. Because noisy miners were not uniformly present in gardens and modified forest, but homogenised species composition where they were present, this would have decreased average similarity between sites. However, as noisy miners were absent from unmodified forest, they did not affect intersite variability in this habitat. Similarly, the relatively lower (compared to Kingborough) levels of intersite similarity for the three disturbed habitats in South Arm (gardens, paddocks and modified forest) is also likely to have been an effect of the noisy miner and its sporadic occurrence in South Arm compared to its absence in Kingborough.

17.4.4 Implications of Exurbanisation

The exurban regions of Hobart have rich assemblages of birds, including forest species observed to be disadvantaged by urbanisation in Australian cities and their suburbs. As a result, exurban avifaunal richness is considerably higher than the avifaunal richness found at higher concentrations of development in Hobart (Daniels and Kirkpatrick 2006). We have shown that the modification of forest understorey shifts the species composition of exurban avifauna away from the composition of wildland avifauna (Fig. 17.2). There is likely to be a critical proportion of unmodified native forest retention that is necessary to maintain the original avifauna in both suburban and exurban landscapes, as there is in rural landscapes, where it appears to be approximately 30 % (Andren 1994; Ford et al. 2001). There may also be critical sizes for retention of native forest, suggested to be 42 ha in western USA (Donnelly and Marzluff 2004) and found to be 30 ha in rural Tasmania (MacDonald and Kirkpatrick 2003).

While habitats with a native tree canopy intact had the highest number of native habitat specialists, gardens provided habitat for some species that suffered from forest modification and were optimum habitat for many others. Similarly, much heterogeneity was evident amongst paddock bird communities. Thus, a large area of unmodified native forest might support greater densities of urban-sensitive species but also lower community diversity than an equivalent area of exurbia.

17.4.5   Conservation Conclusions for Cities, Suburbs and Exurbs

Given the above, planning and land-use regulations that ensure both heterogeneity of habitat and the retention of most of the area of native plant communities are likely to result in exurban conditions that maintain populations of wildland forest birds while creating diverse habitat for other bird species. However, exurban development that destroys forest and other native plant communities may have strong deleterious effects on avifauna. In addition, any form of exurbanisation may result in greater losses of other elements of biodiversity in the wider landscape than more concentrated urbanisation, given the greater land requirements per capita.

Within urban areas, there needs to be a greater focus on ensuring that the rare and threatened bird species that can take advantage of the fertile, well-watered and biodiverse urban conditions do not suffer mortality from easily preventable causes and that their urban habitats are maintained. Examples of management prescriptions that need to flow from recovery plans include requirements for windows that prevent swift parrot collisions and the withdrawal from sale of rat poisons that cause owls and other predatory birds to die of secondary poisoning.

The maintenance of urban habitat for both rare and threatened birds and a wide diversity of other birds can be less straightforward, given that different sets of bird species in Australian suburbia have been shown to occupy different types of garden habitat. It seems that, if Australian suburbanites are left to themselves, they will produce an intimate mix of wildly different habitats for birds at the yard scale (Kirkpatrick et al. 2009). However, birds that require large old trees as part of their habitat can be faced with a dearth (Pearce et al. 2013) as the 8-year average duration of home occupance, the different tastes in trees of different occupants (Kirkpatrick et al. 2012, 2013) and a risk-averse society (Davison and Kirkpatrick 2014) make it unlikely that any Australian private urban tree will survive to old age. This prospect on private land makes it important that governments maintain old trees on public land. Public land is important generally for maintaining a wide range of bird species that require vegetation that approximates the natural.

17.5   General Conclusions

Urban and exurban areas in Australia are better regarded as distinct and diverse habitats for a wide range of birds than an avifaunal void or a harbour for exotics. Individual patch characteristics have a stronger influence on species composition than landscape effects. There are many opportunities for using planning regulations and public land management to improve the prospects for species or groups of species that are in decline over their full range.

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Chapter 18
Ecological and Social Factors Determining the Diversity of Birds in Residential Yards and Gardens

Mark A. Goddard, Karen Ikin, and Susannah B. Lerman

> *I value my garden more for being full of blackbirds than of cherries, and very frankly give them fruit for their songs.*
> (Joseph Addison, English essayist, poet, and politician, 1672–1719)

Abstract Residential landscapes with private yards and gardens are a major land cover in many cities, represent a considerable opportunity for bird conservation and enhance human experiences with wildlife. The number of studies of birds in residential landscapes is increasing worldwide, but a global-scale perspective on this research is lacking. Here we review the research conducted on birds in residential settings to explore how birds respond to this novel habitat and how private gardens can be designed and managed to enhance their value for bird populations and for human well-being. We examine the key ecological and social drivers that influence birds and draw particular attention to the importance of scale, the role of bird feeding, the predation risk from cats and the relationship between native vegetation and bird diversity. The success of bird conservation initiatives in residential landscapes hinges on collaboration between a range of stakeholders, and we conclude the chapter by making recommendations for urban planners and evaluating policy tools for incentivising householders and communities to conserve birds in their neighbourhoods.

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18.1 The Garden Resource

Although we may not all articulate it as eloquently as Addison, people have long sought to cater for birds in their gardens. Indeed, of all the places that we encounter birds in cities, it is in our private gardens and yards (hereafter gardens) that these interactions are often most meaningful. It is here that many of us spend vast amounts of time and money to interact with birds by providing vegetation, food, water or nest sites. Ultimately, whether birds or people (or both) benefit from these activities remains an active area of research, but when this resource provision is scaled up across neighbourhoods, it becomes clear that the collective impact of private gardens in our towns and cities is substantial (Goddard et al. 2010; Lerman and Warren 2011; Belaire et al. 2014). This is especially true in many developed countries where private gardens are often a major urban land cover. For instance, an estimated 87 % of UK householders have domestic gardens (Davies et al. 2009). Collectively, these gardens cover approximately 25 % of the land area of UK cities, which equates to 35–47 % of the total urban green space (Loram et al. 2007). Elsewhere, gardens are even more plentiful; in Dunedin, New Zealand, the vegetated garden area comprises over one third of the total urban area (Mathieu et al. 2007). Although they may differ in their management and form, gardens can also be important components of cities in the global south, e.g. residential gardens in Chile (Reyes-Paecke and Meza 2012), urban home gardens in Brazil (Akinnifesi et al. 2010) and urban 'patios' in Nicaragua (Gonzalez-Garcia and Sal 2008), and their importance is likely to increase further as global urbanisation continues at a rapid pace (Fragkias et al. 2013).

In addition to the extent of gardens across our cities, the management of these residential habitats plays a significant role in their contribution to bird conservation. Over three quarters of US householders participate in some form of gardening (Clayton 2007) and, in 2013, spent an estimated $34.9 billion on gardening supplies and activities (National Gardening Survey 2014). Moreover, 13.4 million Americans maintain vegetation or natural areas specifically for wildlife (US Government 2011). Birds are often the main target of such wildlife-friendly management, as evidenced by the popularity of bird feeding and nest box provision compared to other wildlife gardening activities (Davies et al. 2009; Goddard et al. 2013).

The upshot of the large number of gardens across cities and their potential bird-friendly management is that private gardens can have considerable 'direct' and 'indirect' value for bird conservation (Cannon 1999). On the one hand, residential landscapes within cities provide a direct habitat resource for birds. Early investigations in the USA revealed that residential areas were comparable in bird diversity to the natural habitats on which they were developed (Guthrie 1974; Emlen 1974). Residential developments in the UK have also been shown to have greater value than farmland for thrushes (*Turdus* spp.) as agricultural intensification depletes the

quality of rural habitats (Mason 2000). Urban-rural gradient studies tend to show that dense urban centres have a homogenising effect on bird communities (Clergeau et al. 2006), but intermediate levels of urban development, characterised by residential gardens, are often associated with peaks in bird richness or abundance, where so-called urban adapter species thrive and mix with a few 'urban avoiders' and 'urban exploiters' (Blair 1996; Sewell and Catterall 1998; Blair 2004; Tratalos et al. 2007). Although residential landscapes may not support many habitat specialists, they can be important for species of conservation concern, such as house sparrows (*Passer domesticus*) and starlings (*Sturnus vulgaris*) that are declining in the UK (Fuller et al. 2009). Moreover, gardens certainly contribute to the conservation of common birds which appear to be declining more rapidly than rarer species in Europe (Inger et al. 2015).

In parallel with their direct significance for birds, gardens also have indirect conservation value by increasing people's engagement with birds and fostering a commitment to nature conservation more widely (Cannon 1999). When householders participate in citizen science bird monitoring programmes, it often leads to important data for fundamental scientific research, such as how climate change affects bird communities (Princé and Zuckerberg 2015). Participation also empowers the householder by providing tangible benefits for people, such as improved sense of place (Evans et al. 2005). Evidence is also growing that interacting with wildlife is beneficial to human health. For instance, when controlling for variation in demographic characteristics, the species richness and abundance of birds in southeastern Australian neighbourhoods was positively related to human well-being (Luck et al. 2011).

In the rest of this chapter, we develop the conceptual framework of Goddard et al. (2010) by viewing gardens as socioecological constructs that can influence birds at multiple spatial scales (Fig. 18.1). Our geographic scope is global, but we necessarily focus on the UK, the USA and Australasia as there is a research bias towards these countries. In Sect. 18.2, we discuss the ecological drivers of bird diversity at garden to landscape scales. We then explore the human dimension in Sect. 18.3, highlighting garden management decisions that impact birds (i.e. landscaping, bird feeding and cat ownership) and their underlying socioeconomic drivers. In Sect. 18.4, we turn our attention to urban policy, planning and tools for incentivising and engaging householders and other stakeholders in bird conservation initiatives. We conclude in Sect. 18.5 by highlighting key knowledge gaps and research priorities. Addressing how private gardens can be better designed and managed to strengthen their potential for bird conservation and human well-being will greatly benefit urban planning and policy.

18.2 Ecological Drivers of Bird Diversity

Ecological drivers of garden bird diversity range from the scale of an individual feature (e.g. a tree or a shrub) through to that of an entire city (Goddard et al. 2010). These scales match different events in the life histories of birds, from the
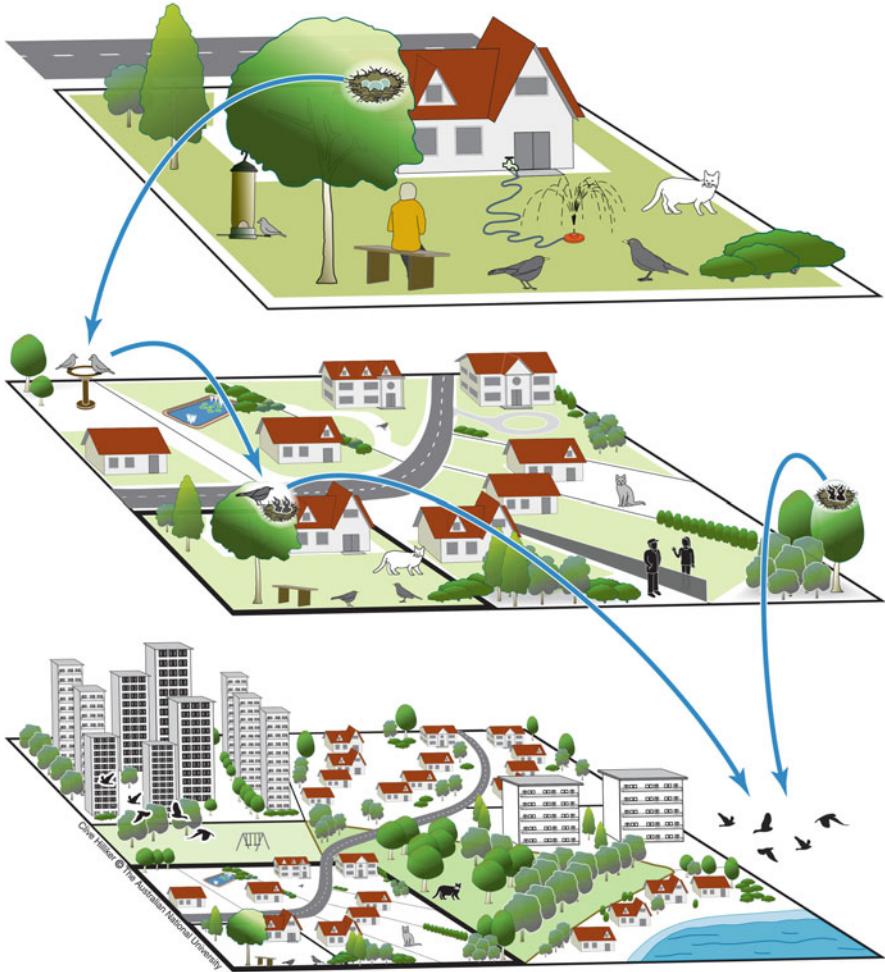
Fig. 18.1 Ecological and social drivers of garden birds at nested spatial scales. At the household scale (*top panel*), individual habitat features (e.g. trees and shrubs) and householder decisions (e.g. to provide supplementary food, to irrigate the garden and have an outdoor cat) affect the ability of birds to find suitable forage and nest sites. At the neighbourhood scale (*middle panel*), the extent, composition and configuration of habitat in groups of adjacent gardens are dictated by variation in socio-economic status and social norms in gardening practices. At the city scale (*lower panel*), the clustering of residential habitat with other urban green spaces reflects urban planning and green infrastructure strategies. *Blue arrows* represent the different life stages of garden birds at different scales in the garden hierarchy, from eggs in an individual nest at the garden scale (*top panel*) to nestlings in multiple gardens (*middle panel*) and fledglings dispersing within and beyond the city (*lower panel*)

consumption of a berry, to the placement of a nest for the season and the interactions of birds within a population or with birds of other species (Fig. 18.1). It is important to note that whilst all birds require habitat to forage, nest, shelter and interact, what constitutes good habitat can vary substantially between bird species,

as does the scale in which an individual species uses that habitat (Hostetler and Holling 2000). For example, cactus wrens (*Campylorhynchus brunneicapillus*) use habitat features at the scale of the individual property, whilst Lesser Goldfinches (*Spinus psaltria*) respond to habitat features at the neighbourhood scale, and Gila woodpeckers (*Melanerpes uropygialis*) are influenced by features from a combination of scales (McCaffrey and Mannan 2012). The ecological drivers of garden bird diversity, furthermore, vary with changing climatic and geographical context. Cultivated gardens with a year-round supply of leafy plants will be perceived by birds in tropical regions much differently to their desert cousins. In this section, we address each scale of ecological drivers in turn and discuss their relevance for different birds and for different geographic contexts.

18.2.1 Garden-Scale Ecological Drivers

Gardens are landscaped with individual vegetation and structural features, such as trees, shrubs, grasses, rocks and water features. These garden-scale features directly link to the availability of habitat resources for birds and are important for shaping urban bird communities (Daniels and Kirkpatrick 2006; Evans et al. 2009; van Heezik et al. 2008; Chamberlain et al. 2004; Parsons et al. 2006). Gardens, however, exhibit individual variability, whereby different styles of gardens emphasise different habitat features with ensuing effects to the bird community. For example, van Heezik et al. (2008) found that gardens in New Zealand with at least 30 % open-vegetated space supported more specialist native bird species, including species that were virtually absent in gardens with minimal vegetation.

Cultivated gardens can be 'oases' of otherwise scarce resources, for example, as sources of water in dry climates (Bock et al. 2008). However, polarisation between intensively managed exotic vegetation and more 'natural' plant communities, especially in urban areas with relatively short histories, can result in decreasing habitat resources for the native bird community (but see Gleditsch 2016). For example, studies from Phoenix, USA, have shown that gardens landscaped with native desert plants contain more abundant foraging resources and have lower foraging costs, as well as a bird community less dominated by aggressive urban birds and more desert bird species, than gardens landscaped with exotic plants (Lerman et al. 2012b; Lerman and Warren 2011). Similarly, in Hobart, Australia, gardens with native plants had significantly more native birds (Daniels and Kirkpatrick 2006). When comparing gardens landscaped with native plants with gardens landscaped with exotic vegetation, Burghardt et al. (2009) found that the native gardens supported a greater abundance and richness of caterpillars and, subsequently, birds, since many species rely on this food source for feeding nestlings. Native gardens were especially important for bird species of conservation concern, supporting eight times the abundance of these species compared with exotic gardens. Interestingly, there is much less evidence for a positive association between native plants and birds in the UK or Europe, where urbanisation has a longer history.

Many birds, including those sensitive to urban landscapes, benefit from vegetation structural complexity, which can be achieved by planting out garden beds with dense shrubs, allowing leaf litter to accumulate under trees, choosing tussock or meadow grasses over lawn or leaving areas of lawn unmown. For instance, in Canberra, Australia, urban-sensitive native species were more likely to be recorded in front gardens characterised by trees, shrubs and ground covers compared with front gardens dominated by lawns (Ikin et al. 2013b). The capacity of gardens to contain these diverse habitat features is positively related to garden size. Smith et al. (2005), for example, found that larger gardens in the UK were more likely to have large trees and a higher diversity and occurrence of vegetation than smaller gardens. Kaoma and Shackleton (2014) likewise found that larger gardens in South Africa had a higher density of trees. It is concerning, therefore, that the current trend in housing development is for smaller gardens that require low maintenance and lack diverse habitat resources (van Heezik et al. 2008; Gaston et al. 2005; van Heezik and Adams 2014).

It is worth noting that the design and management of gardens can result in perverse outcomes for the bird community by leading to the overabundance of some bird species that might have negative consequences for other species. For example, in Australia, nectar-rich cultivars of native flowering shrubs are promoted as being "bird friendly" by nurseries, and people plant them to entice birds to their gardens. However, studies have shown that these flowering shrubs attract aggressive Australian honeyeaters that exclude smaller birds, many of which are declining in urban landscapes (Parsons et al. 2006; French et al. 2005). Further, Davis et al. (2014) showed that these shrubs also provided a year-round source of nectar within suburban areas compared with native forests, supporting high densities of large nectar-feeding parrots whose dominance then enables them to outcompete other species for nesting resources (Davis et al. 2013).

Compared with research focused on other urban green spaces, there have been relatively few studies of bird habitat use in gardens. These studies have had contrasting findings about the relative importance of local garden-scale variables compared with those measured in the surrounding landscape. For example, Lerman and Warren (2011) found that front garden habitat, particularly the presence of desert trees and shrubs, was twice as important as regional landscape features for explaining variation in the urban bird community of Phoenix, USA. In comparison, French et al. (2005) found that the abundance of nectivorous species in gardens within Sydney, Australia, was better predicted by the vegetation characteristics of adjoining and more distant gardens than the vegetation characteristics of a single garden. In the next section, we explore the influence of neighbourhood and city-scale ecological drivers on garden birds.

18.2.2   Neighbourhood and City-Scale Ecological Drivers

Birds are highly mobile and most species use the landscape at multiple scales, including scales larger than an individual garden (Hostetler and Holling 2000; Hostetler and Knowles-Yanez 2003, Litteral and Shochat 2016; but see Daniels and Kirkpatrick 2016). This leads to scale mismatch, whereby the capacity of gardens to provide habitat for birds is constrained or enhanced by the suitability of habitat in the surrounding landscape (Goddard et al. 2010; Warren et al. 2008; Catterall 2004). For example, Gambel's quail (*Callipepla gambelii*) needs areas of desert vegetation larger than the average garden, but when a garden adjoins parkland or a group of gardens are planted with desert vegetation, the cumulative effect could provide sufficient habitat (Hostetler and Knowles-Yanez 2003). Recent research has demonstrated that whilst local-scale factors may well be most important, acknowledging the contribution of landscape-scale attributes can improve our understanding of birds in urban environments (Melles et al. 2003; MacGregor-Fors and Ortega-Álvarez 2011; Suarez-Rubio and Thomlinson 2009; Donnelly and Marzluff 2004).

The collective attributes of neighbouring gardens represent important drivers of garden bird diversity. Belaire et al. (2014), for example, investigating birds within groups of gardens in the Chicago region, USA, found that the richness of native birds was strongly related to the aggregated wildlife value of the gardens (e.g. the presence of trees, plants with fruits or berries and mix of evergreen and deciduous trees). In contrast, the vegetated area and canopy cover within the neighbourhood and amount of green space within the wider landscape provided a weaker explanation of native bird richness within gardens. Chamberlain et al. (2004), in comparison, found that the occurrence of garden birds across the UK was strongly influenced by neighbourhood attributes, such as the presence of brownfield and green space areas.

Neighbourhood attributes influence local-scale garden characteristics and landscape-scale habitat suitability (Catterall 2004). For example, gardens in the inner city (i.e. located in areas of high housing density) support different bird assemblages to gardens in exurban developments (Kluza et al. 2000; Germaine et al. 1998). Several studies have found higher bird diversity when residential streets were planted with native trees (Ikin et al. 2013b; White et al. 2005; Young et al. 2007). For example, native forest bird species richness within residential landscapes of Seattle, USA, was positively related to tree density in the landscape (Donnelly and Marzluff 2006). These positive relationships suggest that tree cover could be used as a surrogate measure of available bird habitat. However, caution is needed when using tree cover as a proxy of habitat for all species. Urban-sensitive birds in Canberra, Australia, for example, had no relationship with tree cover but instead were related to habitat structural complexity, i.e. diversity of strata, including shrubs and ground layer (Ikin et al. 2013b). How cities are planned and developed can also strongly influence the habitat values of gardens for birds (see Sect. 18.4.2).

18.3 Social Drivers of Garden Bird Richness and Abundance

18.3.1 Socio-economic Status

In recent decades, urban ecology has emerged as an important discipline that integrates natural and social sciences in order to understand what drives ecological functioning in and around towns and cities (Tanner et al. 2014; Grimm et al. 2008). Perhaps more so than any other urban habitat, private gardens can be seen as 'hybrid' creations (Power 2005) or 'socioecological constructs' (Goddard et al. 2010) such that understanding residential landscapes demands an interdisciplinary approach (Cook et al. 2011). A central tenet of urban ecology is the association between human social stratification and urban biodiversity (Warren et al. 2010), and studies of urban vegetation have consistently found that wealthier neighbourhoods support greater levels of vegetation cover or higher plant diversity (e.g. Hope et al. 2003; Martin et al. 2004; Lubbe et al. 2010; but see: Meléndez-Ackerman et al. 2014). There are a number of putative mechanisms for this so-called luxury effect, but given the cost of planting trees and shrubs, economics can certainly hinder people's choices for adding to or replacing existing vegetation to their property. Financial constraints can be particularly prohibitive for renters who are at the mercy of their landlord's landscaping decisions (Lerman and Warren 2011). On the other hand, the luxury effect suggests an avenue of outreach to work with higher income areas to landscape more sustainably and with wildlife in mind, given they have the financial capacity to do so. Interestingly, Kirkpatrick et al. (2012) show that household income can also predict attitudes towards vegetation, with wealthier people more likely to value trees (see also Sect. 18.3.2.1).

The human-dictated plant community can be seen to form a 'template', and it has been suggested that birds and other higher taxa are indirectly influenced by social factors via this plant template (Faeth et al. 2011; Luck et al. 2012). As predicted, a positive correlation between bird diversity and neighbourhood income (or related measure of socio-economic status) has been demonstrated in North America (Lerman and Warren 2011; Kinzig et al. 2005; Melles 2005), Australia (Luck et al. 2012) and Europe (Strohbach et al. 2009). These findings have led to concerns about environmental injustice, with lower-income neighbourhoods exposed to lower native bird diversity (Lerman and Warren 2011). However, in the gardens of Dunedin, New Zealand, van Heezik et al. (2013) found only a weak positive association between house value and bird richness, whilst in Chicago, USA, Loss et al. (2009) document an inverse relationship between neighbourhood income and native bird richness. These counter examples suggest that more work is needed before we can generalise findings to cities in different regions and with different development histories (Warren et al. 2010). Other measures of socio-economic status, such as education level or occupation, as well as demographic factors, such as householder age, can also predict the provision of bird-friendly garden habitat

(e.g. Goddard et al. 2013; Lepczyk et al. 2004b). These patterns can be complicated by the legacies of past management due to the maturation of vegetation over time (Luck et al. 2009). For instance, Boone et al. (2010) found that tree coverage in Baltimore, USA, in 1999 was better explained by the 1960 demographics than by 2000 demographics.

There are a number of other confounding spatio-temporal factors that obscure the association between socio-economic status and bird diversity. For example, neighbourhood house prices are positively associated with proximity to urban green spaces and natural habitats (e.g. Morancho 2003; Bolitzer and Netusil 2000; Gibbons et al. 2014); avian diversity also tends to increase with greater green space provision in the wider landscape (Sect. 18.2.2). A number of studies have found that bird species richness increase with neighbourhood age, a pattern that is typically explained by the maturation of vegetation (Munyenyembe et al. 1989; Palomino and Carrascal 2006). In contrast, Mason (2006) found no relationship between avian richness or abundance and housing development age in a small English town, whilst Loss et al. (2009) document higher species richness in newer developments in Chicago because they tend to support *more* natural habitat than older suburbs. These findings underline the fact that the provision of vegetation in residential landscapes is key to supporting avian diversity, even though the factors predicting the extent of vegetation may vary with urban context. Individual bird species may also respond differently to variation in habitat structure that correlates with socio-economic status. For example, Shaw et al. (2008) show that house sparrow (*Passer domesticus*) decline in UK cities has been more prevalent in affluent neighbourhoods that offer reduced nesting and feeding opportunities.

18.3.2 *Individual Behaviour, Attitudes and Beliefs*

Householders undertake a variety of actions to encourage birds in their gardens, including providing food and water, installing bird boxes and planting or maintaining vegetation (Lepczyk et al. 2004b; Davies et al. 2009). A primary motivation for these gardening choices may be to observe or protect nature (Clayton 2007; Goddard et al. 2013). However, for many households, their decisions are driven by other underlying factors, including social norms and financial constraints, which might pose as barriers for widespread participation in wildlife gardening (Goddard et al. 2013). This section highlights how individual behaviour, attitudes and beliefs interact with gardening decisions, the extent of these choices and the consequences of these decisions on people and garden birds. We focus initially on planting vegetation and bird feeding since the majority of research addresses these two wildlife garden activities, but we also highlight the considerable threat provided by domestic cats in residential landscapes.

18.3.2.1   Vegetation and Landscaping

Gardening decisions are underpinned by a series of value judgements that influence the habitat quality of gardens for birds. Gardens are often viewed as an extension of the home, blurring the line between 'wild' and 'domestic' (Clayton 2007). Therefore, householders have the urge to tidy-up the garden space, which might be at odds with supporting wildlife (Lerman et al. 2012a). An 'ecology of prestige' explains this phenomena whereby a householder places importance on maintaining gardens to a standard that adheres to neighbourhood expectations, as well as reflecting aspirational social goals (Larsen and Harlan 2006; Grove et al. 2006; Kurz and Baudains 2012). Implications for this include that the homeowner landscapes with their neighbours in mind rather than for wildlife, even though they may have pro-environmental intentions (Nassauer et al. 2009; Goddard et al. 2013). Householders can also be constrained by the legacy of previous owners; most homeowners inherit a garden and thus what exists does not necessarily reflect their taste or choices for landscaping (Larsen and Harlan 2006; van Heezik et al. 2013). This can detract from the garden as "an expression of me" (Freeman et al. 2012) and the intrinsic value of gardens in providing a connection with the natural world.

The influence of social norms on gardening decisions highlights the need to encourage wildlife gardening at the neighbourhood scale (Goddard et al. 2010; Cooper et al. 2007; Warren et al. 2008). Neighbourhood associations, incentive programmes and greater communication by conservationists can help achieve these goals (Belaire et al. 2014). For example, one key message is that specific plant choices (e.g. native vs. non-native) have cascading impacts for native biodiversity (Daniels and Kirkpatrick 2006; Burghardt et al. 2009; Lerman and Warren 2011). Expressing this message as positive and regionally relevant, i.e. that native birds are what makes the particular city unique (Aronson et al. 2014), can help improve communication effectiveness and thus uptake (van Heezik et al. 2012). Individual homeowners may also find that they share common values. In an extensive survey of households in New Zealand, Freeman et al. (2012) found that over 80 % of respondents saw value in planting native plants for birds. Neighbour mimicry is another way that gardening practices spread. This can be advantageous when a "keystone neighbour" champions landscapes with wildlife in mind (Goddard et al. 2013; Warren et al. 2008; Hunter and Brown 2012).

18.3.2.2   Bird Feeding

Feeding garden birds has become the most widespread and popular wildlife gardening activity in the Western world (Gaston et al. 2007; Jones and Reynolds 2008) and can influence bird populations at multiple spatial scales (Fuller et al. 2012; Fuller et al. 2008; Galbraith et al. 2015). In the UK, nearly 50 % of householders feed garden birds (Davies et al. 2009), spending £200 million per year (British Trust

for Ornithology 2006). This equates to approximately one bird feeder for every nine birds in the UK (Davies et al. 2009). A similar percentage of householders feed birds in the USA (approximately 50 million people; USA Government 2011), Australia (Rollinson et al. 2003; Jones and Reynolds 2008) and New Zealand (Galbraith et al. 2014).

The social drivers of garden bird feeding have received recent interest. Fuller et al. (2008) show that feeding was more prevalent in wealthier neighbourhoods of Sheffield, UK. In contrast, other studies have found neighbourhood income to be unrelated to bird feeding (Davies et al. 2009, Goddard et al. 2013) or unrelated to the total prevalence of bird feeding but related to the type of food provided (Lepczyk et al. 2012). People who feed birds are more likely older and less mobile, living in single-dwelling houses and have a greater interest in nature (Fuller et al. 2008; Lepczyk et al. 2012; Galbraith et al. 2014; Goddard et al. 2013). People feed birds for a wide variety of reasons, ranging from the personal (e.g. increased happiness: Jones and Reynolds 2008; Galbraith et al. 2014), to the moral (e.g. to "give something back" or to "help the birds": Jones and Reynolds 2008; Goddard et al. 2013; Galbraith et al. 2014) and the environmental (e.g. to increase over-winter survival or to provide habitat resources for threatened species: Jones and Reynolds 2008; Mason 2000). In Australia, where bird feeding is discouraged (Jones and Reynolds 2008), people's decision *not* to feed may also be environmentally motivated, i.e. through the belief they are helping garden birds by not feeding (Rollinson et al. 2003).

In addition to the number and types of people feeding birds, the kinds of food provided also strongly influences garden bird populations. Typical items include sugar water, commercial seed and meat (Lepczyk et al. 2012; Rollinson et al. 2003); bread is also provided, particularly in lower-income neighbourhoods (Lepczyk et al. 2012). Galbraith et al. (2014) estimated that householders in New Zealand were putting out a staggering 5.1 million loaves per year, causing a shift in the bird community towards species tolerant of this food source.

The implications of feeding on garden birds are varied, and both benefits and risks to bird populations have been identified (Jones and Reynolds 2008; Fuller et al. 2008; Galbraith et al. 2014). However, the majority of supplemental food studies are not conducted at home feeders and thus might not mimic garden conditions nor do they control for human factors (Robb et al. 2008). Nonetheless, these data provide an insight as to the ecological consequences of bird feeding. Positive effects on the bird community include higher garden bird richness and abundance (Fuller et al. 2008), increased survival over winter or when food is scarce (Jones and Reynolds 2008) and increased breeding success (Schoech and Bowman 2001). For example, Orros and Fellowes (2015) found that supplementary feeding by over four thousand households in Reading, UK, provided food for up to 320 red kites (*Milvus milvus*), explaining their high abundance in the urban area. However, the benefits of feeding birds are more often articulated in terms of their benefits to humans, through increased well-being (Fuller et al. 2008; Goddard et al. 2013), opportunities to interact with nature (Lepczyk et al. 2012) and ecosystem services (Orros and Fellowes 2012).

Despite these positive aspects of bird feeding, this practice can also have negative implications for garden birds. Putting out food too frequently, or too unreliably, can cause dependence on supplementary feeding, and using food with low nutritional value might decrease individual fitness (Rollinson et al. 2003). High-fat and high-protein supplemental foods might lead to earlier laying dates, which might be detrimental when insect foods required for nestlings are not in synchrony (Schoech and Bowman 2001). Garden bird feeding also increases competition from other species attracted to gardens/feeders, causing novel interspecific associations. For instance, Bonnington et al. (2014) found that bird visitation to feeders in Sheffield, and the amount of food removed by birds, declined by more than 90 % due to competition with squirrels. Other risks associated with the increased aggregations of birds around feeding stations include predation (although this may be counteracted by increased vigilance and the dilution effect; Dunn and Tessaglia 1994) and disease transmission (Robb et al. 2008). Providing supplementary food might also alter garden bird communities. For example, in Australia and New Zealand, garden bird feeding has favoured exotic species, especially when seeds are the primary supplemented food item (Galbraith et al. 2014; Daniels and Kirkpatrick 2006; Galbraith et al. 2015). Fuller et al. (2008) found that feeders in UK gardens do not entice new bird species to urban areas but are associated with an increase in the abundance of species that use feeders frequently. If the negative implications of garden bird feeding outweigh positive aspects, householders might be creating an ecological trap (Schlaepfer et al. 2002). For example, this may occur when supplementary food creates a false cue that gardens are high-quality habitat, but there are insufficient resources for breeding or increased stresses, leading to nest failure (Balogh et al. 2011).

Many organisations provide guidelines on when and whether to feed birds (Cannon 1998). In the UK, the British Trust for Ornithology encourages bird feeding and promotes the practice as a conservation action, e.g. through supporting populations of song thrushes (*Turdus philomelos*) (Mason 2000). In the USA, householders in the northeast are encouraged to remove bird feeders between April and November to reduce conflicts with American black bears (*Ursus americanus*) and to encourage birds to take advantage of the abundant natural food sources, e.g. insects for nestlings and berries (MassWildlife 2014). However, there appears to be a mismatch between public and private spaces, with feeding discouraged in National Parks yet a proliferation of bird feeding supply stores, which leads to mixed messages to the pubic (Lepczyk et al. 2012). In Australia, on the other hand, bird feeding is discouraged in both public and private places, yet it is still a very popular activity so the message does not seem to be working (Jones and Reynolds 2008).

18.3.2.3 Cats

Cats represent the most severe anthropogenic threat to bird populations in residential landscapes. In the USA, domestic outdoor cats, both owned pets and unowned,

kill roughly 1.5–3.7 billion birds per year (Loss et al. 2013). In southeastern Michigan, an estimated one bird is killed per km each day, including species of conservation concern (Lepczyk et al. 2004a). In a study documenting nest success and post-fledgling survival in Washington, DC, almost half of gray catbird (*Dumatella carolinensis*) predation was attributed to domestic cats (Balogh et al. 2011). Cats also induce fear and alter behaviour of suburban birds causing sublethal impacts. For example, the fear instilled by domestic cats can reduce fecundity by one offspring per year which results in up to a 95 % reduction in bird abundances (Beckerman et al. 2007; see also Bonnington et al. 2013). In Chicago neighbourhoods, native birds (predominantly migratory species) were less abundant with the presence of owned outdoor cats (Belaire et al. 2014). Cats are known to roam, and their impact is not restricted to their owner's garden. For example, Thomas et al. (2012) found that cats moved within a daily range of 1.94 ha, van Heezik et al. (2010) found that mean home range size was 3.2 ha, and Eyles and Mulvaney (2014) found that cats may travel up to 900 m into nearby protected habitats. Susceptibility to cat predation can vary with natural history traits. For example, Cooper et al. (2012) found that ground-foraging and cavity-nesting birds, including individuals using nest boxes, were as much as three times more susceptible to cat predation.

The majority of information on cat impact relies on owner surveys documenting the number and type of prey brought home. However, many cat owners are in a state of denial regarding their pet's negative impact on wildlife. This primarily stems from the fact that their pet does not necessarily bring home all their prey items, and, hence, the owner does not perceive a conservation problem (van Heezik et al. 2010). To quantify this mismatch, Loyd et al. (2013) fitted "KittyCam" video cameras on 55 owned, free-roaming cats in Athens, USA. They found that cats returned only 23 % of prey items to their household, 28 % of prey items were consumed and an additional 49 % remained at the capture site (Loyd et al. 2013). Similarly, in Reading, UK, Thomas et al. (2012) found that although cats were killing on average 18.3 birds per year, only 20 % of cats returned four or more dead prey to their households. Thus, many studies relying on surveys grossly underestimate the sheer volume of wildlife falling victim to domestic cats.

The devastating impact caused by owned cats has led to a number of mitigation strategies. One obvious strategy is for pet owners to prevent cats from going outside. The American Bird Conservancy "Cats Indoors" campaign has spearheaded this conservation issue through promoting partnerships between wildlife biologists, veterinarians, humane societies, wildlife rehabilitators and nature centres. The key message being that keeping your cat indoors is better for the cat, better for birds and better for people (abcbirds.org). A modified version of this strategy is to keep cats indoors at night. In a study from Florida, USA, video-monitored northern mockingbird (*Mimus polyglottos*) nests had the majority of cat predation events occurring at night. Thus, recommending cats indoors at night time might lessen the impact during the vulnerable nestling stage (Stracey 2011). However, in Dunedin, New Zealand, cats brought more prey home during the day compared with night time, whereas evening prey items consisted largely of

introduced mice and rats (van Heezik et al. 2010). Another strategy is to prohibit cats within defined buffer zones surrounding important wildlife sites (Thomas et al. 2012). Belled collars have also been shown to be effective in reducing predation, with one study demonstrating a halving in prey items returned home after belled collars were fitted and no evidence that cats adjusted their hunting behaviour to become stealthier (Ruxton et al. 2002). Thomas et al. (2012), however, found that only a quarter of cat owners use collars due to perceived risks to their pets.

18.4 Policy, Planning and Tools for Incentivising and Engaging Householders

18.4.1 Engaging the Householder

Sympathetic management for birds in residential ecosystems can arise through a combination of 'bottom-up' and 'top-down' mechanisms. Given that the management of private gardens lies largely outside direct government control, the diversity of plants and birds in gardens is mainly a result of bottom-up processes, i.e. the collective outcome of individual landscaping decisions (Kinzig et al. 2005). Therefore, initiatives that incentivise householders and local communities to increase the diversity of vegetation in their gardens should be a priority for avian conservation in residential settings. There is a long history of 'wildlife-friendly' gardening in the UK (Ryall and Hatherell 2003; Knight 1954) and the USA (Thomas et al. 1973), and conservation NGOs, government agencies and local agricultural extension programmes have adopted various initiatives for engaging householders in bird-friendly gardening activities. Examples include the Royal Society for the Protection of Birds' (RSPB) 'Homes for Wildlife' scheme in the UK (http://www.rspb.org.uk/hfw/) and the National Audubon Society's 'Audubon at Home' project in the USA (http://www.audubon.org/bird/at_home/). A recent review of the National Wildlife Federation's (NWF) Certified Wildlife Habitat™ programme shows that householders who certify their gardens have greater quality and quantity of habitat than random non-certified gardens, but the effect on birds is unknown (Widows and Drake 2014). The NWF and other organisations are also scaling up their efforts and developing tools for certifying neighbourhoods and communities (e.g. the National Audubon Society's Bird-Friendly Communities programme) to better capture the spatial-scale birds use (Warren et al. 2008). Homeowner and similar neighbourhood associations also have the potential to influence garden designs at a larger scale but from a top-down approach. The institutional framework of these private entities, combined with their prescriptive landscape guidelines, could provide a vehicle for delivering wildlife-friendly gardening features. In fact, neighbourhoods governed by homeowner associations in Phoenix, AZ, supported greater native bird diversity compared with ungoverned neighbourhoods (Lerman et al. 2012a). Hostetler

et al. (2011) also recommend the introduction of policies that provide incentives for housing developers to engage residents through environmental education programmes.

Putting these programmes into practice raises more challenges, but this implementation gap has the potential to be bridged through citizen science. Private gardens are ripe for the public to participate in scientific research, and researchers are increasingly partnering with households for assistance with data collection. Often, citizen science projects have multiple goals that benefit both the citizen and the scientist (Bonney et al. 2009). For example, the Cornell Lab of Ornithology based in New York, USA, and the British Trust for Ornithology have a number of citizen science projects focused on documenting garden birds, breeding success and winter bird populations (see Table 18.1). These programmes have the potential to provide important data for fundamental scientific research. For example, using data from the Cornell Lab of Ornithology's Project FeederWatch, scientists were able to link a warming climate to a shift in garden bird communities (Princé and Zuckerberg 2015). Further, these programmes provide an opportunity for the public to learn about their local birds with the hope of a return investment in conservation initiatives, such as providing wildlife habitat in private gardens, which will ultimately benefit these birds (Cooper et al. 2007; van Heezik et al. 2012).

18.4.2   Garden Birds in Urban Planning and Policy

The value of residential habitats for birds is also influenced by top-down processes such as urban planning. There is an urgent need to understand how best to plan and design cities to minimise their impact on biodiversity, and the extent of residential green space is a key consideration in the urban 'land sparing' vs. 'land sharing' debate (Lin and Fuller 2013; Soga et al. 2014). For instance, under a land-sharing scenario, increasing the size of individual gardens in new developments will increase the likelihood that householders will plant or retain trees and other vegetation (Loram et al. 2008; Smith et al. 2005) with positive knock-on effects on garden-scale bird diversity (van Heezik et al. 2013). However, compact development under a land-sparing scenario, comprising high residential density and small backyards, could support greater bird diversity at the city scale, due to a trade-off between maximising population viability of urban birds and people's interactions with birds in their own gardens (Sushinsky et al. 2013).

In addition to the amount of habitat present in gardens and the surrounding neighbourhood, how that habitat is spatially configured also affects birds (Ikin et al. 2013a; Pellissier et al. 2012; Huste and Boulinier 2011; Huste et al. 2006). Habitat connectivity throughout the city is especially important to allow birds to disperse through the urban matrix (Tremblay and St. Clair 2011; Fernandez-Juricic 2000; Shanahan et al. 2011; Donnelly and Marzluff 2006). Rudd et al. (2002) demonstrated that gardens are essential for providing connectivity; urban green spaces were found to be unviable for a hypothetical indicator species unless

Table 18.1 Selected garden bird citizen science initiatives in the UK, the USA, Australia and New Zealand

Programme name	Geog. scope	Year launched	Design	Institution	Website	Example academic references
Big Garden Birdwatch	UK	1979	One-hour survey within 2-day winter period each year	Royal Society for the Protection of Birds	www.rspb.org.uk/birdwatchbbc	–
Garden BirdWatch	UK	1995	Weekly survey	British Trust for Ornithology	http://www.bto.org/volunteer-surveys/gbw	Cannon et al. (2005), Morrison et al. (2014)
Neighborhood Nestwatch	USA	2000	Mentored programme of individual visits by scientists to private gardens. Nest monitoring during the breeding season and tracking annual survival of colour-ringed backyard birds in six US cities	Smithsonian Migratory Bird Center	http://nationalzoo.si.edu/scbi/migratorybirds/research/neighborhood_nestwatch/newsletter/about_nn.cfm	Ryder et al. (2010)
Great Backyard Bird Count	USA	1998	Minimum 15-minute survey within 4-day winter period each year	Cornell Lab of Ornithology, National Audubon Society	http://gbbc.birdcount.org/	Guralnick and Van Cleve (2005)
Project FeederWatch	USA	1976	Weekly survey over two consecutive days between November and April	Cornell Lab of Ornithology, Bird Studies Canada	http://feederwatch.org	Princé and Zuckerberg (2015)
Birds in Backyards	AUS	2000	Various survey methods (single day, 20-minute survey; 1-week list; 1-year list)	BirdLife Australia	http://www.birdsinbackyards.net/	Parsons et al. (2006)
Garden Bird Survey	Canberra, AUS	1981	Weekly tally over whole year	Canberra Ornithologists Group	http://canberrabirds.org.au/observing-birds/frequently-asked-questions/surveys/	Grarock et al. (2013)
New Zealand Garden Bird Survey	NZ	2007	One-hour survey within 10-day winter period each year	Landcare Research	http://www.landcareresearch.co.nz/science/plants-animals-fungi/animals/birds/garden-bird-surveys	Spurr (2012)

networks of garden habitat were enhanced to allow movement through the urban matrix. It is therefore critical that gardens are planned in relation to the larger network of green infrastructure, drawing on Colding's (2007) theory of 'ecological land-use complementation' that advocates the clustering of private and public green spaces to maximise ecological functioning in urban ecosystems. This approach is exemplified by 'conservation development' (of which Conservation Subdivisions are a type), an alternative form of residential development in which homes are built on smaller lots and clustered together (Reed et al. 2014). To better inform the design of such conservation development, it is imperative to collect data on existing bird-habitat relationships in natural lands designated for urbanisation (Stagoll et al. 2010).

Management of existing gardens can also be 'scaled up' to maximise habitat heterogeneity at the city scale. For instance, Goddard et al. (2010) recommend the creation of 'habitat zones', whereby groups of gardens and adjacent habitats are managed under a common theme depending on landscape context (e.g. woodland, wetland). The creation and maintenance of bird-friendly residential landscaping will also require the engagement of housing developers. For example, in the USA, the Texas Parks and Wildlife Department has worked with developers to certify 'Texas Wildscapes' neighbourhoods, wherein the removal of trees and shrubs is minimised during construction. The Wildscapes neighbourhood was found to have higher bird diversity than a traditionally developed neighbourhood and a local natural area (Aurora et al. 2009). The academic community can also have an important role in encouraging developers, planners and policymakers to conserve urban avian biodiversity using university extension programmes (Hostetler 2012). Through a combination of sympathetic and collective management of existing gardens coupled with pre-emptive and more holistic urban planning, bird diversity could be retained in residential landscapes, despite smaller lot sizes, such that the urban land sharing vs. land sparing debate becomes somewhat of a false dichotomy.

18.5 Future Directions

McDonnell and Hahs (2013) call for renewed strategies in the discipline of urban ecology to better inform urban biodiversity planning and management. In addition to better temporal, spatial and cultural contextualisation, they recommend that urban ecological research (1) moves beyond patterns of distribution to the mechanisms and drivers of urban biodiversity and (2) ensures place-based studies can be generalisable by expanding to more cities, regions and countries. Although their call to action is at the city-wide scale, their points can also apply to the more specific urban environment of gardens.

When research questions incorporate an experimental approach, we can better identify some of the drivers of garden bird diversity. In 2006, Shochat and colleagues (Shochat et al. 2006) called for a more mechanistic approach to studying urban systems, but very few researchers have risen to the challenge of undertaking

such studies in gardens, and this is a barrier to the implementation of effective conservation strategies (but see Lerman et al. 2012b on how birds perceive garden quality comparing foraging decisions). In addition to the mechanistic approach, conducting these studies at multiple scales, from the individual garden through to the design of neighbourhoods and cities (Hostetler 1999), will further assess how garden birds interact with the urban matrix. And finally, designing additional studies that document vital rates such as fecundity and annual survival can further our understanding of source-sink dynamics, genetic flow and dispersal (Balogh et al. 2011).

Urban bird studies are often conducted within one city, and although this has advantages for local policy, it makes generalisations difficult. Establishing multi-city networks can be challenging, but introducing standardised methods not only provides rich opportunities for comparative studies but also has the potential to further frameworks and general principles of garden bird ecology (Table 18.1; Magle et al. 2012). Further, there is a research bias in garden bird ecology towards northern, temperate and developed cities, despite the fact that developing nations, which are often in tropical regions, are experiencing rapid urban growth (Seto et al. 2012).

Research questions and tools that have direct management and policy implications will have a stronger likelihood of implementation when we also address the decision-making process. There is a need for more socioecological interdisciplinary studies that examine the motivations behind, and barriers to, the creation of bird-friendly habitat from household to city scales and the subsequent ecological outcomes of management decisions (Cook et al. 2011). Social science can also inform how best to address environmental injustices with regards to unequal access to species-rich bird communities (Lerman and Warren 2011). Further, providing detailed information about specific habitat requirements also helps bridge the implementation gap. For example, identifying the composition, configuration and coverage of vegetation in gardens and neighbourhoods that is required for supporting native birds moves beyond the many recommendations of 'plant more trees' (Lerman et al. 2014). The scientific information should be transferable to urban planners and practitioners. In return, testing the efficacy of the policies and initiatives will further ensure conservation goals are being met.

In conclusion, understanding the drivers of bird diversity in gardens and residential neighbourhoods is crucial for the conservation of urban biodiversity and for maximising the encounters between people and wildlife that are beneficial to human well-being. The suburban mosaic of gardens supports a diverse avifauna, including species of conservation concern. However, individual gardens and neighbourhoods differ widely in their ability to sustain birds. These differences are driven by a complex and interacting range of ecological and social factors operating across scales. Vegetation structure is the most consistent predictor of garden avifauna, and management by householders and community groups should focus on the provision of habitat complexity by retaining tall and mature trees and planting new woody species and berry- and fruit-producing shrubs. Householders can also increase the abundance and richness of birds within their gardens through

the provision of supplementary food and the containment of cats. In addition, the spatial arrangement of gardens and other green spaces is an important predictor of garden birds, suggesting that gardens should be given a higher priority in urban green infrastructure plans. However, the provision and management of habitat in cities is inextricably associated with human social processes, and understanding the underlying socio-economic drivers of garden landscaping decisions is critical for making management recommendations.

Encounters between birds and people in gardens are beneficial to quality of life in an increasingly urban world. Community initiatives exist for incentivising sympathetic landscaping across gardens, and these can be promoted through engagement in citizen science. The scientific community has an important role in guiding city-scale development of green infrastructure to improve habitat connectivity for garden birds. Key areas for future research include experimental studies to understand drivers and mechanisms of garden bird diversity, comparative studies to test generalisations across regions and climates and interdisciplinary studies to better understand the link between the human and avian inhabitants of residential ecosystems.

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Chapter 19
Birds on Urban Wastelands

Peter J. Meffert

Abstract Responses of birds to urbanisation are manifold. Urbanisation directly influences birds by changing ecosystem processes, habitat and food supply; urbanisation indirectly influences birds by affecting their predators, competitors or disease organisms. A special urban habitat is wasteland since it occurs only for short periods in urban agglomerations. Their habitat characteristics could rarely be found in other urban land-use types. In earlier times, large herbivores, fire, floods, windfall, shifting dunes or dynamics of natural river courses removed vegetation and created open landscapes. In human-dominated landscapes, these processes are mostly prevented. In urban settings, building work, demolition and removal of industrial or railroad areas simulate ecological processes that became rare in human-dominated industrial landscapes. Whereas the population dynamics of open-land species in agricultural areas were intensively studied, urban wastelands were rarely examined. These 'unintentional' habitats are populated by a number of rare species. Thereby, species differ considerably from each other with regard to their requirements. Some bird species are sensible to human intrusion, some avoid densely built areas, and some are sensitive to the surroundings of habitat patches that are irrelevant for others. Most bird species that prosper in urban habitats are generalists, but also some habitat specialists are under certain conditions able to exploit the resources of an urban environment. The aim of this chapter is to show the state of knowledge on birds on urban wastelands, their value as habitat for endangered bird species and the influence of the urban space that surrounds wastelands on their avifauna.

Keywords Urban wastelands • Vacant lots • Urbanisation • Intrusion • Urban matrix

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19.1   Urban Wastelands

While urbanisation spreads rapidly and entire human population is continuing to grow (Heilig 2012), another contrary tendency can be observed. Mainly in the industrial nations, many cities are shrinking (Oswalt et al. 2006). Conversion processes mostly involve abandoning of former uses. In consequence, urban wastelands emerge. Wastelands occur in all urban agglomerations, often only for short periods. Their habitat characteristics could rarely be found in other urban land-use types and differ considerably from other urban habitats such as housing areas or parks (Maurer et al. 2000). Indeed, wastelands are known to provide valuable habitats for wildlife (Eyre et al. 2003; Angold et al. 2006; Strauss and Biedermann 2006). In the *Natural History of Vacant Lots* (Vessel and Wong 1987), the authors describe urban wastelands, or vacant lots, as ecosystems and address several groups of plants and animals that can be found on such sites in California, USA, among several endangered species. Similarly, many of the rarest and endangered species in the municipality of Valencia (Spain) inhabit wastelands (Murgui 2005). However, since avifaunal composition is affected by soil properties, climate, biogeography (especially regarding invasive species) and other circumstances, processes may differ considerably between urban wastelands of different locations and genesis.

Urban wastelands could have the potential for improving living conditions, enhance biodiversity, and may contribute to species conservation (Fritsche et al. in Langner and Endlicher 2007). But there is a lack of attention and research on nature conservation issues in urban agglomerations (Miller and Hobbs 2002), and there are only a few studies on endangered open-land birds (e.g. Jones and Bock 2002; Sorace and Gustin 2010) and on urban wastelands since they are often inaccessible, less attractive to ornithologists and of a temporary nature. For these reasons, not much research has been done on this topic in urban agglomerations in Europe or on other continents.

This chapter is mainly based on research done on urban wastelands (Fig. 19.1 in Berlin, Germany) (Meffert et al. 2012; Meffert and Dziock 2012; Meffert and Dziock 2013). It aims to show the state of knowledge on birds on urban wastelands, their value as habitat for endangered bird species and the influence of the urban space that surrounds wastelands on their avifauna.

19.2   Birds on Urban Wastelands

The avifauna of urban wastelands (Fig. 19.2), of course, includes the avifauna of other urban habitat types, such as housing areas, industrial areas or parks. Birds particularly make use of their special vegetation for foraging. Beyond this typical urban bird species, there are habitat specialists that do not occur in other urban habitat types. Applying the concept of Blair (1996), who categorises into urban avoiders, urban exploiters and (sub)urban adaptables, these habitat specialists

Fig. 19.1 Exemplary wasteland sites in Berlin, Germany

belong to the latter group and tolerate the urban setting of wastelands and settle because of certain habitat characteristics. Consequently, there is a mix of two types of bird: Firstly, there are typical urban bird species that dwell in cities anyway and also use urban wastelands. Secondly, there are habitat specialists that in cities only occur on wastelands. The three factors that strongly influence a wasteland's avifauna should be addressed in the following way: the size of a wasteland, its surroundings and the impact of direct disturbance by human intrusion.

19.2.1 Size of Wastelands

The size of a habitat patch is one of the most important features that determine its biodiversity. For example, Drinnan (2005) found it to be the best and most significant predictor of species richness of birds, frogs, plants and fungi on woodland remnants. Matthies et al. (2013) show that, for the diversity of birds and vascular plants, only patch size matters but not the distance to the urban edge. Many openland birds inhabit the interior and avoid the edges of a habitat patch (Yahner 1988). They are especially sensitive to the reduction of habitat patches in size (Vickery et al. 1994; Helzer and Jelinski 1999) since larger sites have more interior habitat that is less affected by edge effects (Soulé 1991). However, the demands for area

Fig. 19.2 Characteristic open-land bird species (row-wise): white wagtail *Motacilla alba*, northern wheatear *Oenanthe oenanthe*, goldfinch *Carduelis carduelis*, crested lark *Galerida cristata*, red-backed shrike *Lanius collurio* and black redstart *Phoenicurus ochruros*. Northern wheatear by Florian Möllers, others by the author. Northern wheatear, drawing by Caroline Greiser

vary widely among species and even regionally within the same species (Johnson and Igl 2001). This also applies for birds of conservation concern that settle on urban wastelands in Berlin, Germany (Meffert and Dziock 2012). Some species strongly depend on a certain minimum size of a habitat patch, e.g. tawny pipit *Anthus campestris*, northern wheatear *Oenanthe oenanthe* or tree sparrow *Passer montanus*, while for others size emerged to be not relevant at all (linnet *Carduelis cannabina*). These differences may be caused by several reasons. Firstly, home ranges and demands for foraging, nesting, etc. differ between species, causing different spatial patterns. Furthermore, the suitability of the urban matrix may also differ among species.

19.2.2   Impact of the Urban Matrix

Birds are, together with bats, the most motile organisms. Therefore, fragmentation and isolation of habitats should affect their ability to invade a habitat patch much less than, for example, mammals, reptiles or insects. This has important implications for fragmented landscapes. Habitats with a patchy distribution, such as urban parks or urban wastelands, may therefore be especially valuable for birds that are able to reach isolated habitats. In contrast, less motile organisms may not be able to overcome the resistance of the urban matrix, such as higher mortality due to traffic, predation or insurmountable obstacles. For example, the sand lizard *Lacerta agilis* also occurs on sandy wastelands but is much more dispersal limited due to fragmentation. Also within birds there might be differences in the response to fragmentation. In consequence, only fragmentation-tolerant species might settle in patchy urban habitats.

Patch size and on-site vegetation is obviously determining species composition, also on urban wastelands. Meffert and Dziock (2012) compared 55 urban wasteland sites with no or few woody vegetation and found that habitat structure explained about half of the variability in species composition. However, about the same amount of variability in species composition was explained by characteristics of the area that surrounds the wasteland site within 50 m, 200 m or 2 km. Despite habitat characteristics in this study were similar among all wasteland sites, species composition changed along with matrix features. Hence, at a spatial scale of several hundred metres to some kilometres, the urban matrix seems to filter certain species and to favour others. In consequence, some species (urban exploiters) become more abundant, whereas at the same time, others (urban avoiders) drop with increasing urbanisation. The response to features of the urban matrix that surrounds wasteland sites differs considerably among species. Some species were only marginally affected, such as tawny pipit and northern wheatear (Meffert and Dziock 2012). They are habitat specialists that inhabit only the wasteland itself and thus do not respond to the characteristics of the surroundings. Species that are supposed to make more use of the urban matrix, such as tree sparrow or linnet, showed stronger responses to the matrix characteristics. Overall, the landscape context is of high importance for the species composition (see Litteral and Shochat 2016), which is in line with many other studies on birds (Mazerolle and Villard 1999) and might be connected to their high mobility.

19.2.3   Disturbances by Humans and Dogs

In general, there is strong evidence that direct human disturbance by intrusion has negative impacts on bird diversity, density and reproduction (e.g. Fernández-Juricic et al. 2001; Flemming et al. 1988; Gutzwiller et al. 1998; Miller et al., 1998; Westmoreland and Best 1985). Schlesinger et al. (2008) found that influence of

disturbance on bird communities in forest remnants was two times higher than that of habitat loss. Many studies have found interspecific variations in the behavioural responses to human disturbance (Blumstein et al. 2005).

In a study of urban wastelands in Berlin, Germany, there was only a very small impact of direct disturbance by humans on birds (Meffert and Dziock 2012). None of the eight modelled threatened species were measurable negatively affected by human intrusion. Another study (Meffert and Dziock 2013) showed that data on vegetation explained all the variance in species composition that was also explained by disturbances. In other words, certain vegetation coincides with a higher degree of disturbance. At least for wastelands in Berlin, intrusion by humans and dogs seems not to have a remarkable impact on bird's occurrence. Possibly, especially disturbance-sensitive species avoid the whole urban area and never settle on urban wastelands. In a study of the reproduction of an urban population of the northern wheatear in Berlin, its breeding success indeed correlated with the presence of humans. However, nests have been lost due to removal of breeding structures at construction sites. Thus, not the presence of humans itself caused the nest failures.

There are several possible explanations for these findings. Firstly, if sites are large enough, birds are able to avoid encounters with humans or dogs. For the common sandpiper *Actitis hypoleuca*, Yalden (1992) showed that direct costs of disturbance to adult birds were not a serious problem as long as there was enough free space for them to fly off and feed elsewhere. Secondly, species adapt to humans. Flight distances have been shown to be shorter in urban populations compared to rural ones (Cooke 1980). Additionally, Møller (2008) was able to show that flight distances are shorter in bird species that live longer in cities. Another reason might be the contrary attractiveness of certain wastelands for birds and humans: large, sparsely vegetated areas attract rare bird species but may be avoided by most joggers or dog walkers.

In the study of Meffert and Dziock (2012), disturbance intensity was positively correlated with occurrence of crested larks *Galerida cristata*. This corresponds well with the described behaviour of this species, that is, takeoff distances of 1–2 m to humans and 1 m to moving cars (Glutz von Blotzheim et al. 1985). Explanations for this pattern could be artificial food supply, for instance, in front of supermarkets, or a lower risk of predation close to humans.

Direct disturbance of birds by human intrusion has been investigated intensively (Van der Zande and Vos 1984; Flemming et al. 1988; Yalden 1992), also in urban environments (Bergen and Abs 1997; Fernández-Juricic et al. 2001). Increased disturbance intensity by human intrusion is reported to result in decreased breeding densities (Van der Zande and Vos 1984; Fernández-Juricic et al. 2001) and lower reproductive success (Westmoreland and Best 1985; Flemming et al. 1988; Miller et al. 1998) by several mechanisms (Chace and Walsh 2006). To date there is only very few research on birds living in open habitats within urban areas and on passerines except very common ones such as house sparrow *Passer domesticus*. Overall, there is much interspecific variation in the responses to disturbance (Blumstein et al. 2005). Estimates of the relative importance of direct disturbance on community structure are very contradicting.

19.3   Conservation Issues

The significance of urban wastelands as habitats for birds is mostly overlooked for several reasons: often they are temporary, unattractive or inaccessible. However, these 'unintentional' habitats are populated by a number of rare species. Thereby, species differ considerably from each other with regard to their requirements. Some bird species are sensible to human intrusion, some avoid densely built areas, and some are sensitive to the surroundings of habitat patches that are irrelevant for others. Most bird species that prosper in urban habitats are generalists, but also some habitat specialists are under certain conditions able to exploit the resources of an urban environment. One example is the northern wheatear that is threatened by extinction in Germany and breeds successfully on many wastelands in Germany's capital Berlin (Meffert et al. 2012).

Urban wastelands have been found to provide habitat for various groups of organisms (Eyre et al. 2003; Angold et al. 2006; Strauss and Biedermann 2006; Öckinger et al. 2009). They are particularly interesting for urban green systems. With their various stages of vegetation, they are able to provide a broad habitat mosaic and, with this, opportunities to increase biodiversity (Mathey and Rink 2010). After Maurer et al. (2000), the most important group for nature conservation purposes within urban agglomerations are species of dry sward communities, typical for railway areas or urban wastelands in the city. Meffert and Dziock (2012) also found a considerable amount of threatened bird species on this type of habitat. Thus, the most valuable wastelands in regard to bird species conservation seem to be those of early successional stages. Without management, shrubs and trees grow up, open-land species disappear, and widespread and common edge and woodland species invade the habitat. Thus, the vegetation has to be removed consistently to maintain biodiversity. The same effect could be achieved if periodically new wastelands would be created. Different authors emphasise that the spatio-temporal dynamic of urban wastelands is crucial for their species diversity (Flores et al. 1998; Gibson 1998; Meffert and Dziock 2012). According to Schadek et al. (2009), high plant species richness on sandy wasteland sites can be achieved by strong disturbances, that is, extensive removal of vegetation at an interval of 3–7 years. Most plant, grasshopper and leafhopper species that were modelled by Kattwinkel et al. (2009) could be maintained at a turnover interval of 10–15 years, whereas the rarest insect species occurred on sites with an age of 3–6 years.

In this way, wastelands that are poor in woody vegetation may serve as surrogate for natural open-land habitats and agricultural areas. In earlier times, large herbivores, fire, floods, windfall, shifting dunes or dynamics of natural river courses removed vegetation and created open landscapes. Nowadays these processes are mostly prevented. In urban settings, building work, demolition and removal of industrial, housing or railroad areas simulate ecological processes that became rare in human-dominated landscapes.

Here, it has to be kept in mind that the number of species, i.e. alpha diversity, of those communities that inhabit open wastelands might be low compared to parks or

cemeteries. Considering not only breeding birds but all present species, wastelands can harbour about the same amount than parks, as occurs in the city of Valencia during both winter and the breeding season (Murgui 2005). However, beta diversity, i.e. compositional heterogeneity between urban wastelands and other urban habitat types, might be high because some species exclusively settle on wastelands.

19.4   Implications for Urban Planning

Studies of urban systems have been approached along several kinds of contrasts: ecology *in* as opposed to ecology *of* cities, biogeochemical compared to organismal perspectives, land-use planning versus biological and disciplinary versus interdisciplinary (Pickett et al. 2001). Also people see their environment as a dichotomy of 'nature' versus 'non-nature'. This concept causes segregative attempts of nature conservation strategies that create severe problems. For instance, agricultural biodiversity in Europe declines dramatically since the European Union pursues a policy of strict protection of threatened species and habitats, whereas simultaneously agricultural practice becomes more and more intensified to maximise crop yields (Donald et al. 2001).

In the last years, there is growing belief that this segregative approach neither stops the loss of biodiversity nor leads to a healthier environment. That applies in particular to Europe that has become almost completely altered by men. Instead, nature and man-made environments such as cities can no longer be considered dichotomic (Thrift and Amin 2002). Kowarik (2011) argues not only to focus on relict habitats and native species in urban settings but to consider the whole range of urban ecosystems, also for conservation approaches. By their nature, urban wastelands are often of economic interest, undesired by residents and the municipality and rarely examined in terms of biodiversity. Consequently, urban wastelands are hardly integrated in nature conservation strategies (Herbst and Herbst 2006).

Meffert and Dziock (2012) showed that some endangered open-land bird species inhabit urban wastelands. As unintentionally provided habitats, wastelands differ in various aspects from planned green spaces. Urban planners may use these findings for the design of green spaces to enhance biodiversity and break with our traditional image of urban green consisting of lawn and trees that not only reduces overall biodiversity but also separates us from nature (Turner et al. 2004).

The early successional stages of newly created wastelands will vanish by themselves. Thus, a dynamic cycle of spatio-temporal shifts between disturbance in terms of removal of vegetation and secondary succession could maintain open spaces and thereby increase biodiversity. These mechanisms have been shown for plants and insects on urban wastelands (Kleyer et al. 2007; Kattwinkel et al. 2009) and should be considered by urban planners.

To provide habitat for open-land birds, territories have to be large enough. In Berlin, Germany, sites above 5 hectares harbour some rare bird species; those above 7 hectares are especially valuable for threatened open-land bird species (Meffert

and Dziock 2012). To decrease disturbance levels by humans and dogs, areas exceeding a size of 10 hectares are recommended. Some species can be helped by providing structures for nesting, such as piles of stones or gabions as breeding structures for the northern wheatear.

With regard to vegetation, open space should not be dissected by trees or high shrubs. Open soils and sparse and short vegetation are of high value. Thus, planners should forego high woody vegetation or at least concentrate it in certain places on the edge of the area. In the grass layer, spontaneous vegetation should be included and potentially enriched with varied and local seeds.

First examples of agricultural-like green areas in Berlin showed both high acceptance by the residents and high biodiversity (Köstler et al. 2006). In addition, predictions of climate development for the region predict less precipitation and desertification (Gerstengarbe et al. 2003). Essential adaptation to these changes in the design of green areas could be used for rethinking by avoiding woody vegetation that needs watering and admits patches with open soils and sparse vegetation.

Urban wastelands can be used for various kinds of purposes and have ecological, economical and social functions; therefore, all these aspects should be considered by planners (Hoffmann et al. 2010). Summarising the up-to-date knowledge, four aspects regarding biodiversity issues that have to be considered by urban planners and managers should be addressed in the following:

1. Think of urban wastelands as habitats: early successional stages enhance urban biodiversity.

    Urban wastelands in early successional stages are valuable habitats for birds. Checking routinely wasteland sites for the occurrence of threatened species is recommended, in particular sites larger than 5 hectares.
2. Regard the size: the larger the better but at least 5 hectares.

    The results of Meffert and Dziock (2012) suggest a minimum size of about 5 hectares for the occurrence of several endangered open-land bird species. Beyond this, the number of threatened bird species still increases with the size of wastelands.
3. Keep it disturbed: remove vegetation periodically.

    If wastelands are created continually by deconstruction of buildings, industrial constructions or track installations, there are constantly sites in an early successional stage. If no new wastelands are created, these open habitats will disappear by growing vegetation. To maintain valuable open-land habitats, vegetation will have to be removed periodically. Based on the literature, removing the complete vegetation after 5–10 years is recommended.

    There are several methods to clear wasteland sites from vegetation or to decelerate succession. One possibility would be to use caterpillars to remove plants and topsoil completely. Beyond that, there are several less expensive methods to remove vegetation. Circuses, temporary selling (e.g. Christmas trees), fairs or festivals, other events or mass meetings, sports or art already happen on wasteland sites. If these uses are properly managed and coordinated, they can be employed to remove vegetation and thus enhance overall urban biodiversity.

4. Human intrusion: care about dog walkers?

    Meffert and Dziock (2012) show that management of human intrusion into wastelands is not necessary in Berlin, Germany. Although, it seems to be important to create hideaways for birds that enable them to avoid encounters with humans and dogs. This becomes the more important the smaller the site is.

Another aspect of urban wastelands is their sociocultural role. While most areas like parks, cemeteries or housing areas are very determined in their usage, wastelands allow processes and unrestricted development. Pyle (2002) stated that 'As the vacant lots go, so goes a source of intimacy and education that contemporary culture can scarcely afford to lose'. Further, larger areas like former airports enable city dwellers to sense width and with that a kind of freedom that does seldom exist in a city's landscape. An example is the former airport Tempelhof in Berlin, Germany. In 2014, the population of Berlin decided in a referendum to prohibit the development or selling of the 386 hectare large area as it was planned by the administration. In the centre of the areas lives a population of about hundred pairs of field larks *Alauda arvensis*, whereas around people are barbecuing, biking and flying kites.

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Chapter 20
The Role of Invasive Plant Species in Urban Avian Conservation

Jason M. Gleditsch

Abstract The implications of invasive plant species on urban avian conservation are complicated and often species or context specific. In the past 20 years, research into the effects of invasive plant species on bird ecology and conservation has increased immensely, thus allowing conservationists to create management practices for the benefit of bird populations. However, until recently, the potential of invasive species to create positive relationships with bird species has been absent from the literature. Recent findings have created a complex puzzle for management of invasive species in order to conserve avian populations in any environment, especially urban areas. Bird communities utilize invasive plants for various aspects of their life histories. In this chapter, I provide evidence for the positive, negative, indirect, and direct effects of invasive plant species on avian communities with a strong focus on the relationship of fruiting invasive plants with native birds. In order to create a relevant discussion, I will use current case studies that are consistent with research from many different areas across the globe. I will then synthesize this discussion into a theory on how invasive plants should be viewed in the paradigm of urban avian conservation. This theory can then be used to discuss possible habitat design and management plans for urban environments and how those may influence other aspects of the environment through their conservation of bird communities.

Keywords Avian conservation • Invasive plants • Birds • Urban conservation • Plant-animal interactions

20.1 Introduction

As the world's population grows, so do urban environments, creating novel challenges for birds to overcome (see Lepczyk et al. 2016). One such challenge is the introduction and establishment of invasive plant species that have arisen as a result of

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increased globalization. A large proportion of plant species in urban areas are now nonnative, indicating that cities can be hot spots for invasive plants. In Europe, an average 40 % of plant species are nonnative (Pyšek 1998), which is similar to North America which has an average of 35 % nonnative (Clemants and Moore 2003), and in Beijing, China, an average of 53 % of species are nonnative (Zhao et al. 2010). High proportions of nonnative vegetation in urban areas suggest that these environments are not only impacted by the effects of urbanization but also by the introduction of invasive plants. Surprisingly, studies that investigate the response of birds to invasive plant species have predominately been focused on less urbanized environments, even though the influence of invasive species on avian life histories often changes along a rural to urban gradient (Rodewald et al. 2010). This paucity of empirical data poses a difficult challenge for bird conservationists that attempt to implement conservation regimes in urban environments. Here, I present a review of the effects of invasive plant species on avian life histories and food availability (for a previous review, see Reichard et al. 2001), and use this information to discuss how invasive plants should be viewed in urban bird conservation policies.

In this review, I use the term *exotic* to denote a plant species in an area that is separated by a geographic barrier which prevents the natural (not human-mediated) dispersal from their native or historical distribution. An example of this is ornamental plants from Europe that are planted in gardens of North America. I use the term *invasive* to denote exotic species that have established self-sustaining, reproductive populations. Note that with these definitions, an exotic species is not necessarily invasive, and native species that can be considered "invasive" (i.e., *Acer rubrum* in North America) is not included in these definitions and this review.

Control of invasive plants has historically involved attempts at complete eradication of exotic species, often at extreme expense and labor. It was estimated that the United States of America spends approximately $9.5 billion for invasive plant control (Pimental et al. 2005). A potential problem with these attempts of eradication is that across the globe, researchers have been finding that heavily invaded habitats can support high numbers of native bird species (Aslan and Rejmánek 2010). During the fall months in Pennsylvania, USA, the abundance of frugivorous (fruit-eating) birds was positively correlated with the amount of shrub honeysuckles (*Lonicera* spp.). This relationship was so strong that some bird species were absent from habitats that had reduced abundances of honeysuckle (Fig. 20.1; Gleditsch and Carlo 2011). Similarly, American robins (*Turdus migratorius*) were observed in higher numbers along the edges of forest fragments where honeysuckles tend to grow in high density (Watling and Orrock 2010). Other studies show similar patterns in Australia (French and Zubovic 1997), France (Debussche and Isenmann 1990), South Africa (reviewed in Breytenbach 1986), and India (Aravind et al. 2010).

The use of invasive plants by birds creates a management challenge for urban conservationists. Since birds are known to use invasive plants, could the eradication of them reduce or change bird communities? The answer to that question is not as straightforward as it seems. The effect of invasive plants on bird species and their
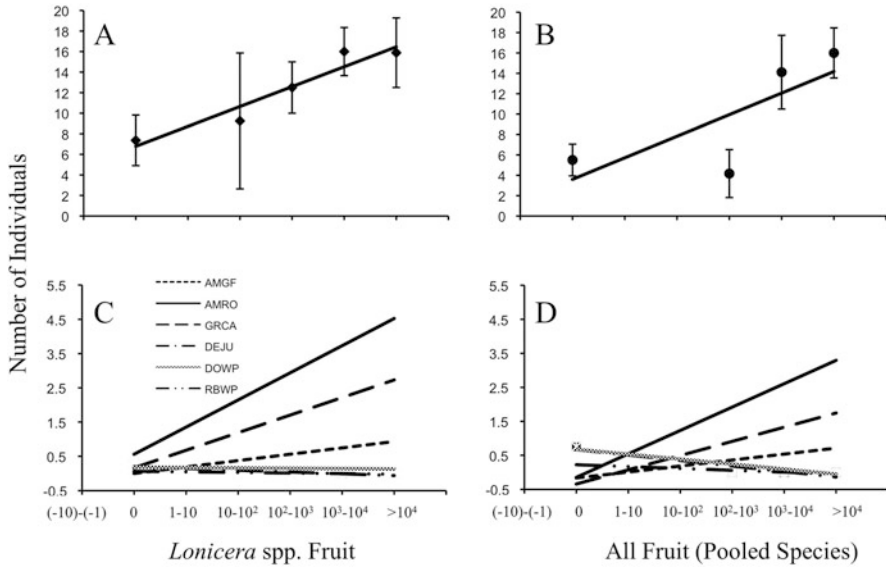
Fig. 20.1 When the correlation of the total bird abundance and *Lonicera* spp. is compared to the bird abundance correlation with the fruit of all pooled plant species, it is evident that honeysuckle is the main driving factor for the abundance of birds. This correlation holds for some pair-wise comparisons. (**a**) The linear correlation of average total number of birds with *Lonicera* spp. fruit abundance [with log(# of birds): $N = 30$, $r = 0.5149$, $p = 0.0036$]. (**b**) The linear correlation of average total number of birds with total fruit abundance [with log(# of birds): $N = 30$, $r = 0.3999$, $p = 0.0285$]. (**c**) Simple regression lines fitted between the average number of bird individuals of important bird species and the fruit abundance of *Lonicera* spp. at point counts display a stronger effect of *Lonicera* on frugivorous species than (**d**) the effect of pooled fruit abundance on such bird species. Figure reprinted from Gleditsch and Carlo (2011) with permission

use is often species specific in regard to both the plant and bird species. Indeed, many of the studies mentioned earlier showing positive relationships with invasive plants also showed negative relationships with avian species in other guilds such as canopy foraging and insectivorous species (French and Zubovic 1997; Aravind et al. 2010; Gleditsch and Carlo 2011; Schneider and Miller 2014), a pattern that is consistent across land use types and global regions. As a result, attempts to generalize the influence of invasive plants on bird ecology have evolved from all invasives negatively affect birds to a nesting or foraging guild approach. A more thorough understanding of the influence of invasive species on bird species, to include all aspects of avian life history, is needed in order to make informed conservation decisions that conserve one ecosystem characteristic without undue harm to another.

20.2   Breeding and Post Fledging

One of the most important and highly researched life history stages of birds is the breeding season. Much time, effort, and expense have been expended to elucidate the effects of invasive plants on the breeding ecology of birds across the globe, and yet many aspects of the issue remains unknown. A particular invasive plant species may be beneficial for some bird species and prove to be an ecological trap for others, compromising their annual productivity. Other species avoid nesting in invaded habitats all together, leading to restricted ranges and populations.

Mate Choice: The first potential effect of invasive shrubs on breeding is with mate choice and sexually derived cues. An example of this is the northern cardinal (*Cardinalis cardinalis*) of eastern North America (Jones et al. 2010). Male cardinals develop a bright red plumage to indicate their quality as a mate. These colors are created by diet-derived carotenoids that are largely obtained during the fall months during their molting period. In much of this region in North America, populations of the invasive shrub honeysuckles (*Lonicera* spp.), which produce red fruits, have exploded, thus creating a high availability of carotenoids on the landscape. This increased source of easily obtained carotenoids, particularly in rural habitats, has decoupled the red plumage signal of quality (Jones et al. 2010). However, this effect of increased dietary carotenoids brought on by invasive honeysuckles is reduced in urban habitats probably due to the reduction in other sources of dietary carotenoids (Jones et al. 2010).

Nesting: The appropriate selection of nesting habitat is critical for bird species to successfully fledge young and thus maintain viable populations. Nest-site selection often takes place at the level of specific plant communities that provide the habitat structures, such as cover, nest-building materials, and food resources, that birds and their nestlings need for incubation, growth, and survival (Martin 1993). Cues that birds use to judge habitat quality can be altered and misinterpreted with the introduction of invasive plants (Remeš 2003). For example, honeysuckles in Ohio have been shown to be ephemeral "ecological traps" for nesting northern cardinals (*Cardinalis cardinalis*; Rodewald et al. 2010), because honeysuckle is attractive to birds for nesting but causes declines in the birds' nesting success. Interestingly, this pattern is ephemeral with negative effects only evidenced during the early breeding season and overall effect on yearly productivity ambiguous.

Many theories have been presented to explain why birds would choose habitats dominated by invasives that are of poor quality. One such theory is that invasive woody species tend to have an earlier leaf flush than natives, which creates the appearance of a habitat that would be good for concealing nests and providing resources. However, some evidence suggests that certain habitats dominated by invasive species may have the opposite effect with higher rates of nest predation for some bird species and reduced abundance of foliar arthropods. The structural complexity of shrubs can make it easier for certain predators to move through the substrate increasing their prey searching effectiveness (Borgmann and Rodewald 2004). In addition, invasive shrubs often cause birds to nest closer to the ground,
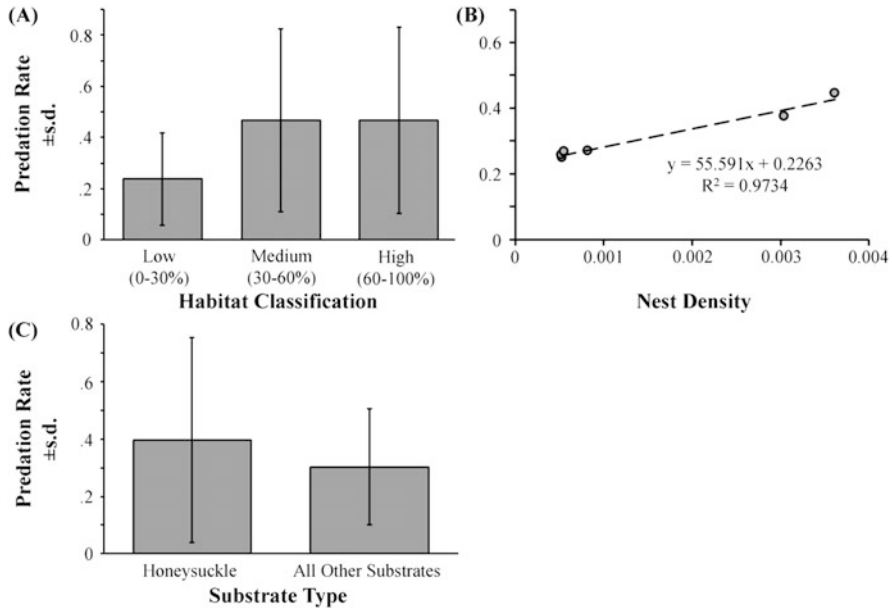
Fig. 20.2 There was no relationship between honeysuckle (*Lonicera* spp.) abundance or honeysuckle use as nesting substrate and the predation rate of nests. Panel **a** shows the average nest predation rates in the low (0–30 % honeysuckle cover), medium (30–60 %), and high (60–100 %) honeysuckle habitats. Panel **b** shows the nest predation rates of the sites regressed with the nest density of each site. A strong relationship was observed between nest density and the predation rate of nests. Panel **c** shows the average nest predation rates in the different substrate classifications (honeysuckle spp. and all other species). Figure reprinted from Gleditsch and Carlo (2014) with permission

which makes those nests more vulnerable to predators. Another theory of how invasive shrubs can increase nest predation is through decreased nest-site partitioning and creation of a homogenized habitat, allowing predators to focus their searching on a specific type of habitat or nest site (Borgmann and Rodewald 2004). However, nest density is an obvious confounder in these studies since many invaded sites have higher nest density, and nest density is highly related to nest predation (Fig. 20.2b; Gleditsch and Carlo 2014). Since some of the negative effects of invasive plants can be ephemeral, migratory birds that arrive later in the breeding season should not be attracted to the early leaf flush of some invasive plants, so the increased predation risk may be mediated (Rodewald et al. 2010).

Conversely, and as evidence of the species-specific influences of invasive plant species on avian reproduction, numerous studies have shown the invasive species may actually have positive effects on nesting birds. Tamarisk (*Tamarix* spp.), one of the most undesirable invasive plants in the arid southwest United States, is an attractive nesting substrate for the endangered western willow flycatcher (*Empidonax traillii extimus*) and has positive effects on their populations (Sogge et al. 2008). Additionally, in New England, one study found that the influence of invasive species on nesting birds is species specific, positively affecting nesting
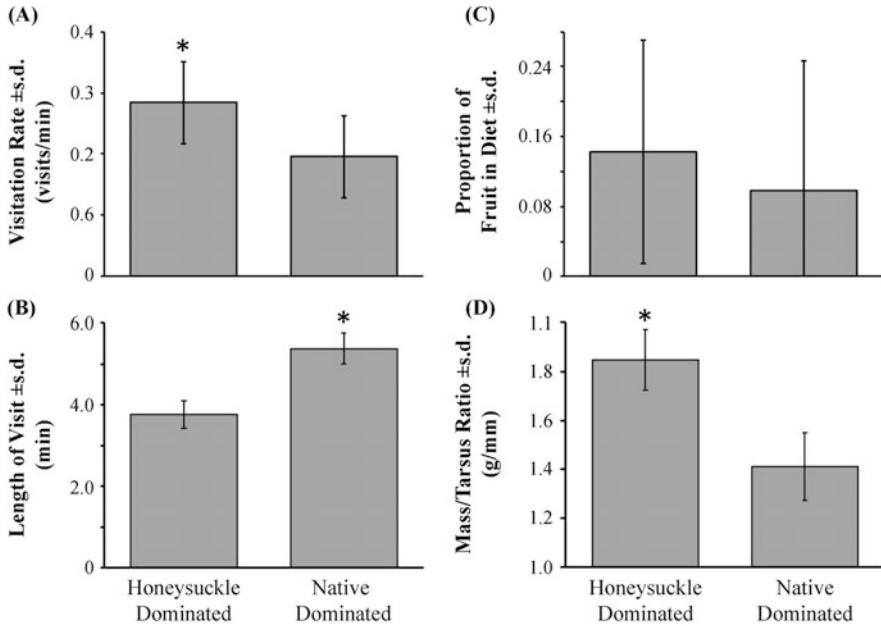
Fig. 20.3 Higher visitation rates and shorter nest visit lengths were observed for catbird nests found in honeysuckle (*Lonicera* spp.)-dominated habitats. In addition, nestlings were observed to be in equal or better condition at the time of fledging. Panel **a** shows the average visitation rate in the honeysuckle-dominated (HSD) and the native-dominated (ND) habitats. Higher visitation rates were found in HSD habitats. Panel **b** shows the average length of each visit in HSD and ND habitats. Parents were at the nest longer in ND habitat. Panel **c** shows the average proportion of fruit in the diet of the nestlings in HSD and ND habitats. No significant difference between habitat types was observed for this response. Panel **d** shows the average mass: tarsus ratio of nestlings in HSD and ND habitats. Higher mass: tarsus ratio was measured in HSD habitats (*$p \leq 0.05$). Figure reprinted from Gleditsch and Carlo (2014) with permission

success of species like the gray catbird (*Dumetella carolinensis*) but having neutral effects on other species, such as the chestnut-sided warbler (Schlossberg and King 2010). Similarly, Japanese barberry (*Berberis thunbergii*) seems to become a refuge of sorts for veeries (*Catharus fuscescens*) in years where rodent populations are high (Schmidt et al. 2005). Another study in the USA found similar results to the Schlossberg and King (2010) study where there was no difference in the predation rates between habitats dominated by invasive bush honeysuckles and habitats dominated by native shrubs (Fig. 20.2a; Gleditsch and Carlo 2014). Interestingly, the Gleditsch and Carlo (2014) study also provided evidence that fledgling gray catbirds may have equal or even better physiological condition in honeysuckle-dominated habitats (Fig. 20.3d).

Beyond nest placement and nest predation, invasive plants can cause shifts in nesting behaviors that could directly or indirectly influence the population dynamics of a bird species. Gray catbirds in the USA exhibit higher nest visitation rates

and less time per visit in habitats dominated by invasive honeysuckle (Fig. 20.3a and b; Gleditsch and Carlo 2014). The higher visitation rates could mean that parents must feed their young more due to the lower nutritional quality of their high fruit diet, or it could mean that the parents are able to feed their young more because there are more food resources in the habitat. This distinction is important because higher visitation rates could attract predators (Martin et al. 2000). Yet, if the parents are able to feed their young more, then they might have better development and be able to evade predators both while still in the nest and after they fledge.

Post-fledging Survival An important aspect of avian life histories is post-fledging survival. Birds are often extremely vulnerable to not only predators but also starvation and exposure during the beginning of the post-fledging period. Unlike nesting, our understanding of how urban environmental characteristics affect fledgling survival is greatly limited due the surprisingly small number of studies that have investigated this issue. A study investigating the fledgling survival and habitat use of northern cardinals and Acadian flycatchers (*Empidonax virescens*) in urban environments suggests that fledgling survival is higher for northern cardinals in the habitats of urban areas that were dominated by Amur honeysuckle (*Lonicera maackii*) because of the structural complexity provided by honeysuckle species (Ausprey and Rodewald 2011). In addition to the concealment from predators, it has been suggested that gray catbirds that have access to invasive plants produce fledgling of equal or even higher physiological condition which may lead to higher post-fledging survival (Gleditsch and Carlo 2014) nesting in urban areas. Interestingly, the association of post-fledging survivorship with invasive shrubs may be consistent across bird guilds (Vitz and Rodewald 2006). Northern cardinals (Ausprey and Rodewald 2011), Acadian flycatchers (Ausprey and Rodewald 2011), ovenbirds (*Seiurus aurocapilla*; King et al. 2006; Vitz and Rodewald 2006; Vitz 2008), worm-eating warblers (*Helmitheros vermivorum*; Vitz and Rodewald 2006; Vitz 2008), hooded warblers (*Wilsonia citrina*; Rush and Stutchbury 2008), Swainson's thrushes (*Catharus ustulatus*; White et al. 2005), white-throated thrushes (*Turdus assimilis*; Cohen and Lindell 2004), dickcissels (*Spiza americana*; Berkeley et al. 2007), and Botteri's sparrows (*Aimophila botterii*; Jones and Bock 2005) differ in their breeding and foraging ecology, but all show the same pattern in selecting habits with high understory structural complexity for the post-fledging period. Many invasive shrubs have high structural complexity that could provide post-fledging habitat for bird species in anthropogenically disturbed habitats.

20.3 Food Availability

Invasive plants can influence the food resources available to birds in multiple ways. All of the already discussed life history traits can be influenced through the altering of food resources by invasive species. It is thought that due to the lack of evolutionary history between exotic plants and native invertebrates, exotic plants can be unpalatable to native herbivores. In Delaware, USA, invasive shrubs have been shown to support not only a lower diversity of foliar arthropods but also lower abundances (Tallamy 2004). The lack of foliar arthropods in invaded habitats has been suggested to be the cause of decreased bird abundance and diversity between invasive and native habitats (Burghardt et al. 2008). Even though foliar invertebrates may be reduced, soil invertebrate biomass may increase with plant invasions causing a shift in invertebrate communities. This shift may be evidenced in the bird community as well with an increase in the number of avian ground and/or generalist foragers.

Another mechanism that may be responsible for shifts in the bird community to more generalist species is that the majority of invasive woody plants produce fruits. The addition of abundant fruit resources to the landscape creates habitats that can sustain much larger populations of frugivores and allow for insectivorous species to switch to a high fruit diet when the abundance of arthropods is low (Gleditsch and Carlo 2011). Traditionally fruit is viewed as a poor resource since it has a very low nutrient density and higher carbon to nitrogen ratio. However, many fruits have secondary compounds in them that could be of high importance, and since the abundance of fruit is high, birds may be able to overcome the nutrient deficits by eating more.

The timing of invasive plant fruiting may also differentially impact bird species with some invasive plants fruiting during temperate breeding seasons, while many natives do not. This can have great consequences to the nutrition and development of birds while nesting. In Central Pennsylvania, USA, gray catbird nestlings were shown to be in good physiological condition at the time of fledging in invasive honeysuckle-dominated habitats likely due to the presence of ripe honeysuckle fruits as a food source (Fig. 20.3; Gleditsch and Carlo 2014). Using fruit to feed nestlings allows for nestlings to have a mixed diet, which has been shown to be beneficial to the overall nutrition of birds (Smith and Hatch 2008). The result of the gray catbird study shows how more analysis into the effects of invasive fruits on the development of nestlings, as well as the parents, is crucial to the understanding of the influence invasive shrubs on bird populations.

Migration is a very important aspect of many species life history, and invasive plant species can affect the food resources at stopover sites during both the fall and spring migrations. Since invasive plants have been shown to support not only less diverse but also less abundant invertebrate communities, spring migration stopover sites that are dominated by invasive species may possess fewer resources for migrating birds. The reduction of food resources could then increase the time and difficulty it takes for birds to replenish their fat stores. If birds have to spend more

time migrating to breeding grounds, then they will arrive later to breeding grounds and potentially in a lesser condition which would cause them to suffer reproductive consequences (Lozano et al. 1996; Sandberg and Moore 1996). Similar consequences can be observed for fall migration as well. However, fruiting invasive shrubs may provide more food resources (i.e., fruit) for some birds which may allow the birds to quickly replenish their fat stores if the fruit is high in nutrients. Still, migrating birds in the USA seem to prefer native fruits over that of invasive fruits (Smith et al. 2013) which may warrant the promotion of native shrubs in important migratory stopover sites.

20.4 Ecosystem Implications

It has been established that many species of birds use invasive shrubs for many aspects of their life history (Aslan and Rejmánek 2010). Some of these interactions are mutualisms that could have the potential to influence other aspects of the ecosystem (Gleditsch and Carlo 2011). For example, through the seed dispersal mutualism with birds (Reichard et al. 2001), invasive honeysuckles also alter the seed dispersal of other, even native, plants. As the abundance of honeysuckle fruit increases, the abundance of birds increases, and, in turn, the removal of fruit from other fruiting plants potentially increases their seed dispersal (Gleditsch and Carlo 2011). In addition, birds act as mobile links between forest fragments, so as bird abundance increases, so does the gene flow between forest patches which is important for the stability of populations (Lundberg and Moberg 2003). High abundance of mobile link species also increase the resilience of ecosystems (Lundberg and Moberg 2003; Lugo 2004), which is highly important in urbanized environment due to the high intensity and frequency of anthropogenic disturbance.

20.5 Conclusion

Urban environments can present challenges for wildlife species, including altered plant communities. Many invasive plants produce more fruit than their native counterparts (Luken and Theiret 1996) and are often positively associated with anthropogenic disturbance (Brothers and Spingarn 1992; Shea and Chesson 2002). Therefore, in highly disturbed urbanized environments, invasive plants might be able to support greater populations of birds. However, the effects of invasive plants on birds can be highly species specific with respect to both the plant and bird species. Table 20.1 attempts to generalize how fruiting and non-fruiting invasive woody plants may affect different feeding guilds of birds in urban environments. However, it needs to be noted that there are unequivocally exceptions to the rule. The western willow flycatcher is an example of this. Tamarisk is a non-fruiting shrub and the western willow flycatcher is insectivorous. So according to their

Table 20.1 Generalized effects of fruiting and non-fruiting invasive plants on different foraging guilds of birds

Foraging guild	Fruiting	Non-fruiting
Foliar insectivore	−	−
Frugivore	+	−
Generalist	=/+	=
Other	=	=/−

Not included in the table are nectarivorous birds because of the often species-specific nature of nectar resources available to birds. "−" denotes a negative effect, "+" denotes a positive effect, "=" denotes no or equal effect of invasive vegetation abundance as native vegetation abundance

guilds, tamarisk should have a negative effect on the flycatcher, yet any deleterious effects seem to be mitigated through the availability of much needed nesting habitat (Sogge et al. 2008).

Although eradication of invasive plant species is often a goal of land managers, removal of certain species may have unintended negative effects on the local bird community. This relationship has been demonstrated in studies that have experimentally removed fleshy fruits from habitats in the Block Islands, USA (Parrish 2000), longleaf pine savannas in South Carolina, USA (Borgman et al. 2004), and the Amazon (Moegenburg and Levey 2003). Because of the potential to cause unintentional harm, conservationists need to proceed with extreme caution when employing eradication methods for the control of invasive plants.

The question that all urban conservationists have to ask themselves is: *What am I trying to conserve?* The answer to that question will dictate how invasive plants are viewed in urban conservation plans. If a conservationist wants to conserve an endangered or threatened bird species, then research into the particular effects certain invasive plants have on that species, and then act accordingly. However, if the primary goal is to conserve the ecosystem services of birds, then invasive plants should be viewed not as villainous but as any other species in the plant community, and, as such, they may want to promote plant diversity instead of eradication of the invasive.

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Chapter 21
Species Richness and Species of Conservation Concern in Parks of Italian Towns

Alberto Sorace and Marco Gustin

Abstract The richness of all bird species and conservation concern species were investigated in 40 parks and their surrounding built-up areas of 27 Italian towns. Data were obtained from published urban atlases of breeding birds (25 parks) and additional personal communication of Italian ornithologists (15 parks). We define species of conservation concern as those included in the Annex I of EC Directive 09/147/CE and/or in the categories 1–3 of the Species of European Conservation Concern (SPEC). Total species richness and species of conservation concern were compared between the parks and the surrounding built-up areas (500 m around the parks). The role of park features such as size and distance from the centre was investigated for these two parameters. The analysis was repeated for single bird species of conservation concern and for a selection of functional groups of these species. According to homogenising theories of urban areas, no significant differences were observed between parks and surrounding built-up areas for the investigated parameters of breeding bird community and for the frequency of single species. Woodland bird species and woodpeckers of conservation concern were the only groups more diffuse in parks. Conversely, the frequency of building-nesting and aerial feeders was higher in built areas. Variables related to town size and distance from the centre appeared to produce higher effects than park size on species frequencies in parks.

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21.1   Introduction

Due to the dramatic growth of urbanisation over the world (Antrop 2004; United
Nations 2010; Haase et al. 2014), knowledge of processes affecting urban ecosys-
tems has become a priority (Flores et al. 1998; Niemela 1999; Marzluff et al. 2001).
Urbanisation is considered one of the strong forces causing biotic homogenisation
and the loss of biodiversity (Blair 2001; Miller and Hobbs 2002; McKinney 2006).
In particular, several studies have shown that urban habitats are characterised by a
decrease in species richness and diversity to the advantage of a few broadly adapted
species that may be particularly abundant (Jokimäki et al. 1996; Marzluff 2001;
Sorace 2002; Garaffa et al. 2009; Møller 2012). However, information on the
response of biological communities to the ecosystem changes caused by urbanisa-
tion requires further investigation (Jokimäki and Kaisanlahti-Jokimäki 2003;
Clergeau et al. 2006). This information is critical for wildlife conservation and to
enable correct management of large sectors of land surface. In particular, it may be
interesting to investigate the response to urbanisation by species whose populations
are decreasing.

   The low predation pressure on adult birds (including the absence of hunting
activity), combined with increased availability of food and milder microclimatic
conditions, may attract certain species to urban areas (Jerzak 2001; Chace and
Walsh 2006; Sorace and Gustin 2009). In some countries, urban areas may have an
important value for the conservation of some thrushes such as *Turdus merula*,
T. philomelos and *T. viscivorus* (Batten 1973; Gregory and Baillie 1998; Cannon
1999; Mason 2000). Some species of conservation concern might be even more
abundant in urban areas than elsewhere. For example, in Italy the majority of
Apulia and Lucania populations of *Falco naumanni*, a globally threatened species
(BirdLife International 2004), breed in towns (Palumbo 1997). In Finland, *Accipiter
gentilis* brood size is greater in urban areas than in rural areas (Solonen 2008).
Non-built areas and urban parks, when managed to benefit biodiversity, can host
rare species [Lerman et al. 2014; see Goddard et al. (2016) and Meffert (2016)],
and, despite being located in an urbanised matrix, small protected parks may
contribute to regional biodiversity conservation (Goodwin and Shriver 2014).

   Among birds, the granivorous species (*Passer* and *Carduelis* sp.) and the aerial
feeders (swifts) seem to better adapt to urban environments (Emlen 1974; Allen and
O'Conner 2000; Jokimäki and Kaisanlahti-Jokimäki 2003; Lim and Sodhi 2004).
As far as nesting sites are concerned, the ground and bush-shrub nesters appear to
be disadvantaged in town as compared to the species nesting at greater heights
(Luniak 1981; Jokimäki 1999, Clergeau et al. 2006; Luck and Smallbone 2010).
Therefore, it is expected that the species of conservation concern that are more
likely to settle in towns may include granivorous and aerial feeder species, hole-
nesters and species nesting at greater heights above the ground. However, some
recent data collected in Italian towns (Sorace and Gustin 2010) indicate that
urbanisation negatively affects most bird species of conservation concern (see
also Rayner et al. 2015), including those belonging to groups that are apparently

better suited to urban conditions. Nevertheless, some decreasing species (*Falco tinnunculus*, *Upupa epops*, *Jynx torquilla*, *Delichon urbicum*, *Phoenicurus phoenicurus*, *Monticola solitarius*, *Muscicapa striata*) do accept high degrees of urbanisation (Sorace and Gustin 2010).

In this study, based on a sample of 40 parks in 27 Italian towns, we compared the richness of breeding bird species and some functional groups of these species between parks and the adjacent surrounding area. Urban parks represent the best preserved fragments of natural area in Italian towns; thus the richness of bird species including those of conservation concern is expected to be higher in parks than in surrounding built areas although built areas include greenery as well. However, if urbanisation homogenises breeding bird communities, scarce differences should be highlighted between these two urban environments. In addition, we evaluated if some variables (town size, park size, distance from centre) can affect the bird community parameters. All analyses were repeated for bird species of conservation concern with the aim of understanding which decreasing species can settle in town and penetrate in built areas thanks to the presence of natural fragments. Although some information is available on the distribution of single species of conservation concern and on the variation of the composition of bird communities along urban gradients (e.g. Luniak 1996; Blair 2001; Marzluff et al. 2001; Clergeau et al. 2006; Sorace and Gustin 2010), data on the response of species of conservation concern to different degrees of urbanisation is still limited.

21.2   Methods

Data on 40 parks and surrounding built areas of 27 Italian towns were obtained from published urban atlases of breeding birds (25 out of 40 parks; see Sorace and Gustin 2009, 2010) and personal communication of Italian ornithologists (15 parks; see Fig. 21.1 and, for the features of these parks and relative towns, Table 21.1). Most study parks are characterised by meadows (in some cases, very large, e.g. P. Mario Carrara, P. delle Cascine, Villa Pamphili), tree rows and woods (including often old trees, e.g. P. del Popolo, P. Ducale, P. Cittadella, P. delle Cascine, Villa Groppallo, Villa Borghese, P. di Capodimonte). Some parks contain other natural habitats like old woods (e.g. Bosco Negri), rivers and wetlands (e.g. P. Mario Carrara, P. Lambro, P. delle Cave, P. della Vernavola, P. Ducos, P. Golena del Po, P. Fluviale, P. Ducale of Parma). In few parks, orchards and vegetable gardens (e.g. P. Pini) and agricultural patches (P. Fluviale) are present.

In our analysis, we included species that were surely breeding (e.g. nest) and species probably breeding (e.g. singing male). The presence of nocturnal breeding species was not investigated because the research effort for these species differed between the studied towns. As species of conservation concern, we considered those birds included in the Annex I of EC Directive 2009/147/CE and/or in the categories 1–3 of the Species of European Conservation Concern (SPEC; BirdLife
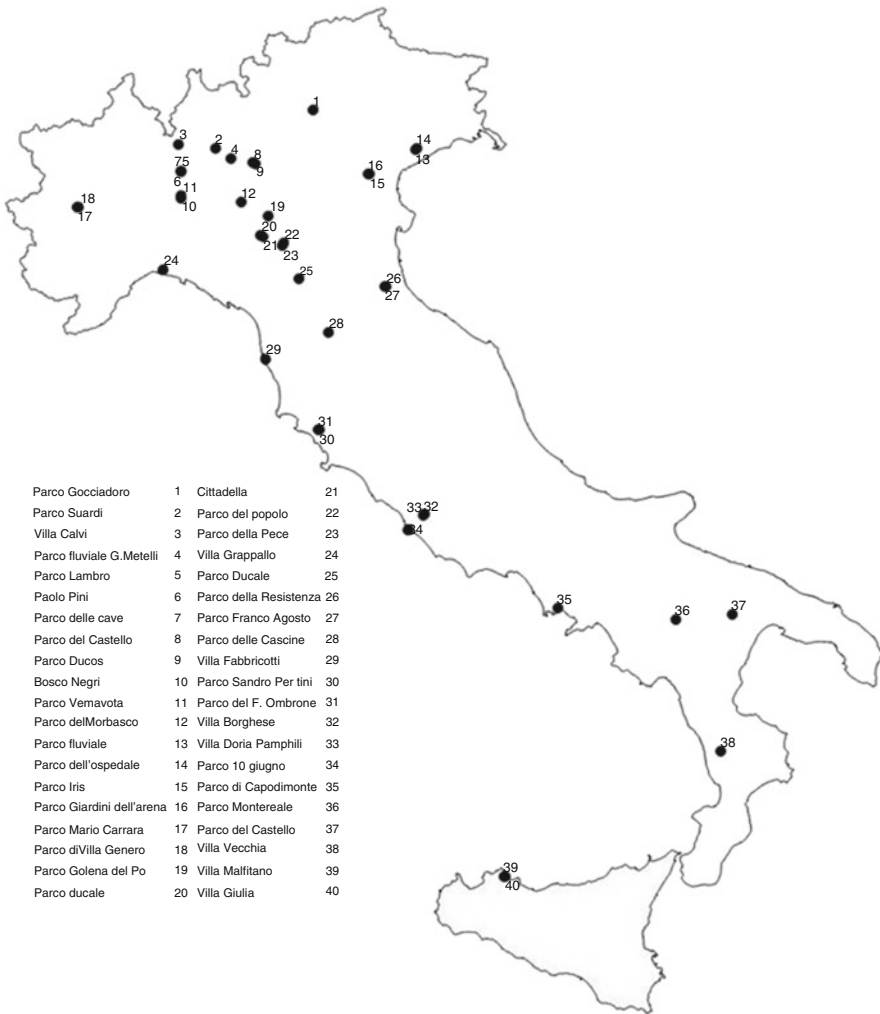
Fig. 21.1 Map of the cities in Italy where the 40 studied parks were located

International 2004). Although *Sturnus vulgaris* is SPEC 3, it was not considered among the species of conservation concern, because the Italian populations of this Passerine are increasing (BirdLife International 2004; Brichetti and Fracasso 2013).

Richness of all bird and conservation concern species was compared between the parks and the surrounding built areas (500-m buffers). The 500-m area surrounding parks is not completely built-up, but encompasses a wide range of habitat types including wetland, woodland, riverine habitats, farmland and even other parks and private gardens. In particular, for the areas surrounding the parks, the percentage of built area was on average 58.9 % (±17.7 SD) with green areas measuring on average 24.2 ha (±19.5 SD) (for comparison the mean size of parks was

Table 21.1 Features of the study parks and of the relative towns

Town	Park	Latitude	Longitude	Altitude (m a.s.l.)	Park size (ha)	Distance from the centre (km)	Town size (km²)	Number of inhabitants	Population density
Trento	Parco Gocciadoro	46° 03.393′	11° 8.244′	194	22	1.9	40.0	11,5905	2897.62
Cantù	Villa Calvi	45° 43.049′	09° 6.908′	369	0.93	0.1	9.6	39,900	4178
Bergamo	Parco Suardi	45° 42.093′	09° 40.592′	249	2.2	0	38.7	1,18,786	3069.4
San Donà di Piave	Parco dell'Ospedale	45° 38.016′	12° 34.472′	3	6.5	0.75	12.1	41,702	3446.45
San Donà di Piave	Parco Fluviale	45° 37.568′	12° 34.017′	3	8.8	0.5	12.1	41,702	3446.45
Palazzolo sull'Oglio	Parco Fluviale G. Metelli	45° 35.788′	09° 53.183′	166	10	3	5.9	20,040	3379.42
Brescia	Parco del Castello	45° 32.486′	10° 13.544′	149	9.6	0	18.2	1,92,749	10590.6
Brescia	Parco Ducos	45° 31.654′	10° 15.009′	149	5.5	3	18.2	1,92,749	10590.6
Milano	Parco Lambro	45° 29.695′	09° 15.096′	122	90	6	105.0	13,58,627	12939.30
Milano	Parco Paolo Pini	45° 28.608′	09° 11.523′	122	8	9	105.0	13,58,627	12939.30
Milano	Parco delle Cave	45° 28.176′	09° 5.997′	122	130	10	105.0	13,58,627	12939.30
Padova	Parco Giardini dell'Arena	45° 24.697′	11° 52.795′	12	2.7	0.5	42.0	2,13,594	5085.57
Padova	Parco Iris	45° 23.584′	11° 53.930′	12	3.25	2.5	42.0	2,13,594	5085.57
Pavia	Parco Vernavola	45° 12.364′	09° 10.015′	77	35	2.5	62.9	84,000	1335.45
Pavia	Bosco Negri	45° 10.248′	09° 8.677′	77	34	2	62.9	84,000	1335.45
Cremona	Parco del Morbasco	45° 08.172′	10° 0.909′	45	9.5	1.5	10.3	72,000	6990.3
Torino	Parco Mario Carrara	45° 06.491′	07° 38.688′	239	83.7	4	106.6	9,08,551	8522.99

(continued)

Table 21.1 (continued)

Town	Park	Latitude	Longitude	Altitude (m a.s.l.)	Park size (ha)	Distance from the centre (km)	Town size (km²)	Number of inhabitants	Population density
Torino	Parco di Villa Genero	45° 03.431′	07° 42.578′	239	4.3	2.5	106.6	9,08,551	8522.99
Casalmaggiore	Parco Golena del Po	44° 55.841′	10° 27.893′	26	200	0.5	6.0	15,348	2558
Parma	Parco Ducale	44° 48.303′	10° 18.905′	57	208	1	35.0	1,89,151	5404.31
Parma	Cittadella	44° 47.535′	10° 19.893′	57	120	1.2	35.0	1,89,151	5404.31
Reggio Emilia	Parco del Popolo	44° 42.146′	10° 37.839′	58	7.6	0	56.8	99,528	1751.94
Reggio Emilia	Parco della Pace	44° 40.805′	10° 37.107′	58	4	2.8	56.8	99,528	1751.94
Genova	Villa Groppallo	44° 22.942′	09° 2.605′	19	3.6	10	57.0	6,08,826	10681.16
Pavullo nel Frignano	Parco Ducale	44° 20.196′	10° 50.014′	710	35	0.4	5.0	17,463	3492.6
Forlì	Parco della Resistenza	44° 12.970′	12° 2.912′	34	9.45	0.2	42.3	1,17,859	2789.56
Forlì	Parco Franco Agosto	44° 12.800′	12° 1.811′	34	26	1.5	42.3	1,17,859	2789.56
Firenze	Parco delle Cascine	43° 47.010′	11° 13.012′	50	118	3	102.0	3,76,498	3691.16
Livorno	Villa Fabbricotti	43° 32.190′	10° 18.974′	3	5.4	0.85	38.1	160,937	4219.64
Grosseto	Parco del F. Ombrone	42° 45.389′	11° 7.410′	10	10	1	14.7	82,284	5597.55
Grosseto	Parco Sandro Pertini	42° 45.331′	11° 6.142′	10	6.4	1.1	14.7	82,284	5597.55
Roma	Villa Borghese	41° 54.773′	12° 29.112′	20	79	2	360.0	43,21,244	12003.45
Roma	Villa Doria Pamphili	41° 53.346′	12° 26.775′	20	187	2.5	360.0	43,21,244	12003.45

Lido di Ostia	Parco 10 giugno	41° 43.923′	12° 17.805′	1	20	0.9	10.3	90,000	8780.49
Napoli	Parco di Capodimonte	40° 52.036′	14° 14.947′	4	130	2.6	117.0	9,93,386	8490.4
Matera	Parco del Castello	40° 39.826′	16° 36.355′	401	80	1.1	6.3	60,556	9612.06
Potenza	Parco Montereale	40° 37.984′	15° 47.909′	819	40	0.8	10.0	66,405	6640.5
Cosenza	Villa Vecchia	39° 17.896′	16° 15.224′	238	3	0.7	37.2	67,910	1823.5
Palermo	Villa Malfitano	38° 07.400′	13° 20.482′	14	7	0.8	158.9	6,55,979	4128.77
Palermo	Villa Giulia	38° 06.806′	13° 22.537′	14	6.2	0.02	158.9	6,55,979	4128.77

44.3 ha ± 63.4). In the majority of small parks (16 out of 20 parks with surface < 10 ha), green areas in the 500-m buffer were larger than park size. The role of some park features (size, distance from the centre) and town features (latitude, longitude, altitude, n. of inhabitants, town size, population density) on richness of all bird and conservation concern species was investigated too. The analysis was repeated for some functional groups of species. In particular, bird species were subdivided in four ecological groups according to their feeding habitat (wetland, 20 species; open habitat, 38 species; aerial, 10 species; wood, 33 species) and four groups according to their nesting site (ground, 14 species; building, 17 species; tree, 36 species; bush, 13 species). Grouping was based on Cramp and Simmons (1977, 1980, 1983), Cramp (1985, 1988, 1992, 1993) and Cramp and Perrins (1993, 1994a, b). In the grouping based on nesting site, *Cuculus canorus* and *Muscicapa striata* (due to their not univocal choice) and wetland species were not considered. For the 12 cities including more than one study park (Table 21.1), the above-reported comparisons were carried out also between the most central and the most peripheral park (or the most central and the most peripheral 500-m buffer).

Pairwise comparisons were carried out with *T*-test for dependent samples. When data were not normally distributed (Kolmogorov–Smirnov test), in spite of data transformation attempts (Fowler and Cohen 1995), non-parametric tests were used (Wilcoxon matched-pairs test). Comparisons for the relative frequencies of single species between the parks and the 500-m buffers or between the most central and the most peripheral park were conducted by means of χ^2 test with Yates correction. Simple linear regressions were performed between some independent variables (i.e. those ones describing park and town features, see above) and the number of species per park of the following group: all species, all species of conservation concern, species belonging to different ecological groups, species of conservation concern belonging to different ecological groups and families of species of conservation concern. However, autocorrelation between variables might complicate the correct interpretation of results. Therefore, when more than one independent variable was significantly related to one of the considered parameters of bird community, a multiple regression analysis (forward stepwise) was carried out.

Since the use of the data of more parks for some towns might affect the results, we repeated the statistical analyses also with two 27-park subsamples. In both cases, only one park per each town with two to three study parks was considered: in the first subsample, the most central park was taken into account (27-park sample A); in the second subsample, the most peripheral park (27-park sample B). The majority of results obtained with samples A and B were similar to those obtained for the 40-park sample, with a reduction of significance levels most likely due to the smaller sample. Therefore we did not report them.

If not specified otherwise, values presented throughout are means ± SD or median with interquartile range (i.r.). Statistical analysis was performed with Statistica software package (StatSoft Inc. 1984–2000).

21.3   Results

On the whole in the 40 parks and surrounding 500-m buffer, 101 breeding species were recorded including 40 nonpasserines (39.6 %) and 61 passerines (60.4 %) (Table 21.2). In the parks, 94 species were observed among them; the most frequent (>30 parks) were in decreasing order *Sylvia atricapilla* (39 parks), *Parus major* (39), *Serinus serinus* (38), *Carduelis chloris* (38), *Turdus merula* (35), *Passer italiae* (34), *Fringilla coelebs* (34), *Carduelis carduelis* (34) and *Streptopelia decaocto* (32) (Table 21.2). In the 500-m buffers, 89 species were found among them; the most frequent were *Streptopelia decaocto* (38), *Corvus cornix* (37), *Apus apus* (36), *Sylvia atricapilla* (36), *Parus major* (36), *Passer italiae* (36), *Serinus serinus* (34), *Carduelis chloris* (34), *Delichon urbicum* (33), *Turdus merula* (33), *Carduelis carduelis* (31) and *Columba livia* var. *domestica* (30) (Table 21.2).

The mean number of species per park (25.6 ± 8.4) and in relative 500-m buffer (25.7 ± 8.9) was not significantly different ($t_{39} = 0.08$, $P = 0.93$). Moreover, the differences between the parks and relative 500-m buffers for the mean number of open-habitat species ($t_{39} = 1.22$, $P = 0.23$), the median number of wetland species in the parks ($Z_{40} = 0.41$, $P = 0.68$), the median number of ground-nesting species ($Z_{40} = 0.63$, $P = 0.53$), the mean number of bush-nesting species ($t_{39} = 1.40$, $P = 0.17$) and the mean number of tree-nesting species ($t_{39} = 1.41$, $P = 0.17$) were not significantly different (Figs. 21.2 and 21.3). However the mean number of woodland bird species was higher in the parks than in relative 500-m buffer ($t_{39} = 2.09$, $P = 0.04$), whereas the median number of aerial species ($Z_{40} = 4.49$, $P = 0.000007$) and the mean number of building-nesting species ($t_{39} = 5.39$, $P = 0.000004$) was lower in the parks (Figs. 21.2 and 21.3).

In three cases, the relative frequencies of single species were significantly higher in the 500-m buffers than in the parks: *Apus apus* ($\chi^2_1 = 11.96$, $P = 0.0005$), *Delichon urbicum* ($\chi^2_1 = 20.3$, $P = 0.0000006$) and *Corvus cornix* ($\chi^2_1 = 4.24$, $P = 0.039$) (Fig. 21.3). The relative frequency of *Picus viridis* was higher in the parks being on the verge of statistical significance ($\chi^2_1 = 3.72$, $P = 0.053$; Fig. 21.4).

In the 12 towns in which more parks were investigated, the differences between the most central and the most peripheral park for the (i) richness, (ii) the number of species of the four functional groups based on feeding habitat and (iii) the number of species of the four groups based on nesting site were not significant; in addition, the relative frequencies of single species did not significantly change between the two kinds of parks (data not shown). Similar results occurred for the 500-m buffers (data not shown).

Considering data of the 40 study parks, species richness was positively related to altitude, park size and number of inhabitants (Table 21.3). However, the relationship with park size was not significant in the multiple regression analysis ($t_{36} = 1.83$, $P = 0.08$). Other positive relationships were observed between population density and the number of open-habitat species; latitude and the number of aerial species; and altitude and the number of woodland species, ground-nesting

Table 21.2 Number of parks and relative 500-m buffers in which each species was recorded

	Parks	500-m buffer		Parks	500-m buffer
Cygnus olor	0	2	*Luscinia megarhynchos*	17	16
Anas platyrhynchos	12	9	*Phoenicurus ochruros*	7	10
Coturnix coturnix	0	2	*Phoenicurus phoenicurus*	18	19
Phasianus colchicus	8	9	*Saxicola torquatus*	3	5
Tachybaptus ruficollis	1	1	*Turdus merula*	35	33
Podiceps cristatus	1	0	*Turdus philomelos*	2	2
Phalacrocorax carbo	1	0	*Monticola solitarius*	3	7
Ardea cinerea	3	0	*Cisticola juncidis*	5	4
Ixobrychus minutus	2	0	*Cettia cetti*	7	10
Pernis apivorus	2	1	*Acrocephalus palustris*	2	1
Milvus migrans	2	1	*Acrocephalus scirpaceus*	1	0
Circus pygargus	0	1	*Acrocephalus arundinaceus*	2	0
Buteo buteo	4	5	*Hippolais polyglotta*	5	3
Accipiter nisus	2	7	*Sylvia cantillans*	0	1
Falco tinnunculus	11	14	*Sylvia atricapilla*	39	36
Falco naumanni	1	1	*Sylvia melanocephala*	9	11
Falco subbuteo	4	3	*Phylloscopus bonelli*	1	0
Falco peregrinus	0	3	*Phylloscopus sibilatrix*	0	1
Gallinula chloropus	15	15	*Phylloscopus collybita*	9	6
Fulica atra	3	0	*Regulus ignicapilla*	12	7
Charadrius dubius	1	1	*Regulus regulus*	2	2
Actitis hypoleucos	1	0	*Muscicapa striata*	27	26
Larus michahellis	2	5	*Aegithalos caudatus*	25	22
Columba palumbus	17	14	*Poecile palustris*	2	3
Streptopelia turtur	7	6	*Periparus ater*	6	9
Streptopelia decaocto	32	38	*Cyanistes caeruleus*	27	28
Columba livia domestica	24	30	*Parus major*	39	36
Psittacula krameri	4	3	*Sitta europaea*	12	8
Cuculus canorus	12	6	*Certhia brachydactyla*	15	11
Apus apus	21	36	*Remiz pendulinus*	2	2
Apus pallidus	2	7	*Oriolus oriolus*	6	5
Apus melba	0	3	*Lanius collurio*	2	2
Alcedo atthis	8	7	*Garrulus glandarius*	11	13
Merops apiaster	1	1	*Pica pica*	23	23
Upupa epops	9	4	*Corvus cornix*	29	37
Caprimulgus europaeus	1	1	*Corvus monedula*	9	14
Picus viridis	17	8	*Sturnus vulgaris*	26	29

Table 21.2 (continued)

	Parks	500-m buffer		Parks	500-m buffer
Dendrocopos major	21	17	*Sturnus unicolor*	1	0
Dendrocopos minor	3	1	*Passer italiae*	34	36
Jynx torquilla	19	13	*Passer montanus*	26	24
Galerida cristata	2	1	*Passer hispaniolensis*	2	2
Alauda arvensis	1	4	*Fringilla coelebs*	34	29
Ptyonoprogne rupestris	1	6	*Serinus serinus*	38	34
Hirundo rustica	18	22	*Carduelis chloris*	38	34
Delichon urbicum	12	33	*Carduelis carduelis*	34	31
Motacilla flava	1	1	*Carduelis cannabina*	1	1
Motacilla cinerea	8	8	*Loxia curvirostra*	1	1
Motacilla alba	18	21	*Coccothraustes coccothraustes*	1	0
Cinclus cinclus	1	1	*Pyrrhula pyrrhula*	2	0
Troglodytes troglodytes	20	12	*Emberiza cirlus*	2	2
Erithacus rubecula	15	10			
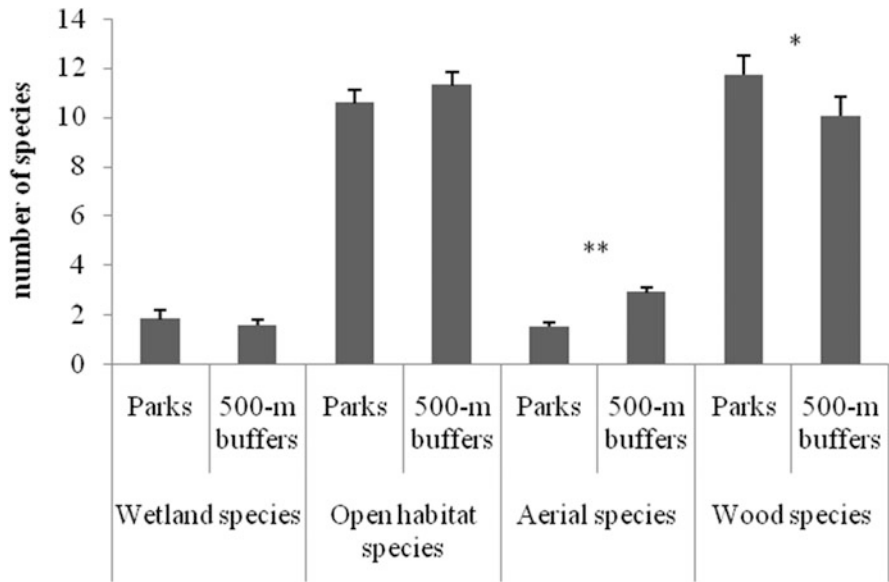
Fig. 21.2 Mean (+ SE) number of species for the wetland, open-habitat, aerial and wood groups in parks and in relative 500-m buffers. *P < 0.05; **P < 0.01
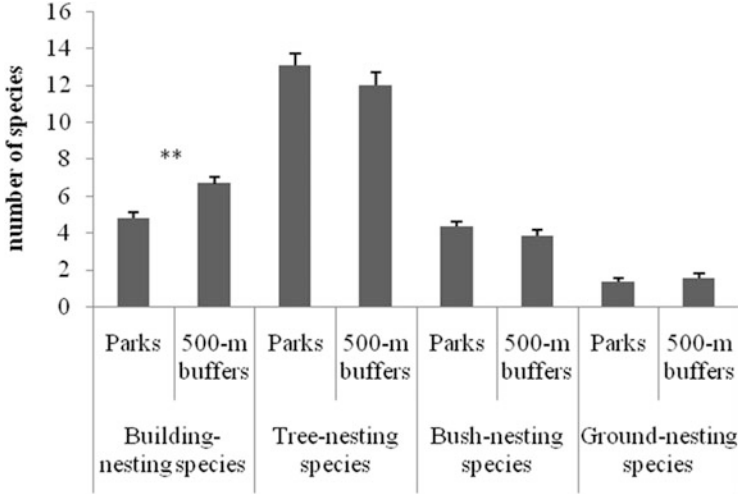
Fig. 21.3 Mean (+ SE) number of species for the ground-nesting, bush-nesting, tree-nesting and building-nesting groups in parks and in relative 500-m buffers. **$P < 0.01$
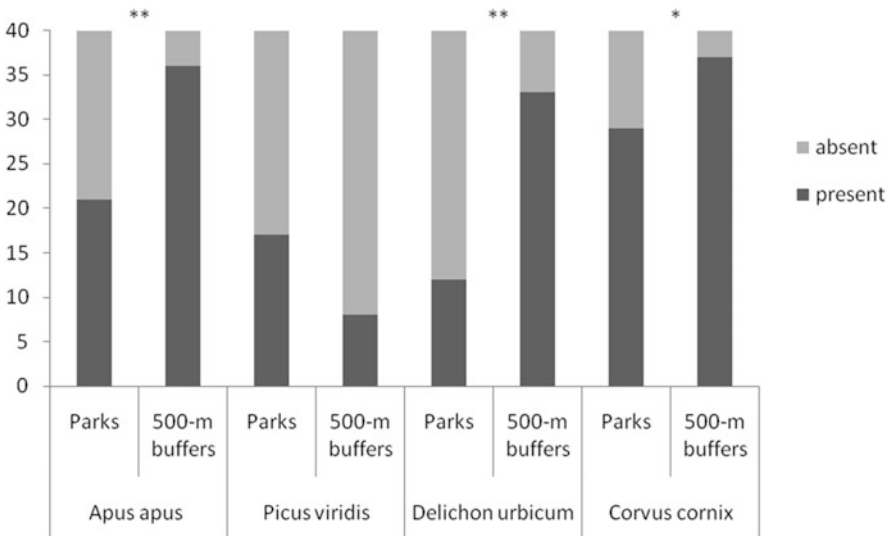
Fig. 21.4 Number of the 40 parks and 500-m buffers in which *Apus apus*, *Delichon urbicum*, *Corvus cornix* and *Picus viridis* were present.*$P < 0.05$; **$P < 0.01$

species and tree-nesting species (Table 21.3). The number of wetland species was positively related to park size, distance from the centre and number of urban inhabitants (Table 21.3). However, number of inhabitants did not enter in the model of multiple regression analysis. The number of bush-nesting species was positively related to town size and number of inhabitants and negatively to latitude

Table 21.3 Significant correlations between independent variables (see methods) and the number of species per parks of different bird groups

Relationships for parks					
Independent variable	Bird group	r(X,Y)	r²	t	P
Altitude	All species (richness)	0.48	0.23	3.38	0.0017
Park size	*All species (richness)*	0.34	0.11	2.19	0.0344
N. of inhabitants	All species (richness)	0.34	0.12	2.25	0.0300
Latitude	Aerial species	0.34	0.12	2.26	0.0297
Population density	Open-habitat species	0.38	0.14	2.50	0.0169
Altitude	Woodland species	0.58	0.34	4.42	0.0001
Park size	Wetland species	0.42	0.18	2.85	0.0071
Distance	Wetland species	0.35	0.13	2.34	0.0249
N. of inhabitants	*Wetland species*	0.34	0.12	2.23	0.0316
Latitude	*Bush-nesting species*	−0.31	0.10	2.03	0.049
Town size	*Bush-nesting species*	0.33	0.11	2.17	0.036
N. of inhabitants	*Bush-nesting species*	0.34	0.11	2.21	0.033
Altitude	Ground-nesting species	0.37	0.14	2.45	0.019
Altitude	Tree-nesting species	0.55	0.31	4.09	0.0002
Town size	*Building-nesting species*	0.41	0.17	2.74	0.009
N. of inhabitants	Building-nesting species	0.46	0.21	3.17	0.003
Population density	*Building-nesting species*	0.49	0.24	3.45	0.0014
Relationships for 500-m buffers					
Altitude	Arial species	0.42	0.18	2.86	0.007
Longitude	Woodland species	−0.32	0.10	−2.10	0.043
Town size	Wetland species	0.33	0.11	2.12	0.040
Altitude	Building-nesting species	0.32	0.10	2.09	0.044

In italic, the not significant relationships in the multiple regression analysis

(Table 21.3). However, only town size entered in the model of multiple regression analysis, but the relationship was not significant ($t_{36} = 1.93$, $P = 0.06$). The number of building-nesting species was positively related to town size, number of inhabitants and population density (Table 21.3). However, only town size and number of inhabitants entered in the model of multiple regression analysis, but the relationship was significant exclusively for number of inhabitants ($t_{36} = 2.06$, $P = 0.047$). Considering data of the 500-m buffers, positive relationships were observed between town size and the number of wetland species and altitude and the number of both aerial species and building-nesting species (Table 21.3). Conversely, a negative relationship was observed between longitude and the number of woodland species (Table 21.3).

On the whole in the 40 parks and surrounding 500-m buffer, 29 breeding species of conservation concern were recorded including 16 nonpasserines (55.2 %) and 13 passerines (44.8 %) (Table 21.4). Out of the 29 species, 25 were observed in the parks and 26 in the 500-m buffers (see Table 21.2). Mean number of species of conservation concern per park (5.7 ± 2.8) and in relative 500-m buffer (6.0 ± 2.9) were not significantly different ($t_{39} = 0.77$, $P = 0.44$). In addition, the differences

Table 21.4 Species of conservation concern recorded in the 40 study parks

Family	Species	Annex I Dir. 2009/147/CE	SPEC
Phasianidae	*Coturnix coturnix*	–	3
Ardeidae	*Ixobrychus minutus*	X	3
Accipitridae	*Pernis apivorus*	X	–
Accipitridae	*Milvus migrans*	X	3
Accipitridae	*Circus pygargus*	X	–
Falconidae	*Falco tinnunculus*	–	3
Falconidae	*Falco naumanni*	X	1
Falconidae	*Falco peregrinus*	X	–
Scolopacidae	*Actitis hypoleucos*	–	3
Columbidae	*Streptopelia turtur*	–	3
Alcedinidae	*Alcedo atthis*	X	3
Meropidae	*Merops apiaster*	–	3
Upupidae	*Upupa epops*	–	3
Caprimulgidae	*Caprimulgus europaeus*	X	3
Picidae	*Picus viridis*	–	2
Picidae	*Jynx torquilla*	–	3
Alaudidae	*Galerida cristata*	–	3
Alaudidae	*Alauda arvensis*	–	3
Hirundinidae	*Hirundo rustica*	–	3
Hirundinidae	*Delichon urbicum*	–	3
Turdidae	*Phoenicurus phoenicurus*	–	2
Turdidae	*Monticola solitarius*	–	3
Sylviidae	*Phylloscopus bonelli*	–	2
Sylviidae	*Phylloscopus sibilatrix*	–	2
Muscicapidae	*Muscicapa striata*	–	3
Paridae	*Poecile palustris*	–	3
Laniidae	*Lanius collurio*	X	3
Passeridae	*Passer montanus*	–	3
Fringillidae	*Carduelis cannabina*	–	2

Species included in the Annex I of EC Directive 2009/147/CE and/or in the categories 1–3 of the Species of European Conservation Concern (SPEC; BirdLife International 2004) were considered

between the parks and relative 500-m buffers for the median number of species of conservation concern belonging to the wetland, open-habitat, woodland, ground-nesting, tree-nesting and bush-nesting species were not significantly different (data not shown). However in the parks, as compared to the relative 500-m buffers, the median number of aerial species of conservation concern (1.0, i.r. = 1.0 versus 2.0, i.r. = 1.0; $Z_{40} = 3.85$, $P = 0.0001$) and the mean number of building-nesting species of conservation concern (1.8 ± 1.1 versus 2.6 ± 1.3; $t_{39} = 3.96$, $P = 0.0003$) were lower. The differences between the parks and relative 500-m buffers for the median number of species of conservation concern grouped per family were usually not significant except the median number of Picidae species that was higher in the parks (1.0, i.r. = 1.0) than in relative 500-m buffer (0, i.r. = 1.0; $Z_{40} = 2.43$, $P = 0.02$), and

the median number of Hirundinidae species that was lower in the parks (1.0, i. r. = 1.0) than in relative 500-m buffer (1.5, i.r. = 1.0; $Z_{40} = 3.74$, $P = 0.0002$).

In the 12 towns in which more parks were studied, the differences between the most central and the most peripheral park for the number of species of conservation concern and among them for those ones belonging to the four functional groups of species based on feeding habitat and the four groups based on nesting site were not significant; in addition the relative frequencies of single species or grouped in families did not significantly change between the two kinds of parks (data not shown). Similar results occurred for the 500-m buffers (data not shown).

Considering data of the study parks, the number of species of conservation concern was positively related to altitude, distance from the centre and population density (Table 21.5). However, the relationship with distance from the centre was not significant in the multiple regression analysis ($t_{36} = 1.39$, $P = 0.17$). The number of open-habitat species of conservation concern was positively related to distance from the centre, population density and number of inhabitants (Table 21.5). However, only the relationship with population density ($t_{36} = 3.38$, $P = 0.002$) was significant in the multiple regression analysis. Another positive relationship was observed between altitude and the number of woodland species of conservation concern (Table 21.5). The number of wetland species was positively related to park size and number of inhabitants (Table 21.5). However, both relationships were not significant in the multiple regression analysis ($t_{36} = 1.71$, $P = 0.10$ and $t_{36} = 1.25$, $P = 0.22$, respectively). The number of tree-nesting species was positively related to altitude and population density (Table 21.5). However, only altitude entered in the model of multiple regression analysis, but the relationship was not significant ($t_{36} = 1.65$, $P = 0.11$). The number of building-nesting species was positively related to town size, number of inhabitants, population density and distance from the centre (Table 21.5). However, only number of inhabitants entered in the model of multiple regression analysis, but the relationship was not significant ($t_{36} = 1.33$, $P = 0.19$). The number of Falconidae species of conservation concern was negatively related to latitude and positively related to distance from the centre, population density, town size and number of inhabitants (Table 21.5). However, number of inhabitants did not enter in the model of multiple regression analysis, while the relationship with population density was not significant ($t_{36} = 1.65$, $P = 0.11$). The number of Picidae species of conservation concern was positively related to distance from the centre and population density (Table 21.5). However, both relationships were not significant in the multiple regression analysis ($t_{36} = 1.51$, $P = 0.14$ and $t_{36} = 1.09$, $P = 0.28$, respectively). The number of Turdidae species of conservation concern was positively related to latitude and altitude (Table 21.5). Both relationships were confirmed in the multiple regression analysis (data not shown). Considering data of the 500-m buffers, positive relationships were observed between latitude and the number of woodland species of conservation concern and altitude and the number of Turdidae species (Table 21.5). The number of Falconidae species of conservation concern was negatively related to latitude and positively related to longitude (Table 21.5). However, longitude did not enter in the model of multiple regression analysis.

Table 21.5 Significant correlations between independent variables (see methods) and the number of species per parks of different bird groups

Independent variable	Bird group	r(X,Y)	r^2	t	P
Altitude	All conservation species	0.37	0.14	2.48	0.0178
Distance	*All conservation species*	0.39	0.15	2.63	0.0122
Population density	All conservation species	0.45	0.20	3.07	0.0039
Distance	*Open-habitat conservation species*	0.33	0.11	2.13	0.0401
Population density	Open-habitat conservation species	0.45	0.20	3.08	0.0038
N. of inhabitants	*Open-habitat conservation species*	0.31	0.10	2.02	0.0499
Altitude	Woodland conservation species	0.41	0.17	2.77	0.0087
Park size	*Wetland conservation species*	0.36	0.13	2.37	0.0231
N. of inhabitants	*Wetland conservation species*	0.31	0.10	2.03	0.0492
Altitude	*Tree-nesting conservation species*	0.55	0.31	4.09	0.0002
Population density	*Tree-nesting conservation species*	0.32	0.10	2.10	0.042
Distance	*Building-nesting conservation species*	0.46	0.21	3.22	0.0026
Town size	*Building-nesting conservation species*	0.44	0.19	3.02	0.0045
N. of inhabitants	*Building-nesting conservation species*	0.51	0.26	3.68	0.0007
Population density	*Building-nesting conservation species*	0.65	0.42	5.38	0.000005
Latitude	Falconidae conservation species	−0.36	0.13	−2.35	0.0238
Distance	Falconidae conservation species	0.51	0.26	3.61	0.0009
Town size	Falconidae conservation species	0.59	0.35	4.49	0.0001
N. of inhabitants	*Falconidae conservation species*	0.60	0.36	4.60	0.00005
Population density	*Falconidae conservation species*	0.60	0.36	4.64	0.00004
Distance	*Picidae conservation species*	0.40	0.16	2.71	0.0101
Population density	*Picidae conservation species*	0.36	0.13	2.37	0.0232
Latitude	Turdidae conservation species	0.32	0.10	2.05	0.0469
Altitude	Turdidae conservation species	0.42	0.18	2.86	0.0068
Relationships for 500-m buffers					
Latitude	Woodland conservation species	0.36	0.13	2.40	0.021
Latitude	Falconidae conservation species	−0.48	0.23	−3.33	0.002
Longitude	Falconidae conservation species	0.36	0.13	2.42	0.021
Altitude	Turdidae conservation species	0.57	0.32	4.22	0.0001
Latitude	Tree-conservation-nesting species	0.36	0.13	2.35	0.024

In italic, the not significant relationships in the multiple regression analysis

21.4   Discussion

Urbanisation is considered one of the strong forces causing biotic homogenisation and the loss of biodiversity leading to the reduction of populations of specialist and native species and to the expansion of generalist and exotic species (Blair 2001; Jokimäki and Kaisanlahti-Jokimäki 2003; Devictor et al. 2008; Sorace and Gustin 2008; van Heezik et al. 2008). Since data on exurban areas were not available for our data sample, we did not evaluate the entire "homogenisation effect" due to urbanisation. In any case, some our results seem to support the observation that urbanisation homogenises breeding bird communities. In particular, we observed few differences between Italian parks and surrounding 500-m buffer and reduced effects of park size and distance from the centre on the examined parameters of breeding bird communities (richness, number of species of conservation concern, frequency of some functional groups of species). Moreover, although based on a small sample (12 towns), no significant differences were highlighted between central and peripheral parks or central and peripheral 500-m buffers.

The woodland bird species was the only group that showed higher frequency in parks than in the 500-m buffers. Urban forestry sites can connect urban areas with the natural landscape promoting town penetration by several species (Miller 2005; Croci et al. 2008, Ortega-Álvarez and MacGregor-Fors 2009; Caula et al. 2010, 2014). In particular, urban parks, when managed for wildlife, have the potential to support species of conservation interest (Sorace and Gustin 2010; Lerman et al. 2014). Among them, in the present study, two woodpeckers of conservation concern (*Picus viridis*, *Jynx torquilla*) were more recorded in the study parks than in surrounding areas. Given the sensitivity of woodpeckers to habitat fragmentation (Hinsley et al. 1995; Frank and Battisti 2005), they should be scarcely present in towns. However, a limiting factor for woodpeckers is the availability of mature and decaying trees for feeding and nesting (McCollin 1993). In urban parks and in private gardens, the availability of mature and old trees may be higher than in the nearby countryside (Nilsson and Cory 2009 in Heyman 2011; Sorace and Gustin 2009; Carpaneto et al. 2010, but for dead wood see Hedblom and Söderström 2008). The habitat characteristics (the presence of mature trees, habitat heterogeneity and availability of insects) that satisfy the requirements of some species such as *Picus viridis* and *Jynx torquilla* (Cramp 1985; Südbeck 1994; Tomiałojć 1994) tend to disappear in areas subject to intensive agriculture. Urban parks and gardens might serve as refuges for these species, provided that they preserve such characteristics (see also Mörtberg and Wallentinus 2000; Fernández-Juricic and Jokimäki 2001; Marzluff 2001; Daniels and Kirkpatrick 2006; Sorace and Gustin 2010). According to Hedblom and Söderström (2010), the importance of urban woodland cover for some forest-breeding birds in towns increased when peri-urban woodland cover decreased, so to maintain populations of specialised forest birds in towns of southern and western Europe placed in farmland landscapes (with little peri-urban woodland) is most important to preserve any remaining woodlands in urban environments. In addition, large and old trees should be protected because they are of

pivotal value in urban areas as keystone structures for bird species and, in general, wildlife (Harper et al. 2005; Carpaneto et al. 2010; Stagoll et al. 2012; Lerman et al. 2014). However, our results only partially support the suitability of parks for all woodland species. In particular, the fact that in the comparison between parks and relative buffers we did not find significant effects for the group of tree-nesting species and for most woodland bird species might be due to the presence of tree rows and green areas in the urban matrix around the parks that reduce fragmentation effects (Marzluff and Erwing 2001; White et al. 2005; Suarez-Rubio and Thomlinson 2009; Chiari et al. 2010; Litteral and Wu 2012).

For species belonging to other groups (open-habitat and wetland species, ground- and bush-nesting species, raptors), the presence of natural spaces is usually not sufficient to occupy urban sites. According to Sorace and Gustin (2010), the ecological requirements of most species of conservation concern are often incompatible with urban sprawl. In the present study, these species were very scarcely observed and showed in the parks a frequency similar to the surrounding areas. Large- and medium-sized raptors require large areas of contiguous habitat (Newton 1979; Phillips et al. 1984; Hostetler 2001; Marzluff 2001; Chace and Walsh 2006; including sectors with reduced human disturbance, see, e.g. Møller 2012), which urban areas, even in the presence of careful biodiversity protection efforts, cannot support. Conservation efforts for such species should focus on non-urban areas (but see Solonen 2008 for the presence in town of *Accipiter gentilis*, a forestal species). Towns offer few opportunities also for species linked to rural environments (see also Filippi-Codaccioni et al. 2008; Caula et al. 2010) and for species nesting and/or feeding on the ground or in low scrub (Luniak 1981; Marzluff 2001; Lim and Sodhi 2004). Although the decline of galliforms and passerines (Alaudidae, Passeridae, Fringillidae, Emberizidae) of farmland and open habitats (Tucker and Evans 1997; Robinson and Sutherland 2002; BirdLife International 2004) is attributed largely to agricultural intensification (Donald et al. 2001, Newton 2004, Vickery et al. 2004), urban growth may constitute a further dramatic threat for these species (Filippi-Codaccioni et al. 2008; Caula et al. 2010; Sorace and Gustin 2010).

The present investigation confirms that residential areas is a favourable environment for some species that feed on flying insects and, above all, place their nest on buildings (Emlen 1974; Allen and O'Conner 2000; Marzluff 2001). Several species such as *Falco tinnunculus*, swifts, *Columba livia*, *Passer domesticus* and *Sturnus vulgaris* respond positively to building features that provided nesting and resting places (Clergeau et al. 1998; Evans et al. 2009; Latta et al. 2013; Mikula et al. 2013). Therefore, the building features promoting the settlement of species of conservation concern such as *Falco naumanni*, *F. tinnunculus*, *Delichon urbicum*, *Monticola solitarius* and *Passer montanus* should be preserved or increased in urban areas. Besides the building-nesting species, we found that, as expected, the built areas favour also urban exploiters such as *Streptopelia decaocto* and generalist species such as *Corvus cornix* (McKinney 2002, 2006; Bonier et al. 2007; Sorace and Gustin 2008, 2009; Luck and Smallbone 2010).

In the present study, the town size (or variables related such as number of inhabitants or population density) seems to produce higher effects than park size

and distance from the centre on the investigated parameters. The positive relationship between town size and richness of species was described and might be steeper in towns than for samples taken within the surrounding landscape or similar in cities and surrounding natural environments (MacGregor-Fors et al. 2011; Pautasso et al. 2011; Ferenc et al. 2014). Major town size might increase the spatial heterogeneity of habitats leading to a higher richness of species (Cadenasso et al. 2007; Ferenc et al. 2014), and this might partially explain our results.

Several studies reported a positive relationship between park size and richness of species that was clearly more marked as compared to our findings (e.g. Sarrocco et al. 2002; Evans et al. 2009; Bräuniger et al. 2010; Strohbach et al. 2013). However, the relationship may be modified by factors, such as human-induced disturbance, recreational use and seasonal variation (Fernandez-Juricic 2000; Caula et al. 2008, 2014; but see Murgui 2007, 2010) as well as the features of surrounding built matrix (Oliver et al. 2011; Latta et al. 2013; Nielsen et al. 2014). In addition, some studies highlighted that park age (or age of trees present inside it) may be a factor affecting mostly the richness of species more than park size and insulation degree (Fernandez-Juricic 2000; Miller et al. 2003; Biaduń and Zmihorski 2011).

Although the present study was not specifically addressed to investigate the effects of geographic variables (altitude, latitude, longitude), the results highlighted a more remarkable effect of altitude on the frequency of all species, including those ones of conservation concern, in parks than in relative 500-m buffers. The results obtained for latitude were less clear since significant relationships were observed for different groups either in parks or in relative 500-m buffers (except for the relationships with the frequency of Falconidae of conservation concern recorded in both environments), and the number of significant relationships was similar in parks and in relative 500-m buffers. Previous studies showed that the effect of geographic variables on urban bird communities can be reduced in more urbanised sectors (Jokimäki and Suhonen 1993; Jokimäki et al. 1996; Clergeau et al. 2001; McKinney 2006; Luck and Smallbone 2011; Ferenc et al. 2014). Sorace and Gustin (2008) observed that the similarity indices between towns were negatively correlated with differences in both latitude and altitude between towns in each urban sector, including town centres. However, according to the results obtained for the latitude variable by Clergeau et al. (2006), these authors showed that the values of the regression coefficient decreased in the more urbanised sectors.

In conclusion, Italian town parks and their surrounding built-up areas show similar avifauna. Parks appear to have a positive influence for the presence of woodland bird species and woodpeckers of conservation concern, whereas for some decreasing urban specialists, the built areas have a critical value for their settlement. It is important to observe that the study on the effects of parks on birds in Italian towns should be repeated with a new data sample based on species abundance rather than the simple recording of species presence since the two approaches might emphasise different results (Sorace and Gustin 2008).

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Chapter 22
Indicators of the Effects of the Urban Greening on Birds: The Case of Barcelona

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Javier Quesada, and Xavier Ferrer**

Abstract Building and maintaining an urban green infrastructure, which can be understood as a network of urban parks, private gardens or forest areas, can potentially contribute to reverse the trend of biodiversity loss. In this context, developing indicators of the changes produced by green infrastructures on urban biodiversity represents a task of particular interest for planning and governance approaches. The results of long-term bird monitoring schemes in many cities, mainly based on volunteer programmes, may provide a good opportunity to obtain robust data on the spatial patterns and temporal trends of species populations. In addition, recent development of multispecies indicators can now be implemented to make use of common bird monitoring datasets with the aim to generate robust

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policy relevant evaluation tools. In this chapter we show a procedure to track the effects of urban greening on birds using common bird monitoring data from the city of Barcelona (north-east Iberian Peninsula). Essentially, the proposed approach requires to quantify the species' response to the green infrastructure at a population level and to integrate all this information in combined indicators of the effect of urban greening. Using this approach we developed a first indicator to track temporal changes on bird populations linked to the greening and a second indicator to determine the areas of the city in which the level of development of the green infrastructure is already having a positive effect on biodiversity.

Keywords Indicators • Bird monitoring • Breeding bird atlas • Urban planning • Green infrastructure

22.1 Introduction

22.1.1 The Challenge of the Urban Green Infrastructure

Urban areas are composed of a combination of built-up surfaces and patches of vegetation, often named grey and green infrastructures, respectively. After a long period of developing intensively grey infrastructures, in 2013, the European Commission adopted a Green Infrastructure Strategy to promote its development both in urban and rural areas (EC 2013). This strategy defines the green infrastructure as a strategically planned network of natural and seminatural areas designed and managed to deliver a wide range of ecosystem services (TEEB 2011). The urban green infrastructure plays a major role in densely populated areas since it is not only a natural capital itself but also an essential component to help reducing the fragmentation of the ecosystems (Benedict and McMahon 2006; see also Goddard et al. 2016; Heyman et al. 2016; Meffert 2016).

Developing a green infrastructure in urban regions implies accounting for a matrix of different components of vegetation in and on the edge of cities and towns, either cultivated or spontaneously developed (e.g. remnants of natural vegetation such as forests or shrublands, riparian or coastal vegetation, urban parks, wastelands, tree plantations, farmland, house gardens, green roofs, green walls and scattered shrubs and trees). Greening cities and towns usually represents a challenge since mentalities favouring grey infrastructures for immediate and single purposes should be at least partially shifted towards principles aimed at protecting and enhancing natural processes from which human societies get different ecosystem services. One of the contrasted differences between the grey and the green approach is that the outcomes of the latter deeply depend on the interaction between human management and natural processes.

Undoubtedly biodiversity is one of the elements more intrinsically linked to the natural processes occurring in the green infrastructure, and urban greening represents an immense opportunity for restoring biodiversity and its associated functional traits, as expressed by the Goal D of the Strategic Plan for Biodiversity

2011–2020 (SCBD 2014). Within this context, there is an evident interest in implementing indicators to track if the development of the urban green infrastructure is actually unfolding positive responses in biodiversity, and this unequivocally requires an appropriate monitoring for at least some of their biological components.

22.1.2 Monitoring Urban Birds for Developing Indicators

Monitoring biodiversity is not a trivial task either in natural or human-modified environments. The complexity of biodiversity is so high that there is a clear need of developing essential biodiversity variables (EBV) to track the effects of environmental change in organisms (Pereira et al. 2013). Developing EBVs is crucial for a robust assessing of progress towards the 2020 targets of the convention on biological diversity. They should be sensitive to change over time, of relevance to the broader community (including scientists/researchers, governments, decision/policymakers, assessment bodies, conservation professionals and conventions), and feasible in terms of monitoring. One of the examples of EBV is provided by data from population abundance for species sets representative of some taxa (Pereira et al. 2013).

Birds represent the most popular taxonomic group for delivering indicators of population change in the framework of EBVs. In Europe, birds account for almost 40 % of all species monitoring schemes (EuMon 2015). To understand the prominence of birds in this context, it should be taken into account the ease with which they can be monitored, the involvement of amateur ornithologists in citizen science projects, the existence of scientifically robust methods for monitoring their populations and a general acceptance of their use as indicators of environmental change (Furness and Greenwood 1993; Gregory et al. 2008).

Bird monitoring projects have been particularly successful in providing relevant indicators to track the loss of biodiversity in farmlands (e.g. Gregory et al. 2005), and the European Union has adopted the farmland bird indicator as a structural indicator, a sustainable development indicator and a baseline indicator for monitoring the implementation of the rural development regulation under the common agricultural policy (EEA 2015). However, indicators based on urban bird data have been poorly developed, and their acceptance as policy relevant tools in Europe is still an ongoing process. This could be at least partially explained by the lack of unambiguous messages regarding what urban bird indicators actually indicate in the framework of planning and conservation strategies. Many urban bird indicators actually show trends composed of species that usually live in cities, towns and villages, with more or less strict approaches on the species urban-related ecology depending on each case (e.g. Zbinden et al. 2005; Sudfeldt et al. 2013; SEO/BirdLife 2014). In general urban bird indicators have been developed at a country level, and only in few cases, the focus has been a particular metropolitan area (e.g. Herrando et al. 2012; see van Heezik and Seddon 2016). All these methodological approaches represent interesting experiences to inform on the

population changes for a number of species associated to urban habitats, but cannot provide unambiguous information on the degree of achievement of the goals of strategies aimed at improving biodiversity by means of urban greening. The evaluation of the process of urban greening should be definitely conducted by means of a species set closely related to urban green habitats and not to man settlements.

22.1.3   Indicators to Track the Effect of Urban Greening on Birds

The development of indicators capable to specifically track the response of birds to urban greening should be situated within the general context of indicators of "pressure" upon biodiversity (Butchart et al. 2010). Ideally, these indicators should not track the magnitude of the pressure itself (urban greening) but its direct effect on biodiversity (population response to urban greening), thus being more informative than indirect data based on implicit assumptions linking the environmental change and the response of biodiversity (Collen and Nicholson 2014).

Within this framework, Gregory et al. (2009) generated a methodology to evaluate the impact of climate change on bird populations by means of the indicator of climatic impact on bird populations. More recently, Herrando et al. (2014) adapted this methodology to develop indicators of the impact of land abandonment in a Mediterranean region, thus broaden the former methodological approach to land use changes. In this study we develop multispecies indicators to evaluate the effects of the green infrastructure on bird populations both on a temporal and spatially explicit basis. The experience is implemented in the city of Barcelona, where the existence of an active policy to improve the urban green infrastructure and the wealth of bird monitoring data represent an ideal framework to develop these indicators.

The election of birds for this particular purpose is obviously associated to the availability of monitoring data and the development of technical approaches to generate indicators. Nevertheless, birds have also their intrinsic value within the study context of urban greening since this taxonomic group may contribute some of the ecosystem services recognised by the UN Millennium Ecosystem Assessment (Whelan et al. 2008). As in any other terrestrial ecosystem, regulation services such as control of insect populations and plant seed dispersal can be important elements in green urban environments. Finally, the cultural role of birds (spiritual enrichment, cognitive development, reflection, recreation and aesthetics) is particularly important in these green urban areas, where citizens have regular contact to this conspicuous biodiversity component.

22.2 A Study Case in Barcelona

22.2.1 Introduction to the Green Infrastructure in Barcelona

Barcelona is located on the shore of the Mediterranean Sea in the north-east of the Iberian Peninsula (latitude, 41°23′3″N, longitude, 2°10′34″E). With a total of 1,602,386 inhabitants and a size of 10,216 ha, this is a very dense metropolis (157 inhabitants per ha in 2014), and consequently, it is mainly a grey city (Fig. 22.1). The extent of water masses (blue infrastructure) within the city is
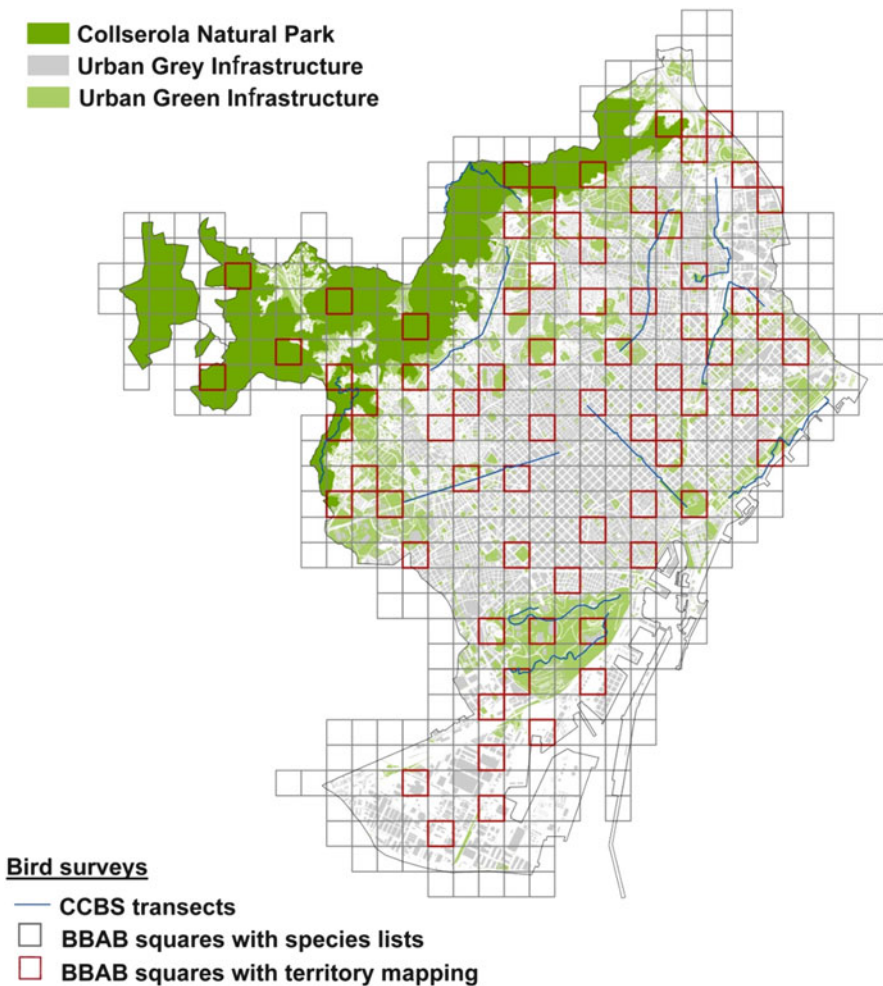
Fig. 22.1 Location of the green and grey infrastructure and of the bird surveys carried out in Barcelona: Catalan common bird survey (CCBS) and breeding bird atlas of Barcelona (BBAB)

very low. Barcelona as a compact city provides only 18 m^2 green space per inhabitant (Barcelona City Council Statistical Yearbook 2014). This low value, otherwise usual in Mediterranean cities, represents a poor green space allocation per capita (Fuller and Gaston 2009). The total green space of Barcelona amounts for 2,911 ha, mostly located in the Collserola Natural Park (1,795 ha), a peri-urban natural green space placed in the Catalan Coastal Mountain Chain. The city green extends over 1,116 ha (7 m^2 of green space per inhabitant) mainly located in two-step hill systems surrounded of built-up areas, i.e. Montjuïc (251 ha) and Els Tres Turons (123 ha). As Baró et al. (2014) showed, this low level of green space is partly counterbalanced by the high number of trees on streets, accounting for 161,423 specimens in 2013 from 150 species, mainly *Platanus hispanica* and *Celtis australis* (Barcelona City Council Statistical Yearbook 2014). This represents a ratio of 100 street trees per 1,000 inhabitants, a high value compared to other European cities which mostly range between 50 and 80 street trees per 1,000 inhabitants (Pauleit et al. 2002). The largest part of the green infrastructure is relatively recent (c. 1980), with some noticeable exceptions such as the first urban park in the city, Parc de la Ciutadella (built in 1872), and a few more from the early twentieth century as El Laberint d'Horta. As a result, most of trees found in city parks are relatively young.

22.2.2 The Strategy of Green Infrastructure and Its Link to Bird Biodiversity

The Barcelona Green Infrastructure and Biodiversity Plan falls in line with the 2020 EU Biodiversity Strategy and the strategies laid out along these lines by the UN by means of the Aichi targets for 2011–2020. This plan envisages the city in 2050 as a place where nature and urbanity interact and enhance one another by ensuring the connectivity of greenery (Barcelona City Council 2015). It is essentially defined by two goals: increasing the connectivity of green infrastructure and renaturalising the city. Green corridors are the tool aimed at achieving connectivity, defined as belts with abundant vegetation where pedestrians and cyclists must be given priority. The renaturalisation of the city is expressed by action points in "opportunity areas" which vary in terms of size and type: unoccupied plots, roofs, balconies and generally speaking all areas that can potentially keep flora and fauna (Barcelona City Council 2015). The plan is organised in ten strategic lines and the urban bird projects fit into mainly number 1 *preserving the city's natural heritage* and 7 *improving knowledge for the management and conservation of green infrastructure and biodiversity* and more indirectly to others.

22.2.3 Bird Monitoring Strategy in Barcelona

Bird monitoring is included in the action plan of the Agenda 21, the local road map for working in accordance with sustainable development principles (Barcelona City Council 2013). Two monitoring programmes are implemented in close collaboration among the Barcelona Local Council, the University of Barcelona and the Catalan Ornithological Institute, organisations that promote the monitoring of urban birds in the city. In particular, these main programmes are the Barcelona's nodule of the Catalan Common Bird Survey (CCBS; known also by its Catalan acronym SOCC) and the Breeding Bird Atlas of Barcelona (BBAB; for a review on urban bird atlases see Luniak 2016). While the main objective of the first is to determine temporal patterns of change, the second aims to determine spatial patterns. These two projects are based on citizen science; people actively participate in fieldwork following basic rules designed to facilitate their collaboration and ensuring minimum standards of robustness for subsequent data analyses. In total, nine ornithologists participate in the CCBS every year, while a total of 318 people have collaborated in the BBAB fieldwork during the years 2012–2014. Recruitment of volunteers is done by the Catalan Ornithological Institute thanks to the support for coordination provided by the regional and local governments. In general urban areas such as Barcelona are not very attractive to ornithologists, but the number of inhabitants interested in the discipline is enough to cover CCBS requirements. For the BBAB, massive dissemination of the project allowed to achieve a high number of participants in the extensive surveys, but territory mapping could not be covered exclusively on a volunteer basis, and five professionals were hired to cover some other additional squares (see below for details on these two methodological protocols). As a whole, these cooperative social projects do not only provide crucial EBVs but also improve the citizen awareness and enjoyment of urban nature.

The CCBS is an ongoing monitoring project that is based on a network of 3 km line transects sampled two times in spring (Herrando et al. 2012). Its coverage remains constant in Barcelona since 2005, with 11 transects (Fig. 22.1). The CCBS is the chosen programme to derive metrics to track the temporal change of urban birds, both native and alien (Barcelona City Council 2013). The CCBS feeds key information for the evaluation of the Barcelona Green Infrastructure and Biodiversity Plan deriving indicators to assess how birds are changing along time as the plan progressively unfolds.

The BBAB attempts to determine the distribution of breeding birds in Barcelona (under publication). For BBAB the municipality is subdivided in 528 500 × 500 m squares, and each of these squares is visited twice during the breeding season (30 min each visit) to generate species lists (Fig. 22.1). These extensive surveys across all the squares of Barcelona are complemented by a more intensive survey in a sample of 69 randomly selected squares to derive detailed information on birds' location. This second type of survey is based on the territory mapping method (Bibby et al. 2000), and its main aim is having a robust dataset to generate fine-grained maps (100 × 100 m resolution) based on niche-based models (Guisan and

Zimmermann 2000). The main project objectives are also closely related to the development of green infrastructure because it allows determining the areas of the city in which bird biodiversity is responding to the targets of the Barcelona Green Infrastructure and Biodiversity Plan.

22.2.4 Assessment of Species' Response to Urban Greening

To develop the indicators of the effect of urban greening on birds, we quantified the responses of bird species to this process as the change in their occurrence in an ecological gradient ranging from urban areas with high coverage of green surface to urban areas with high coverage of grey surface. This statistical analysis was the basis for the selection of the set of species to be included in the indicators and of the relative contribution of each selected species to the final index.

To quantify the species' responses to urban greening, we used the data gathered for the intensive surveys carried out in the territory mapping in a sample of 500×500 m squares. Within each of these squares, we randomly selected five noncontiguous 100×100 m squares and determined the bird species occurrence from the map location of individual birds in field observations. A total of 140 100×100 m squares were selected for this purpose. Information on the area of green and grey infrastructures in each square was obtained from high-resolution land use maps (Barcelona City Council 2012).

We carried out generalised linear models (GLM) to determine the species response to urban greening. GLM were run with a binomial error distribution and a logit link function; the occurrence of the species (0-1) was used as the response variable and the percentage of a green surface as the independent factor. We selected species with significant models at $p < 0.1$ and then used the obtained model parameter as an estimation of their affinity to the focal gradient. These statistical analyses were carried out using the R package (R Development Core Team 2008).

Gregory et al. (2009) provided a new approach to determine the impact of climate change on birds by assessing the overall population response to the set of species positively (+) affected by climate change and that of the populations negatively (−) affected by this driving force. A few years later, Herrando et al. (2014) developed a similar methodological approach to assess the impact of land use changes on birds and applied it to the process of land abandonment and its impact on Mediterranean bird populations. In both cases the number of species in the two sets (+ and −) sufficed to implement multispecies indices. In contrast, in this study, only the set of 18 species positively affected by urban greening were included in the analytical approach (Table 22.1). Only two species (the feral pigeon and the house sparrow) showed a negative response to this environmental change, i.e. their occurrences were negatively related to the amount of green infrastructure (−). Irrespective of its position on the gradient, the particular case of the feral pigeon is useful to illustrate the typical example of nonvalid species in this indicator

Table 22.1 Bird species whose occurrence within the urban area was significantly associated with the amount of green infrastructure

Latin name	English name	Estimate	No. of squares	Trend
Streptopelia decaocto	Collared dove	0.008$^+$	284	(+2 %)
Cyanistes caeruleus	Blue tit	0.012$^+$	148	(+5 %)
Serinus serinus	Serin	0.013*	272	−5 %
Carduelis carduelis	Goldfinch	0.013$^+$	182	(−3 %)
Pica pica	Magpie	0.015**	292	0 %
Turdus merula	Blackbird	0.016**	266	−5 %
Carduelis chloris	Greenfinch	0.019**	166	(−11 %)
Erithacus rubecula	Robin	0.022**	112	(−1 %)
Parus major	Great tit	0.025**	188	(−1 %)
Aegithalos caudatus	Long-tailed tit	0.029**	40	–
Sylvia melanocephala	Sardinian warbler	0.029**	215	(+4)
Periparus ater	Coal tit	0.032**	74	–
Columba palumbus	Wood pigeon	0.032**	260	16 %
Lophophanes cristatus	Crested tit	0.045**	107	(16 %)
Certhia brachydactyla	Short-toed tree creeper	0.049**	63	(−2 %)
Regulus ignicapilla	Firecrest	0.051**	43	(+2 %)
Sylvia atricapilla	Blackcap	0.053**	73	(−2 %)
Phylloscopus bonelli	Western Bonelli's warbler	0.073*	16	–

Estimates correspond to the slope parameters of the GLM; the higher the value, the stronger the response of species occurrence to the amount of green infrastructure. Species sorted from low to high estimates (levels of significance, p: $^+ < 0.1$, $* < 0.05$, $** < 0.01$). For each species, information about the number of occupied squares over a total of 351 500 × 500 m squares within urban area (excluding those located in Collserola Natural Park, BBAB data), and their trend (mean yearly change over the period 2005–2014, CCBS dataset) is also shown. Non-significant trends are shown between brackets

framework since the species is so intensively managed in Barcelona that their population patterns cannot be associated to the greening process. As a consequence, the spatial and temporal indicators of the effects of urban greening were generated using exclusively the 18 bird species whose occurrence were considered to be positively influenced by this driving force (+).

22.2.5 *Indicator of the Effect of Urban Greening Over Time*

Bird monitoring data from CCBS provided a valuable framework for studying the changes revealed by the studied indicators over time. In order to analyse trends in the indicators of the effect of urban greening, we selected monitoring plots located in the city and rejected those located in the Collserola Natural Park (two transects; Fig. 22.1).

Using data from the nine urban transects, we estimated annual population indices and trends (period 2005–2014) for these common bird species that showed a significant positive response to urban greening (+). These population values were assessed using the time-effects model of TRIM, a software package based on the analyses of time series of counts using a Poisson regression (Pannekoek and van Strien 2005). Population trends greatly differed depending on the species, but most of the calculated trends were not statistically significant (Table 22.1). This general lack of statistical significance at species level is at least partially related to the low sample size (number of transects) and hampers interpretation of these trends. In these cases finding procedures for aggregating species data at a multispecies level may help finding ecological patterns of more robust interpretation.

The temporal multispecies indicator developed in this study was based on the geometric mean of abundance indices across species and was computed by taking the average of the log of the annual indices of n species followed by a back transformation. This type of index satisfies the majority of the desirable mathematical properties for indicators of biodiversity change (van Strien et al. 2012). These multispecies indicators were calculated using geometric means, but with a weight (Wi) for each species obtained from its response to urban greening (species estimate/sum of all estimates). This enabled the concept of the unequal relative contribution of each species to the indicator to be introduced into the procedure (van Strien et al. 2012).

For each species we used the annual index obtained by TRIM as the population index for year a (Ia). Then, we obtained a value of change (Xab) between years a and b, where $b = a + 1$, using the formula $Xab = \log (Ib/Ia)$. Subsequently, we calculated the sum of $Wi \times Xab$ for i species, where Wi is the weight of each species in the indicator (considered constant over the study period). The value obtained for this sum represents the logarithm of the proportional change in the index between two consecutive years for a given set of species. We then applied the antilogarithm to obtain the annual index value. By establishing an initial value of the indicator at 100 for the first year (2005), we used the previously calculated values of annual change to calculate the annual values of the indicator. The 90 % confidence limits for each annual value of the indicator were defined by the central 9,000 values of the ranked 10,000 bootstrap estimates (Gregory et al. 2009).

We found that the indicator of the effects of urban greening did not show a clear pattern within a 10-year study period and values for the latest years did not significantly differ from those of the beginning of the studied time series (90 % confidence intervals overlap between the first and last studied years) (Fig. 22.2). This result contrasts with the progressive increase of urban green space in the municipality of Barcelona in the period 2005–2013 (Fig. 22.2), and in fact, the values of the indicator were not significantly correlated with those of the green area (Pearson $r = 0.24$; $p = 0.51$).

There are a number of reasons that could help to explain why we did not find a nice correlation between the results of the indicator and the increase in green spaces in Barcelona along time. The first one is purely methodological since available bird
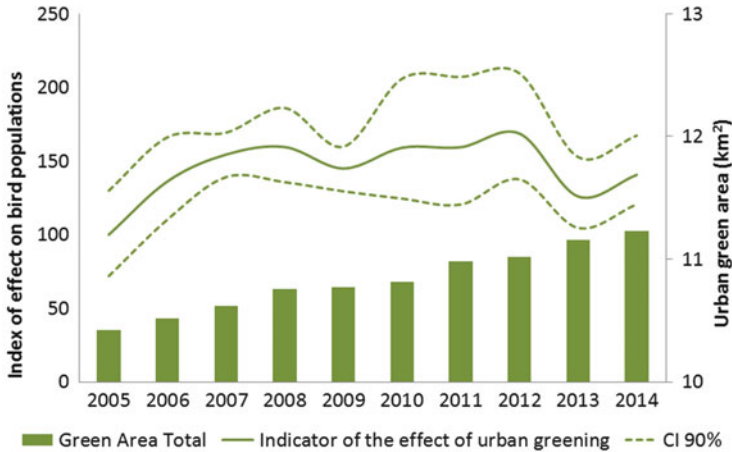
Fig. 22.2 Temporal change in the indicator of the effect of urban greening on bird populations in the city of Barcelona. This composite index was calculated using species yearly abundance indices from CCBS transects ($n = 9$ 3-km transects) and population responses according to BBAB datasets (see Table 22.1). The indicator of the effect of urban greening was set to a reference value of 100 in 2005. Change in the area of urban green in Barcelona is also shown (*Source*: Barcelona City Council 2014)

monitoring sample size is small (only 9 3-km transects), and this may influence the accuracy of this bird indicator. A second potential cause is related to the magnitude of change in the green area, which, although noticeable over the period 2005–2013 (7 %), might constitute an insufficient increase for bird populations. Obviously it is hard to determine which may be the ecological threshold in the amount of green habitat gained to produce a noticeable effect on bird biodiversity (Hedblom and Söderström 2010). A third hypothetical cause of the lack of correlation could be related to the type of green habitats that have been created within the urban matrix. Urban green areas do not always refer to the same wooded habitats, and even within these habitats, the bird species response could be associated to the species of tree or shrub and to its size and age. Finally, creating or improving the green infrastructure does not necessarily imply a simultaneous improvement of their associated biodiversity and time lags could be expected.

The need of long-term monitoring is thus crucial to robustly analyse the effects of urban greening on biodiversity. Altogether, these considerations make us remind on the original aim of this type of indicator that is not informing on the magnitude of the pressure in itself (urban greening) but its direct effect on biodiversity (population response to urban greening). At this point, it might be argued that this indicator is not a valid tool and does not inform on patterns related to urban greening. Fortunately we have a complementary source of information that enables to further explore if we are in the right direction: the spatial patterns of the indicator and its relation with the green surface.

22.2.6 Indicator of the Effect of Urban Greening Across Space

The spatially explicit approach of the indicator of the effects of greening in Barcelona attempts to provide synthetic data on the distribution of the indicator across space at a given time. In our case, this cartographic information corresponded to the period of the extensive atlas survey (2012–2014). It represents a complementary approach to the temporal scale since it allows determining the areas of the city in which the level of development of the green infrastructure is already having a positive effect on biodiversity and where this is intended to be improved in the future.

The procedure implemented in this study to depict the indicator across the municipality of Barcelona is based on the extensive surveys of the BBAB. The selected set of species was well distributed in Barcelona, being the majority present in more than 20 % of 500×500 m square of its urban area, but with some species rather scarce within the urban matrix (Table 22.1). The resolution of the indicator map is 500×500 m, the same of the original species set. Essentially, in order to calculate the indicator value for each square, we followed the same conceptual approach of species-depending contribution, incorporated as the affinity of each species for the green surface (Wi) for all species present in the square. Likewise in the temporal approach, the weight (Wi) for each species is calculated as species estimate/sum of the estimates for all species included in the indicator.

The indicator of the effects of urban greening in Barcelona shows a clear spatial pattern, with high values close to the Collserola Natural Park and the coast line and low values in densely built-up areas of the city centre (Fig. 22.3). Statistically, the pattern is intimately related to the percentage of green space in each square (Pearson $r = 0.46$; $p < 0.0001$). It is important to highlight that results shown in this map were obtained from an independent dataset than that used for calibrating the species response (intensive surveys) and shows that the approach carried out to develop this indicator responds to the amount of available green space. In addition to this technical approach, the spatial representation of the indicator can be considered a valuable tool for managers since it allows to determine the areas where bird biodiversity associated to the green infrastructure is better developed and thus considers this information in the process of ecosystem restoration established in the Barcelona Green Infrastructure and Biodiversity Plan.

The ultimate objective of this study is contributing to develop scientific tools to evaluate urban greening for biodiversity in a way understandable for managers, policymakers and citizens. Although this indicator has not been included so far within the set of indicators of the Agenda 21 of the Barcelona Local Council, the authors of this manuscript and policymakers in the city are currently discussing on its potential future role. We hope that our experience in Barcelona stimulates further research in this field and that robust indicators will be progressively developed and incorporated into such planning strategies.
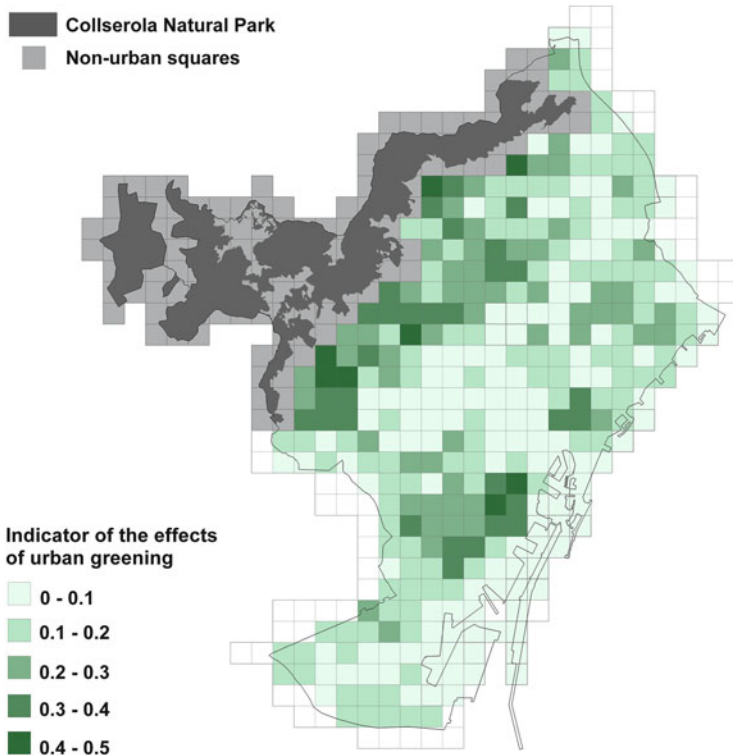
Fig. 22.3 Spatial pattern of the indicator of the effect of urban greening on bird populations in the city of Barcelona using data from BBAB (2012–2014). Since the target of the Barcelona Green Infrastructure and Biodiversity Plan lies in the urban matrix, the evaluation of the birds' response by means of this indicator is projected into the urban squares and not in those located in the Collserola Natural Park. Square size: 500 × 500 m

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Chapter 23
Management of Urban Nature and Its Impact on Bird Ecosystem Services

Erik Heyman, Bengt Gunnarsson, and Lukas Dovydavicius

Abstract Managing urban nature to produce public benefit and environmental quality through ecosystem services is a significant objective of urban nature managers. Ecosystem services provided by birds are highly valued and appreciated as birds provide pest control, seed dispersal, nutrient cycling as well as cultural ecosystem services. The aims of this chapter are to (1) provide a review of published experimental studies relating to the management of green areas and bird ecosystem services, (2) describe the findings of our own field experiments in suburban woodlands in southern Sweden, (3) investigate the status of management plans in Swedish cities and (4) discuss how our findings could be implemented in sustainable management planning of urban nature. The main results are:

(1) Forest management interventions gave responses that were highly species dependent. Interventions with the object to create or improve bird habitat gave almost entirely positive effects on bird communities.
(2) Clearance of bushes and small trees may have a negative impact on the biological control of forest arthropods. The study of bird abundance and understory management showed that clearance of understory can also have negative effects on bird densities if carried out as "complete" clearance (90 % removal of understory). A landscape characterised by high openness in the understory is often favoured by people but may not be an optimal habitat for birds.
(3) The management of urban forests and parks can be improved by including informal green space in management plans, putting emphasis on availability of

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favourable habitats and resources and initiating monitoring programmes for city birds.

(4) Urban woodlands would benefit from being managed with an adaptive approach, where management practices are constantly tested and evaluated.

23.1   Introduction and Aims

In the context of a rapidly urbanising world, urban ecology and ecosystem services in cities receive increasing attention (Young 2010). Biodiversity has key roles at all levels of the ecosystem service hierarchy: as a regulator of underpinning ecosystem processes, as a final ecosystem service or for its own inherent value (Mace et al. 2012). Maintaining diverse ecosystems in cities is a critical investment to improve the quality of life for urban citizens by enriching the experience of visiting urban green areas (Fuller et al. 2007; Hedblom et al. 2014; Wu 2014). Managing urban nature to produce public benefit and environmental quality through ecosystem services is currently a significant objective of urban nature managers (Young 2010). Management plans are a principle tool that is used for achieving goals in urban green planning such as noise reduction, appealing landscapes or conservation of biodiversity. Ecosystem services provided by birds are highly valued and appreciated (Sekercioglu 2006; Belaire et al. 2015). Birds provide pest control, seed dispersal, nutrient cycling, ecosystem engineering (e.g. by providing nest opportunities for other species) and cultural ecosystem services, e.g. bird watchers and hunters (Whelan et al. 2008; Wenny et al. 2011). In urban areas, birds mainly provide cultural ecosystem services (e.g. Fuller et al. 2007; Luck et al. 2011; Hedblom et al. 2014) but also regulate services, for instance, by performing top-down control of pest insects in gardens and parks (e.g. Gunnarsson and Hake 1999).

The aim of this chapter is, first, to provide a review of published experimental studies relating to the management of green areas and bird ecosystem services. The scientific evidence of the effects of management interventions with impacts on birds is reviewed and discussed. Examples of interventions are urban forestry (e.g. different cutting regimes, under- and midstory management), providing nest boxes, providing green roofs and bird feeding. We discuss the experimental evidence, including methods and implications for the management of urban green areas.

In the second part of the chapter, we describe our own field experiments in suburban woodlands in southern Sweden. The experimental design is discussed, as well as suggestions for future management experiments in urban and suburban woodlands.

In the third part of this chapter, we specifically ask: What kinds of managements in forests and parks are practised in urban areas in Sweden? In a survey, we

investigated the status of management plans in Swedish cities and municipalities. We focussed on urban forests and parks and the management plans were contrasted to plans for rural forests. These plans were discussed in relation to the urban bird fauna.

Fourth and finally, we discuss how our findings could be implemented in sustainable management planning of urban nature. We also discuss how future studies and field experiments could be designed to fill current knowledge gaps in the field of urban nature management. The goal is to facilitate a shift in the structure of urban management plans, i.e. to include biodiversity, e.g. insectivorous birds, and thereby improve conditions for wildlife and indirectly city inhabitants. The overall focus in management plans should be to meet the increasing needs of urban people by improving ecosystem services in green space.

23.2   Part One: Review of Experimental Evidence Regarding the Management of Urban Nature and Its Impact on Bird Ecosystem Services

The management of urban nature is a highly relevant topic, as urban green areas and the ecosystem services they provide are highly influenced by management actions. Despite the increasing attention to management questions, relatively few experimental studies on the management of urban nature and ecosystem services have been conducted. Several descriptive and comparative studies on urban nature management have been published (reviewed in, e.g. Konijnendijk et al. 2007; Bentsen et al. 2010). However, such studies have constraints regarding conclusions about causal relationships. Manipulative management experiments, on the other hand, with controls, randomisation and replication, provide more powerful ways of learning about natural systems and causal relationships (Johnson 2002). In general, managers of urban nature do not have the necessary time and resources to document and evaluate the effects of management activities (Lundquist 2005). There is, therefore, a need for more rigorous evaluations of the efficacy and effects of urban forest management, using proper experimental design and data analysis. Properly designed management experiments should include replicating procedures or treatments at proper scales, using reference sites or treatment controls and collecting pre- and post-treatment data to establish the baseline and document the range of variability in responses (Giardina et al. 2007).

The studies included in this review are field experiments with relevance for the management of urban nature and ecosystem services provided by birds. The selection of management interventions included in this review was based on earlier studies about the management of urban nature (e.g. Williams et al. 2012; Aronson et al. 2014) as well as the authors' personal experience in the field. Articles were searched by using available citation databases (Web of Science, Biological Abstracts and Google Scholar) using the keywords "management", "urban",

"nature", "ecosystem services", "birds", "experiment" and combinations of these words. Further literature searches included keyword search (using the same keywords as above) in the following scientific journals that were considered to be the most relevant in the field of urban nature management: *Landscape and Urban Planning*, *Trends in Ecology and Evolution*, *Ecosystem Management*, *Forest Ecology and Management*, *Urban Forestry and Urban Greening* and *Conservation Evidence*.

In total, 24 studies were included in this review, 22 experimental studies and two reviews of experimental studies. A summary of the studies is shown in Table 23.1. The main findings of the experiments are discussed in the following categories: under- and midstory management, cutting methods, the use of coppice, providing nest boxes, providing supplementary food and providing green roofs and walls.

Under- and midstory management (cutting and/or clearance of bushes and small trees) was tested in five replicated and controlled experimental studies (Wilson et al. 1995; Easton and Martin 1998; Rodewald and Smith 1998; Fleming and Giuliano 1998; Orlowski et al. 2008). A study of forest edge cutting found higher bird densities at cut edges than on uncut edges (Fleming and Giuliano 1998), and one study found lower densities of both breeding birds and wintering birds after understory clearance (Orlowski et al. 2008), while the three other experiments received results that were divergent and species dependent (Wilson et al. 1995; Easton and Martin 1998; Rodewald and Smith 1998). Management experiments with under- and midstory thinning are highly relevant for urban forest management. Understory clearance is regularly practised in urban woodlands, as a way to promote aesthetic qualities and a sense of safety by increasing visibility and openness (Hedblom and Söderström 2008). The results of the five studies above suggest that the bird communities' response to under- and midstory management is highly species specific, and this type of management must therefore be adapted to the desired target species of the intervention.

Different cutting methods were tested in nine studies. The interventions that were tested included clear-cuts and creation of open woodland patches of different sizes and variable retention timber management. The responses were often highly species dependent: seven studies found that early-successional species increased in clear-cut areas or opened forests compared to control areas. Two studies report that mature-forest species declined in cut/opened areas of forest (Gram et al. 2003; Wallendorf et al. 2007). A replicated, randomised, controlled study from the USA found no differences in species richness between clear-cuts of different sizes (Rudnicky and Hunter 1993), while another American study found that a mosaic of cut and uncut areas supported a variety of species, with highly season-dependent responses and no clear pattern in bird species responses to management (Yahner 1987). A long-term study from the USA of a landscape with opened patches found that there were no consistent differences between clear-cut and controlled areas, although some species were only seen in clear-cuts (Alterman et al. 2005). A replicated, controlled study from the USA found that nine bird species occurred at higher densities in stands under variable retention management compared to control stands. Five were found at lower densities. The results suggest that the

Table 23.1 Experimental studies with relevance for the management of urban nature and ecosystem services provided by birds

Year conducted	Intervention	Response variable	Main results	Location	Published
1992–1993	Midstory thinning	Bird densities and species richness	Bird species richness and abundances were similar in stands with midstory thinning compared to controls	Arkansas, USA	Wilson et al. (1995)
1992–1995	Manual thinning of the mid- and understory vegetation in a mixed forest	Bird abundance and nesting success	Fewer species but higher nesting success in thinned areas than in controls. No difference in abundance	British Columbia, Canada	Easton and Martin (1998)
1993–1994	Under- and overstory control	Bird abundance of 14 selected species	Responses were species dependent, with both positive and negative responses to management	Ozark Mountains, Arkansas, USA	Rodewald and Smith (1998)
1996	Cutting of forest edges	Bird densities, species richness and nesting success	Cut edges had higher bird densities than uncut edges. No management effect on species richness and nesting success	Pennsylvania, USA	Fleming and Giuliano (1998)
2008	Undergrowth removal in a suburban wood	Bird densities	Lower densities of breeding and wintering birds first year after clearance. Bird densities recovered in the following 1–4 years	Wrocław City, Poland	Orlowski et al. (2008)
1981–1984	Clear-cuttings of different sizes, mosaic of aspen and oak stands	Bird densities	Responses were highly season dependent with no clear pattern	Barrens Grouse Management Area, Pennsylvania, USA	Yahner (1987)

Table 23.1 (continued)

Year conducted	Intervention	Response variable	Main results	Location	Published
1978–1988	Creation of open woodland patches	Number of European nightjars	Nightjar abundance increased significantly following management interventions, including the creation of open woodland patches	Minsmere Reserve, Suffolk, England	Burgess et al. (1990)
1989–1990	Clear-cuttings of different sizes (2–112 ha)	Bird diversity	Some evidence of increased species richness in smaller clear-cuttings. Average species richness showed no trend amongst the range of clear-cutting sizes	Maine, USA	Rudnicky and Hunter (1993)
1993–1994	Clear-cuttings, selective logging and shelterwood	Bird densities	Responses were species dependent with no clear pattern	Missouri Ozarks, Missouri, USA	Annand and Thompson (1997)
1991–2000	Clear-cutting and selective logging in oak-hickory forest	Bird densities and nest success	Responses on abundance were species dependent. Nest success did not change after treatment	Missouri Ozarks, Missouri, USA	Gram et al. (2003)
2001–2002	Cutting management for bird conservation	Bird densities and diversity	Responses to management were species dependent. Total bird abundance and species richness increased over the study period	Pennsylvania, USA	Yahner (2003)
2000–2001	Patch harvest	Bird densities	Early-successional species were more abundant in seed-tree stands compared to openings made by cutting in patches	Ouachita National Forest, Arkansas and Oklahoma, USA	Alterman et al. (2005)

Table 23.1 (continued)

Year conducted	Intervention	Response variable	Main results	Location	Published
1991–2000	Clear-cutting	Bird densities	Responses were species dependent: densities of early-successional species increased after clear-cutting, while some mature-forest species declined	Missouri Ozarks, Missouri, USA	Wallendorf et al. (2007)
2003–2004	Variable retention timber management	Bird densities	In general higher bird densities in stands with variable retention timber management than in control stands	Tensas River National Wildlife Refuge, Louisiana, USA	Twedt and Somershoe (2009)
1950–1952	Use of coppice	Densities of ruffed grouse	The local population of ruffed grouse declined over time, as coppiced woodlands became more mature	Pennsylvania, USA	Sharp (1963)
1975–1984	Use of coppice	Bird diversity and bird densities	Overall bird diversity decreased with coppice age and declined markedly at canopy closure	Longbeech Wood, Kent, England	Fuller and Moreton (1987)
1978–1988	Use of coppice	Densities of European nightjars	The local population of nightjars increased following the coppicing of birch trees	Minsmere Reserve, Suffolk, England	Burgess et al. (1990)
1981–2008	Provide supplementary food for songbirds (review)	Bird densities, survival rate and body weight	A review of 13 studies showed positive responses in seven studies and no response in six studies	USA and Europe	Williams et al. (2012)

Table 23.1 (continued)

Year conducted	Intervention	Response variable	Main results	Location	Published
1945–2007	Provide nest boxes (review)	Breeding densities, nest occupancy, etc.	Only three studies out of 66 found low rates of nest box occupancy	Global	Williams et al. (2012)
1995–2000	Provide nest boxes in woodlands	Breeding densities of great tit	Higher bird densities in areas with nest boxes than in control areas	Pärnu County, Estonia	Mand et al. (2009)
2009–2010	Provide nest boxes in small public gardens	Diversity and abundance of cavity nesting birds	Higher diversity and abundance in parks with nest boxes than in control parks	Paris, France	Shwartz et al. (2014)
2008–2012	Provide nest boxes on farms	Abundance of house sparrow and tree sparrow	Providing nest boxes positive for tree sparrow populations but did not affect house sparrow populations	Southern Sweden	von Post and Smith (2015)
2005–2006	Provide green roofs	Breeding pairs of ground-nesting birds	Northern lapwings and little ringed plovers use green roofs as breeding habitat	Five sites in Switzerland. Buildings with green roofs	Baumann (2006)
2010–2011	Provide green walls	Bird abundance	Birds use green walls for nesting, foraging and shelter	27 sites in Northern Staffordshire, UK	Chiquet et al. (2013)

The table shows the year when the study was conducted, type of management intervention, studied response variable, main findings, study site, author and year of the publication

mosaic of treated stands affords greater community-wide bird conservation value than untreated stands (Twedt and Somershoe 2009).

The use of coppice was tested in three studies. Coppicing is a traditional method of woodland management that takes advantage of the fact that many trees make new growth from the stump or roots if cut down. In a coppiced wood, young tree stems are repeatedly cut down to near ground level, and in subsequent growth years, many new shoots will emerge from the coppiced tree. One study found that a population of European nightjars increased following a series of management interventions, including the coppicing of birch trees (Burgess et al. 1990). Two before-and-after

studies from the USA and the UK found that the use of coppices by some bird species declined over time (Sharp 1963; Fuller and Moreton 1987). Fuller and Moreton (1987) also found that overall species richness decreased with age but that some species were more abundant in older stands. Warblers, finches and buntings were most abundant in young coppice, while thrushes and tits increased in abundance with age since coppicing.

Several studies have documented the effects on bird populations by providing nest boxes. A review by Williams et al. (2012) found that only three studies out of 66 found low rates of nest box occupancy, although this may be partially the result of publishing biases. Relatively few experiments with treatment and controls have, however, been conducted and published. The three experimental studies in our review all showed higher densities of breeding birds in areas with nest boxes compared to control areas, although the response was sometimes species specific (Mand et al. 2009; Shwartz et al. 2014; von Post and Smith 2015). The general conclusion is that providing nest boxes is a simple and effective method to promote bird fauna in urban green areas.

Providing supplementary food for songbirds was tested in 13 studies, reviewed by Williams et al. (2012). Out of 13 studies, seven showed higher densities or larger populations in areas close to supplementary food. Six studies found that population trends or densities in some species were no different between fed and unfed areas. Bird feeding in private gardens has been shown to be the most popular activity amongst "wildlife gardening" and other management activities in private gardens in the UK (Gaston et al. 2007).

Green roofs and walls are known to provide ecosystem services such as storm water retention, carbon dioxide uptake and noise reduction. They can also serve as suitable habitats for animal and plant species that are able to adapt to the local conditions and are mobile enough to reach these habitats. Preliminary data from a long-term study of green roofs as potential bird habitat in Switzerland suggests that green roofs may be able to provide not only food habitat but also breeding habitat for ground-nesting birds such as the endangered little ringed plover and northern lapwing (Baumann 2006). A study, comparing 27 sites with green walls and 27 control walls, in England found that birds use green walls for nesting, foraging and shelter, while no birds were found at the control walls (Chiquet et al. 2013). However, this study does not meet the requirements of a true experiment, as it merely compares green walls and walls without vegetation.

In general, forest management interventions gave responses that were highly species dependent. Bird species known to prefer young forests were positively affected by the creation of small clear-cuts, forest glades, young coppice and similar young forest habitats, while the responses amongst mature-forest bird species were the opposite. Interventions with the object to create or improve bird habitat (providing nest boxes, supplementary food, green roofs, etc.) gave almost entirely positive effects on bird communities.

23.3 Part Two: Example of a Management Experiment in Urban Woodlands

The management experiment described here is an example of a study with a replicated before-after-control-impact (BACI) design (Quinn and Keough 2002), conducted to evaluate management effects on ecosystem services related to birds in urban woodlands.

The aim of the experiment was to evaluate forest management effects on bird communities and ecosystem services delivered by birds in urban woodlands. Here we summarise the results from four publications (Gunnarsson et al. 2009; Heyman 2010; Heyman and Gunnarsson 2011; Heyman 2011). The study was carried out as a large-scale field experiment, with a replicated BACI design, over 3 years (2006–2008) in the county of Västra Götaland in southwestern Sweden. The experiment included five sites with deciduous woodlands dominated by oak (*Quercus robur*) and understory mainly consisting of hazel (*Corylus avellana*), rowan (*Sorbus aucuparia*) and alder buckthorn (*Frangula alnus*). The sites were all located on the fringe of three midsized cities (23,000–63,000 inhabitants): Alingsås, Borås and Skövde. Figure 23.1 shows the location of the five study sites. None of the sites had been subject to any recent (<10 years) clearance or thinning, so the understory was dense before the management experiment.

Fig. 23.1 Location of the five study sites in the management experiment

Fig. 23.2 The experimental setup of the management experiment. The plots were *square* or *rectangular* in shape, with some variation due to the shape of each forest stand. The experiment was replicated at five sites
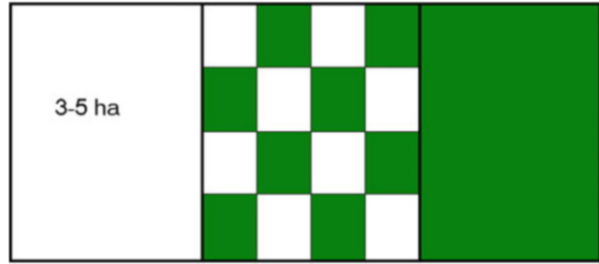
23.3.1 Experimental Setup

The management experiment included two different treatments (randomly assigned to the plots): "complete" and "patchy" clearance of understory and "control" with no clearance. Mean plot area was 3.9 ha ($n = 13$, range 3–5.5 ha). The experimental setup of the management experiment is shown in Fig. 23.2. In total there were four plots with "complete" clearance, four with "patchy" clearance and five with "control" plots.

Clearance of understory was carried out in autumn and winter 2006/2007. Bushes and small trees with a base diameter of less than 10 cm were cut close to the ground, except for multi-stemmed bushes of hazel (*C. avellana*) which were retained. The woody debris was transported out of the forest with light forestry machines. In the plots with "complete" clearance, about 90 % of the bushes, shrubs and small trees (base diameter <10 cm) were cleared in the whole plot area. In the plots with "patchy" clearance, the plot was divided into patches in a regular pattern, each patch roughly square in shape and measuring 50×50 m. Every other patch was cleared, and the rest were left unmanaged. "Control" plots were left untreated during the whole experiment. More details about the management experiment are given in Heyman (2010).

Territory mapping was used to estimate density and diversity of breeding birds in the experimental plots (Heyman 2010). Surveys were conducted in the spring during 3 years (2006–2008). The first survey was carried out before the management interventions (2006), followed by surveys the first (2007) and second year (2008) after the management.

In addition to the measure of breeding bird densities, bird and arthropod interactions were studied to examine the importance of the understory and tree canopies as foraging sites for insectivorous birds. This was done by setting up two field experiments that studied the importance of top-down effects from insectivorous birds on arthropods in bush and tree canopies (Gunnarsson et al. 2009; Heyman and Gunnarsson 2011). In both these experiments, bird nets were used to prevent birds from foraging on certain branches or bush canopies. For each net-enclosed branch or bush, an adjacent branch of the same species and similar size was chosen as a control. The method with net enclosures has been widely used to estimate top-down effects from birds on arthropods (van Bael et al. 2008; Mooney et al. 2010). As the

understory vegetation was to a large extent removed in the management experiment, a measure of bird foraging in the understory in the unmanaged plots would be of interest in relation to the effects on bird abundance that were found in the managed plots. The canopies of rowan (*Sorbus aucuparia*) and alder buckthorn (*Frangula alnus*) bushes were net enclosed for two months at three study sites (Gunnarsson et al. 2009). We compared abundance, biomass and body size distributions of arthropods between experimental and control canopies to estimate top-down effects.

In an additional experiment with net enclosures in tree canopies, we studied bird predation rates on tree-living arthropods in relation to forest management (understory clearance) and foraging height (Heyman and Gunnarsson 2011). Bird exclosures were put up for 1 month at two foraging heights (3–5 and 12–15 m above the ground) in oak (*Q. robur*) canopies in managed ("complete" understory clearance) and control areas (no understory management). The experiment was replicated at two sites. Our experimental design would allow us to analyse bird predation effects in relation to management, height above ground and the interaction between these factors.

23.3.2   Results and Discussion

In the analysis of breeding bird density and diversity, 18 species of forest birds were included. The species had an appropriate territory size and a sufficient number of observations to be considered to be breeding within the experimental plots. The bird surveys showed that total densities of woodland birds were affected by clearance of understory (Heyman 2010). Bird densities decreased in the plots subjected to "complete" (90 %) removal of the understory compared to the plots with "patchy" (50 %) clearance. "Patchy" clearance had no significant effect on bird density compared to "control". Two years after the management, bird densities were reduced by 18 % on average in the plots with "complete" clearance, while there was an increase in bird densities in both "control" plots (15 %) and plots with "patchy" clearance (26 %). Breeding bird diversity, quantified using Simpson's index (D), expressed as the reciprocal value (1/D), was not affected by the management. The reduction in bird densities in plots with "complete" clearance was not unexpected as the understory density was reduced by 90 %. In the plots with "patchy" clearance, understory density was reduced by about 50 %, but, interestingly, there was no decrease in bird densities compared to control plots. Understory density and structure have been shown to be one of the most important factors for habitat selection for woodland passerines (Cody 1985; Marshall and Cooper 2004). The understory provides both nesting and foraging sites as well as protective cover against weather and predators (Willson and Comet 1996). The lack of management effect on bird densities in the plots with "patchy" clearance (with about 50 % removal of understory) was more unexpected. It is possible that "patchy" clearance would provide a similar effect as other small-scale disturbances, such as windfalls,

forest roads and power line corridors, which in previous studies have been shown to have a positive or neutral impact on forest bird densities compared to undisturbed forest (Fuller 2000; Kroodsma 1982; Ortega and Capen 2002). There was no management effect on the diversity of breeding birds, which was somewhat unexpected, given the large number of studies that show the importance of the understory layer for the diversity of woodland birds (e.g. MacArthur 1964; Brokaw and Lent 1999; Forslund 2003; Camprodon and Brotons 2006). An explanation to the lack of effect on breeding bird diversity could be that, due to the limited size of the study plots (3 ha on average), the analysis was carried out on a relatively small number of bird species (18 bird species were considered to be breeding within the study plots).

The two exclosure experiments showed strong top-down effects from insectivorous birds on arthropods, in the understory as well as in the tree canopies (Gunnarsson et al. 2009; Heyman and Gunnarsson 2011). In the understory, arthropod abundance and biomass were higher, and arthropod body sizes were larger on the net-enclosed canopies compared to controls. The strong top-down effects in bush canopies supported earlier experimental results from this geographic region (e.g. Askenmo et al. 1977; Gunnarsson 1996; Gunnarsson and Hake 1999) as well as data from other temperate forests (e.g. Holmes et al. 1979; Marquis and Whelan 1994; Mooney and Linhart 2006).

In the oak tree canopies, higher abundances and biomass of arthropods were found on the net-enclosed branches. The height in the canopy did not affect the bird predation rate, but there was a management effect, with higher rate of bird predation in the control plots compared to managed areas. In the unmanaged plots, the effect of bird predation on arthropod abundance was about twice as high as in areas with understory clearance. This means that the intensity of bird foraging is higher in plots with dense understory compared to the plots where the understory was cleared. The exclosure experiment in the tree canopies also gave support to previous studies that have shown that insectivorous birds significantly decrease arthropod populations in forest and agricultural ecosystems (Eveleigh et al. 2007; Mooney et al. 2010; Philpott et al. 2009; van Bael et al. 2008). Furthermore, the results indicate that the potential for population control of arthropods is higher in the areas with dense understory than in the cleared areas. This supports the idea that bird predation on arthropods can be affected by forest management. We suggest two possible mechanisms behind the observed management effect on avian predation:

(A) Decreased bird abundance in cleared plots (average decrease was 37 % in the cleared plots compared to unmanaged plots).
(B) Reduced predation pressure on arthropods in the cleared plots as a result of a shift in bird foraging behaviour. Possibly, birds avoid foraging in the more open plots to reduce the risk of exposure to predators, e.g. sparrowhawk (*Accipiter nisus*) (Götmark and Post 1996).

These two mechanisms may act simultaneously, decreasing possibilities for avian control of arthropod abundance in plots with removed understory.

Experiments from a range of ecosystems have shown that insectivorous birds are important in controlling the populations of their invertebrate prey (Bock et al. 1992; Fayt et al. 2005; Gradwohl and Greenberg 1982; Mols and Visser 2002; Perfecto et al. 2009). Several studies have shown that bird predation can contribute to dampen the outbreaks of forest pests, even though such predation is most effective in controlling low to moderate invertebrate populations (Crawford and Jennings 1989; Sekercioglu 2006; Whelan et al. 2008). Mass occurrences of insect pests are rather rare in northern Europe except, e.g. *Tortrix viridana* on oak (*Q. robur*) in southern Scandinavia (Ivashov et al. 2002) and *Operophtera brumata* and *Epirrita autumnata* on birch (*Betula* spp.) in northern Scandinavia (Bylund 1997; Tenow et al. 2007). It has been suggested that there might be an ecological and evolutionary relationship between high bird predation pressure and relatively low abundance of pest outbreaks in the forests of southern Fennoscandia (Tanhuanpää et al. 2001). There are, however, few experimental tests on the effects of habitat management on ecosystem services provided by birds. Our study was, to our knowledge, the first to show experimentally that forest management can affect naturally occurring predation pressure on arthropod abundance.

23.3.3 Implications for the Management of Urban Woodlands

We conclude that management for enhanced aesthetic values of forests, such as clearance of understory, may have a negative impact on the biological control of forest arthropods. As the understory is of importance for bird foraging, we suggest that there is a potential management conflict between promoting recreational values and providing foraging sites for birds. A landscape characterised by high openness in the understory is often favoured by people, but may not be an optimal habitat for birds.

The study of bird abundance and understory management showed that clearance of understory can have negative effects on bird densities if carried out as "complete" clearance (90 % removal of understory). "Patchy" clearance (50 % removal of understory) was not found to have negative effects on bird densities. Treatment effects were not dramatic but may be of relevance as this was a relatively short-term study, and it is likely that avian site fidelity may have delayed management effects on the avifauna. Patchy clearance of understory is suggested as a compromise to promote the recreational values as well as bird fauna in urban woodlands. It has been shown that a mix of open and closed woodlands is preferred by the majority of respondents in preference surveys (Gundersen and Frivold 2008; Heyman et al. 2011). Additional research is needed to assess the long-term effects of understory clearance and other forest management practices on bird communities in urban woodlands. Further field experiments with a replicated design would be of

great value to evaluate management effects on ecological and social values in urban woodlands.

23.4 Part Three: Management of Urban Forests

23.4.1 Background: Urban Green Space Management in Sweden

The management of urban green space is key to explain the variation in bird abundance and diversity found in and around cities. The maintenance is usually based on specific management plans, and by developing such plans, green areas may change in a positive direction for urban birds. Here we use management plans in Swedish cities to investigate how the maintenance may affect avian populations.

In Sweden, the planning and management of parks and forests in urban and suburban areas are primarily a task for the municipalities. In recent years, there has been an increasing focus on urban forests for recreational purposes (Rydberg and Aronsson 2004), partly as a consequence of increasing urbanisation. Municipalities own ca 60 % of urban fringe forests (Arnell et al. 1994) but many also own rural forests. In a survey, Lundquist (2005) found that the mean forest area was 1893 ha (median 1000 ha) in Swedish municipalities. The municipalities have the legal responsibility for the planning process. However, the Swedish Forest Agency (Skogsstyrelsen), a national authority, is responsible for making sure that the management of urban and rural forests complies with the forest policy law. This means that the municipalities are being monitored by Skogsstyrelsen, but in practice there is a great amount of freedom to implement various management regimes in the forests. The policy is to put equal emphasis on production and environmental goals. On the webpage of the authority, the aims are summarised as: "It is important that the forest is managed to give sustainable high yields while biological diversity is maintained" (Swedish Forest 2015). Moreover, forest management has to show consideration to the needs of the public. Forests can be used for recreational activities such as walking on paths, picking berries, camping for short periods, etc., according to the right of public access ("allemansrätt")—a right applicable in private- as well as municipality-owned forests (Sandell and Fredman 2010). Thus, the management of rural and suburban forests has to be a balance between different "demands". The concept "multifunctionality" is a good description of how maintenance is practised. However, parks in cities often have a number of restrictions to the utilisation of green space. In practice, the municipalities can decide on much of the management for both formal parks and urban forests in Sweden.

23.4.2 Methods

An invitation to participate in a web-based survey on the management of forests was mailed to the 50 largest municipalities in Sweden. The questions were related to how often different management actions were included in the plans (see Table 23.2). The survey also included questions on ecosystem services but those findings will be reported on elsewhere. We received 23 fully, or partially, completed responses. In all kinds of investigations employing questionnaires, there could be potential problems of bias in the responses. In the present case, e.g. if only officers in cities with high management ambitions respond, the results may not be representative. We interpret the response rate of 46 % in our study as being a consequence of random factors, e.g. the questionnaire not reaching the correct officers, and factors related to institutional conditions, i.e. time and/or economic constraints. A few cities responded that they did not have time to deal with the questionnaire. We did not find any significant difference in population size between cities that responded and those that did not (Mann–Whitney U-test, $p = 0.221$), so we consider the responses to be unbiased in relation to city size. However, a possible bias could be that cities without large forest areas did not reply, as was the case in the study by Lundquist (2005). The number of inhabitants in the cities that responded together represented ca 26 % of the total Swedish population. The majority of the officers who responded were working as ecologists, conservation planners or foresters, but a few were landscape planners, biologists or park managers.

Table 23.2 Action options in management plans for urban forests, urban parks and rural forests in Swedish municipalities

	(Never)	(Rarely)	(Sometimes)	(Often)	(Always)	N
Clear-cutting	59/90/17	23/10/22	18/0/33	0/0/28	0/0/0	22/20/18
Thinning	4/5/6	9/35/0	17/25/11	61/30/72	9/5/11	23/20/18
Selective cutting	0/15/6	17/0/44	39/60/44	39/15/6	4/10/0	23/20/18
Partial removal understory	0/5/6	19/15/47	38/55/29	43/20/18	0/5/0	21/20/17
Complete removal understory	41/15/47	27/50/29	27/20/18	5/10/6	0/5/0	22/20/17
Removal of dead wood	14/11/35	45/21/47	41/32/18	0/37/0	0/0/0	22/19/17
Creating dead wood	5/20/6	10/55/24	52/25/41	24/0/12	10/0/18	21/20/17

Respondents were asked to rate frequency on a 5-point scale: never, rarely, sometimes, often and always. Percentages for urban forests/urban parks/rural forests are shown. N is the total number of responding municipalities

23.4.3 Results and Discussion

First, we asked general questions about the management of urban green space with emphasis on forests and parks. The focus on urban green space with trees and shrubs was chosen because such sites harbour a large number of habitats suitable for birds. Many Swedish cities and municipalities have three types of forests that could be utilised for recreational activities:

(1) Urban forests with predominately indigenous vegetation and less extensive management mainly used for everyday recreational activities, e.g. walking, cycling and jogging.
(2) Urban parks with a mix of indigenous and introduced vegetation and relatively intensive management. In such parks, the public use green space for picnic, walking, playing, etc.
(3) Rural forests in peri-urban and suburban areas that are often used for sports, e.g. horse riding, but also walking, picking berries and hiking. We included these three types of greens in our survey.

The majority of cities had management plans for urban forests (74 %), urban parks (77 %) and rural forests (73 %). Some cities had such plans in progress for urban forests (22 %), urban parks (9 %) and rural forests (10 %). However, only 20 % of the cities had management plans for informal types of urban green space, such as groves of trees between residential buildings. Another 10 % of the cities had such plans in progress. Such types of green space can be important habitats to urban birds (Andersson and Colding 2014), e.g. in providing hiding places and foraging sites, but obviously they are often neglected when it comes to management, which means that ad hoc methods for maintenance can be important in informal greens (for urban wastelands, see Meffert 2016).

Buffer zones with restrictions for buildings close to forests were practised in 20 % of the cities. One third (30 %) of the cities had specific management plans for red-listed birds. The species that were mentioned in such plans were lesser spotted woodpecker (*Dendrocopos minor*), white-backed woodpecker (*Dendrocopos leucotos*) and common kingfisher (*Alcedo atthis*). Only one of the cities had a general monitoring programme for birds. In Sweden, a national monitoring programme for birds has been complemented by a citizen science Internet open-access platform ("Species Gateway") which can be used to assess changes in, e.g. bird populations in urban settings (for some examples in other countries, see Fidino and Mason 2016; Goddard et al. 2016; Herrando et al. 2016). However, the reliability of Species Gateway as a monitoring tool is not perfect suggesting that it should be viewed as a support to the national programme rather than used on its own (Snäll et al. 2011).

As a second part of the questionnaire, we asked what kinds of management that were used in urban forests, urban parks and rural forests, respectively. The respondents were asked how often different management actions were included in management plans, and a multiple choice option was employed for describing the

frequency of the actions (Table 23.2). Percentages given below are related to cities that have the particular type of forest that is discussed, i.e. number of cities can vary because not all cities have, e.g. rural forests of their own. Here we focus on the most relevant management regimes that are used in Sweden.

Clear-cutting as an option for management was "never", or "rarely", used in urban forests in 82 % of the cities. In urban parks, these two management options were the norm in all cities (Table 23.2). However, in rural forests, clear-cutting was used "sometimes", or "often", in 61 % of the responding cities. This means that in 39 % of the cities, clear-cutting was "never", or "rarely", used in rural forests. Thinning was used "often", or "always", in urban forests in 70 % of the cities but in urban parks in 35 % of responding cities according to management plans. This management option was used "never", "rarely" or "sometimes" in 65 % of the urban parks. In rural forests, thinning was used "often" or "always" in 83 % of the responding cities. It was expected that clear-cutting and thinning would be relatively uncommon in urban settings. Especially clear-cutting has dramatic effects on flora and fauna, e.g. bird communities, for several decades (e.g. Väisänen et al. 1986; Edenius and Elmberg 1996; see also part one, above).

Selective cutting was employed "often", or "always", in urban forests in 43 % of the cities and in urban parks in 26 % of the cities (Table 23.2). In rural forests, the situation seemed to be different. Selective cutting was used "often" in only one city (6 %), but in 94 % such cutting was used "never", "rarely" or "sometimes".

In Sweden and other Nordic countries, thinning of understory is a management technique that is well established in order to enhance recreational values (e.g. Tyrväinen et al. 2003; Gundersen and Frivold 2008). Such removal could affect the biodiversity of the habitats, e.g. a nearly complete removal of the understory in deciduous forest reduced the bird abundance (Heyman 2010). According to the management plans, partial removal of understory was generally more common than complete removal (Table 23.2). However, partial removal seemed to be more uncommon in rural forests than in urban forests and parks.

The maintenance of structural variation of trees and bushes in urban forests and parks is of great importance to bird communities as shown in the review in part one (see above). For instance, tree cover is a very important factor that has a strong influence on urban bird abundance and diversity. In a correlative study in three Swiss cities, Fontana et al. (2011) concluded that well-developed vertical vegetation structure together with an optimal mixture of coniferous and deciduous trees enhanced bird species richness and diversity. Findings in several studies have supported similar conclusions (e.g. Evans et al. 2009; Ferenc et al. 2013).

Dead wood is a potentially very important habitat quality for various organisms, e.g. insectivorous birds (e.g. Mörtberg 2001; Fayt et al. 2005). Removal of dead wood was generally uncommon ("never" or "rarely") in management plans of urban (59 % of the cities) and rural (82 %) forests. In urban parks, however, such removal was relatively common ("sometimes" or "often", 68 % of the cities). On the other hand, newly created dead wood as a management strategy was quite common in urban and rural forests according to management plans (Table 23.2). But in urban parks, this type of management was generally uncommon. Although

dead wood has been shown to promote high biodiversity of birds in different types of forests (e.g. Hobson and Schieck 1999), the general public has been quite reluctant to this management option (Gundersen and Frivold 2008). However, a shift in opinion about dead wood might be at hand in younger people. For instance, in a field study of recreational values in urban forests, the respondents (range 19–38 years) did not perceive dead wood as negative (Heyman 2012).

In summary, the conclusion from our survey is that the maintenance of urban forests and parks can be improved by, e.g. (1) including informal green space in management plans, (2) putting emphasis on availability of favourable habitats and resources (e.g. dead wood) and (3) initiating monitoring programmes for city birds. More focus on birds as providers of ecosystem services should also be included in management plans. The concept of ecosystem services is a valuable tool for communicating the role of birds, and other organisms, in urban green space.

23.5 Part Four: Final Conclusions and Suggestions for the Management of Urban Nature

As urban woodlands are intensively used ecosystems, their management is of central importance. Urban woodlands would benefit from being managed with an approach, where management practices are constantly tested and evaluated (Gunderson 1999; Johnson 1999). Our experimental work was based on replicated field experiments with controls, randomisation and replication. Such studies provide powerful ways of learning about natural systems and causal relationships, but are still rare in the field of forest management (Johnson 2002). The results from our management experiment and studies of recreational values suggest that variation in management at the forest stand level would probably be a favourable strategy in urban woodlands. Clearance of understory in small patches is an example of a management strategy that introduces small-scale variation in a forest stand if the understory vegetation is dense. This type of management did not affect forest birds negatively even though more than 50 % of the understory was removed.

It is crucial that results are communicated from researchers to managers. National forest authorities, e.g. the Swedish National Board of Forestry, could serve as a link between researchers and managers, to compile evidence and provide advice to managers of urban nature. It will be a challenge, however, to take another step forward, i.e. to make management plans more flexible. Adaptive management has a number of advantages in an environment that is affected by dynamic systems, e.g. climate change. But there is a tradition, at least in Sweden, that maintenance of green space is based on, at best, fixed management regimes or, at worst, ad hoc methods. A flexible and adaptive management system that also takes changes in the surroundings into account (e.g. Mörtberg 2001; Ferenc et al. 2013) is probably the best basis for successful protection of urban bird faunas. Moreover, to fully implement an adaptive management system, there is a need of a monitoring

programme that can track changes in urban bird populations, including red-listed species (e.g. Mörtberg and Wallentinus 2000). Such monitoring should include all types of urban green space, i.e. both non-residential land (parks, urban forests) and residential land (gardens, yards, etc.) (Smith et al. 2013). However, it takes a lot of effort to implement an adaptive management, so it is not possible to take decisions that are solely based on adaptive systems. Still, our knowledge about management regimes and their effects on urban bird populations usually allow us to make quite robust recommendations about actions to execute (e.g. Taylor et al. 2013).

The Swedish government recently stated that by 2018, it will be mandatory to include the impact on ecosystem services in all relevant economic and political decisions. This suggests that there should be more efforts to include ecosystem services in policies and plans. One of the advantages with the concept of ecosystem services is that it facilitates communication with stakeholders. This also opens up for management that is focussed on ecological functions and relationships between different trophic levels. However, there is a need for more knowledge about ecosystem services by birds in urban areas. A starting point for new investigations could be findings in the present study but also findings by Belaire et al. (2015). We would strongly suggest an experimental approach when possible. Strong evidence obtained from experiments should be the norm. The most challenging part of ecosystem service values is perhaps "cultural services", i.e. perceptions by urban citizens. However, it should be possible to perform various types of experiments linked to experienced values (e.g. Hedblom et al. 2014). But even with good knowledge at hand, the plans need to be implemented on an everyday basis. In the end, the quality of municipal green space management depends on the commitment by people involved in maintenance. A high level of support to personnel working with ecosystem services might be a key to success (Young 2013).

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Part VI
Concluding Remarks

Chapter 24
Improving Research Towards Conservation Objectives

Some Thoughts on Urban Bird Ecology

Enrique Murgui and Marcus Hedblom

Abstract In the last three decades urban bird ecology has experienced a remarkable advance as demonstrated by the rich variety of chapters included in this volume. Nevertheless, there are some research gaps which we try to identify in this chapter, including some issues in current research that to us seem especially pressing. We conclude that a critical examination of bird census techniques in urban areas, an integration of patterns and processes across different spatial scales, the incorporation of temporal dynamics, a more widespread use of experimental or pseudo-experimental design and a deeper insight on sociological and cultural issues are key issues to refine our understanding of the causal connection between urbanisation and bird fauna parameters. Such improvement could help us to shape urban design and management strategies for bird fauna conservation in cities and in the surrounding landscape.

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24.1   Introduction

A rich variety of chapters in this book has contributed to improve our understanding of urban bird ecology, but there are still many gaps in our knowledge of the complex relationships between bird fauna and urbanisation. As we are in the fringe of the book and our task as editors finishes, we here take the liberty to further emphasise some of the research gaps revealed in the chapters of this volume. These gaps are not only academically interesting but entail a potentially deep influence on urban landscape design and management that ultimately promote biodiversity conservation, provision of ecosystem services and environmental justice in cities (Dearborn and Kark 2010; Seto et al. 2012). Thus, the purposes of this chapter are twofold: to identify some gaps in current research on urban bird ecology (as a complement to those that previously reviewed this topic; Marzluff et al. 2001; McKinney 2002; Donnelly and Marzluff 2004; Chace and Walsh 2006; Shochat et al. 2006) and to evaluate how the urban bird research can contribute to bird conservation in different contexts.

To fulfil these objectives in a thorough way is not possible (we would probably need a specific volume and additional expertise on some areas to accomplish that). Thus, accordingly to the title, we will not provide any solutions but merely a general set of reflections over present gaps in urban bird research and conservation issues.

24.2   Filling Gaps in Urban Bird Research

24.2.1   *Bird Census in Urban Settings: Not as Easy as It Seems*

The estimation of bird species richness and population sizes is central to most of the bird ecological research, especially to applied ecology, and thus the development of counting methods is crucial in the advancing of the discipline (see Elphick 2008). Accordingly, there is a considerable investigation on the benefits and limitations of bird-counting methods that is periodically updated trough manuals and papers (for recent examples, see, e.g. Rosenstock et al. 2002; Matsuoka et al. 2014). Urban bird ecology, however, has mostly ignored such approach, adopting in an uncritical way methods developed to census birds in other ecosystem types and being remiss in incorporating an explicit modelling of detection probability in bird census work (van Heezik and Seddon 2016).

Van Heezik and Seddon (2016) provide compelling reasons about the need of reliable estimates of bird populations in urban areas taking into account the probability of detection through different techniques (e.g. distance sampling) and how this objective is constrained by built structures, social factors and a mosaic of many small private parcels of land. Sometimes, a careful consideration of these factors may lead to the uncomfortable but indisputable evidence that sophisticated bird census methods will not render estimates of population abundances more

reliable than indices of population size obtained through simpler field methods (Johnson 2008). Even in the latter cases, urban settings and urban bird communities show some features that entail some difficulties in the business-as-usual bird census work. We shall succinctly examine some of these factors in the following paragraphs.

A first obvious factor is the physical structure of the built-up landscape. In compact cities where high-rise buildings predominate, the upper part of buildings is mostly inaccessible to the observer in such a way that an unknown proportion of the population of bird species that use buildings for roosting, feeding or nesting purposes may be unnoticed. This scenario would resemble a natural cliff system but with the additional trouble that private property makes it challenging to sample the top of the buildings. Similarly, land ownership often interferes a proper sampling of private gardens in cities where these are a relevant landscape feature.

Usually, bird counts (of landbird species) start shortly after dawn and stop to midday coinciding with the greatest output of song and hence of detectability (e.g. Blake et al. 1991; Bibby et al. 1992). However, there is an increasing recognition that urban bird populations exhibit behavioural traits that may differ from populations in natural areas (see Dominoni 2016; Miranda 2016). For instance, in response to anthropogenic sound, urban robins *Erithacus rubecula* sing mostly at night (Fuller et al. 2007), and European blackbirds *Turdus merula* exposed to artificial light extended their activity into the night (Dominoni 2016). Hence, doing censuses as usual (i.e. in the 7–11 a.m. interval) could render inaccurate counts of these species in urban settings, and a shift of census work to nocturnal hours would be necessary, similarly as occurs in the Finnish night-singing bird census scheme (Koskimies and Väisänen 1991) addressed to estimate population size of species that sing mostly at night like, e.g. nightingale *Luscinia megarhynchos*. Note that anthropogenic sound not only may modify behaviour of urban bird fauna but may reduce detectability of birds.

Another important component of urban settings that may heavily influence bird censuses is direct human disturbance. A fundamental difference in doing census work in "natural" and urban settings is that in the former the only source of disturbance (leaving aside natural phenomena like rain or wind) is (ideally) the researcher. In urban settings, this does not occur: bird censuses are carried out simultaneously with a variable degree of human disturbance (pedestrians, dogs, cars, etc.). Furthermore, such disturbance may occur in an unnoticed way as the "ghost of recent disturbance": a low number of birds recorded in one public urban park could be due to that 2 min before the researcher arrived to the park there was a person walking with a dog. As direct human disturbance may exhibit daily patterns, it follows that urban bird censuses maybe should be carried out avoiding peaks of human activity. Regrettably, in working days, the highest affluence of people in urban parks (crossing them to reach the job or the school, footing, walking dogs) often coincides with part of the interval of maximum output of song in many countries. By last, direct human disturbance may influence the behaviour of urban birds and ultimately detectability: flight distance of birds in urban and rural settings may be different (Møller 2008), thus precluding comparisons.

In summary, the automatic application in urban areas of bird census methods developed in other habitat types may be misleading, producing flawed understanding and bad management decisions. It is time to evaluate the situation and try to find solutions if it is necessary.

24.2.2 Research Approaches: There Is Room for Improvement

Overall speaking, we could identify three main approaches (each one relying on underlying theoretical frameworks) in the study of urban bird abundance and diversity: the first two approaches are the "rural–urban gradient" and the "landscape ecology approach" which both have been worldwide employed and the third "urban atlas studies" is very much tied to European cities.

24.2.2.1 Rural–Urban Gradient Studies

The origin of the gradient approach lies on comparative studies initially of two sites showing contrasting level of urbanisation (Pitelka 1942; Tomialojc 1970; Emlen 1974) and then of several sites (Lancaster and Rees 1979; Green 1984) that were firstly described as an urbanisation gradient by Ruszczyk et al. (1987). Later McDonnell and Pickett (1990) coined the term rural–urban gradient to define a conceptual framework that greatly has stimulated research on patterns of urban bird communities (e.g. Blair 1996; Clergeau et al. 1998; Maestas et al. 2003; Chamberlain et al. 2004; Fraterrigo and Wiens 2005). The results obtained through rural–urban gradient studies are quite diverse and taken as a whole do not allow strong generalisations about the response of bird diversity to urbanisation (which was already pointed out in Marzluff et al. 2001). This is hardly surprising since in comparative approaches the findings heavily depend on (i) the quality of what is being compared (McKinney 2002), (ii) the selection and level of precision of the specific measures of urbanisation (McDonnell and Hahs 2008) and (iii) a plethora of other factors including disturbance history (Ramalho and Hobbs 2012), landscape context (Hedblom and Söderström 2012), sampling design and potentially confounding environmental variables to cite a few (for a thorough review, see Catterall 2009). These circumstances not only undermine the understanding of causal relationships in a specific study but made it difficult to compare across studies, especially when they involve a wide interpretation of what a gradient means. Many of the problems described are common to other studies conducted in more natural areas but probably are exacerbated in urban settings where human influence adds complexity and unpredictability to ecological phenomena. Therefore, to reduce sources of variability, a greater effort should be devoted to reach a consensus and to implement a standard protocol of research (see du Toit and

Cilliers 2011). In regard to this, we think that abstract definitions of the ecological gradient (e.g. wildland–urban parks–garden terraces–business district) making difficult comparisons across studies should be avoided.

24.2.2.2   Landscape Ecology Studies

If gradient studies use the amount of habitat type as the main explanatory variable of bird fauna patterns, other approaches have focused on configurational variables, i.e. on habitat as discrete, spatially limited units. Initially studies were made under the powerful influence of island biogeography theory, and thus urban habitat patches (usually green spaces) were envisioned as embedded in a hostile and homogeneous matrix very much like islands in a sea of concrete. Later, according to mainstream ecology (Haila 2002), the concept of the matrix has evolved to a much more complex and dynamic one (Driscoll et al. 2013). Currently, patches and matrix are considered as interacting parts of the landscape mosaic that can be fruitfully studied, applying methods and principles of landscape ecology (Wu 2008). The underlying assumption in all cases is that the number, quality, size and spatial arrangement of patches influence bird population and diversity (and other ecological phenomena) through different mechanisms (movement, resource availability, dispersal, etc.).

Similarly as occurs in research conducted in other landscapes (see Fahrig 2003), there is no general agreement on the relative importance of local (patch area, habitat structure, etc.) and landscape (isolation, contagious, etc.) factors on urban bird diversity, although some reviews however indicate that the former outweigh the latter (Evans et al. 2009; Beninde et al. 2015). That uncertainty is motivated by several factors and we could mention (i) the diverse definition of the observational unit, i.e. the landscape, (ii) the wide availability and diverse use of landscape measurements facilitated by GIS software and (iii) the scarcity of studies exploring the movement of birds among patches (but see Tremblay and St. Clair 2011). As occurred in gradient studies, some agreement on research protocols and methods would alleviate the extreme heterogeneity (and hence incomparability) of studies. Additionally, given the rapid advance in tracking technologies (tag weights and prices are falling noticeably) in a near future, we should expect a considerable progress on the understanding of bird movement across landscape.

24.2.2.3   Urban Atlas Studies

Mapping the distribution of presence and abundances of birds across larger regions or countries is a common approach in mainstream ecology (Gibbons et al. 2007), but in urban areas, it is mostly a European approach (or even Central European; for a comprehensive review of the subject, see Luniak 2016). Bird urban atlases may constitute a powerful tool in engaging citizens in urban science and conservation projects and provide invaluable spatially explicit information useful for urban

planning (Luniak 2016). It is therefore puzzling that the enormous quantity of data gathered in many urban bird atlases across Europe have generated a scarce number of papers published in peer-reviewed journals (but see e.g. Witt et al. 2005). However, data gathered in urban bird atlases can be employed to explore the factors promoting urban bird diversity (Murgui 2009a) and the drivers of the distribution of individual species across the urban landscape (Murgui 2002, 2009b). In short, urban bird atlases allow the examination of many of the topics outlined in this section.

24.2.3   The Forgotten Combination of Scale and Quality Aspects

Already more than 20 years ago, Daniel Simberloff claimed that:

> The "old conservation biology" emphasized the detailed study of habitat use by individual species. This sort of work is less popular in academia than it was formerly. It is not aimed at large generalizations, it is very labour intensive and it is often viewed as old-fashioned natural history. (Simberloff 1995)

The situation depicted by Simberloff describes accurately current research in urban bird ecology. The influence of landscape ecology and metapopulation conceptual framework and the development of technological advances in remote sensing and GIS-based metrics have emphasised broad-scale research (Miller 2012). This makes topics like habitat use/selection, foraging and breeding ecology of individual species relatively rare in urban ecological research.

For instance, a search in ISI Web of Science using the keywords "urban", "habitat" and "bird" rendered only 30 papers published from 1990 to 2014, most of them (23) between 2001 and 2014. Further, some of them employed very large grains and extent (Jokimäki and Suhonen 1998; Hashimoto et al. 2005; Murgui 2009b; Pennington and Blair 2011), thus making them unsuitable to unravel fine-scale patterns of habitat use/selection; only a small quantity of papers addressed at proper scale the topic of bird habitat use/selection in urban areas (e.g. Schwarzová and Exnerová 2004).

The scarcity of this kind of studies (for similar results, see Magle et al. 2012) is unfortunate for three reasons. First, an integration of patterns and processes across different spatial scales is necessary to a full understanding of ecological phenomena in urban areas (Hostetler and Holling 2000) and elsewhere. Secondly, fine-scale ecological knowledge may help to understand some processes (e.g. nest predation, see Stevens et al. 2007) that may influence the distribution of birds across rural and urban landscapes. By last and crucially, the information provided by single-species studies could be decisive to inform specific design and management guidelines in urban areas (Miller 2012). For instance, detailed research on feeding and nesting resources provided by exotic versus native plant species and how bird species use them (see e.g. Gleditsch 2016) would be invaluable in adopting gardening decisions

at different levels of social and institutional organisation from householders to city planners (see Goddard et al. 2016).

24.2.4 Long-Term Bird Monitoring

As a whole, temporal dynamics have been poorly incorporated into the ecological study of urban bird fauna (Garden et al. 2006; Luck and Smallbone 2010 but see Fidino and Mason 2016). Two particularly serious shortcomings are the scarcity of studies of long-term changes of bird fauna and the shortage of studies documenting temporal changes after urbanisation process.

Although some exceptions exist (e.g. Turner 2003; Cannon et al. 2005), the absence of urban bird population monitoring schemes is the rule worldwide (Fergus et al. 2013), and this shortage does not seem to be compensated by monitoring schemes operating at national scale (Bland et al. 2004). Thus, to improve our understanding of central aspects in urban bird ecology, namely, bird population dynamics, schemes addressing breeding success, survival and abundance (similarly as, e.g. the Integrated Bird Population Monitoring in the UK, Peakall 2000) are necessary in urban areas. To accomplish such objective is crucial involving people in urban monitoring programmes, something that should not entail serious problems insofar census plots in urban areas can be reached after a short walking, biking or using public transport. However, it is ironic that remote and depopulated areas often exhibit better census coverage of birds than places where most people live, for example, in the Swedish national bird programme (not including urban areas).

Similarly to the scarcity of monitoring-based studies, there are few examples investigating temporal changes of bird diversity in sites undergoing urbanisation. Most of them have compared historical (or older) records with contemporary survey's data (e.g. Batten 1972; Aldrich and Coffin 1980; Major and Parsons 2010) but using large sampling intervals that prevent the examination of short-term effects of urbanisation. Considering that large-scale processes of land development occur daily worldwide, the scarcity of studies documenting the influence of this phenomenon on birds is absolutely regrettable. Fifteen years after Marzluff et al. (2001) pointed out the need of such studies, no major improvement is seen. Thus we lack a powerful tool to refine and visualise our understanding of the causal connection between urbanisation and changes in bird diversity.

24.2.5 Experiment Is the Key

In the above paragraphs, we outlined how taking into account the temporal dimension of phenomena would benefit our understanding of the causal relationships between urbanisation and bird fauna. But this is only possible up to a certain point since disentangling the influence of the urbanisation process and other concomitant

drivers (e.g. climate change) needs appropriate experimental and sampling design. Several authors have called for a greater contribution of experimental work in urban ecology (Marzluff et al. 2001; Shochat et al. 2006; Felson et al. 2013), but regarding bird fauna, this has been mostly focused on behavioural aspects (e.g. Shochat et al. 2010; Dominoni 2016) and patch management (e.g. Heyman et al. 2016). Conversely, there is an extreme paucity of studies investigating large-scale episodes of land development through experimental (or pseudo-experimental) design, a situation that differs with research on the effects of other human activities on bird fauna like logging (Hache and Villard 2010), industrial activity (Hamilton et al. 2011) or transport infrastructure development (Torres et al. 2011). Experiments are not only important from a pure scientific point of view. Carefully designed experiments would enable to fill the gap between research and practice, improving the often few specific guidelines that urban bird ecology offers to meet the needs of practitioners (Miller 2012), thus contributing to better design and management of urban areas.

24.3 Towards Effective Conservation Strategies

In the previous section, we have explored some (and by no means all) of the research needs that potentially could improve our understanding of urban bird ecology. Such improvement in turn could collaborate to shape bird conservation strategies in urban areas. In the following paragraphs, we will briefly emphasise three issues that to us seem especially pressing.

24.3.1 Urban Design

Urbanisation may occur through many different ways ranging from infilling city centres to rural housing (Milder 2007), but in all cases, it entails negative consequences to the bird community that existed prior to development through different processes (from habitat loss to air pollution, to cite a few). Therefore, a first need would be to assess the benefits and shortcomings of a compact city versus urban sprawl (see Lin and Fuller 2013). Compaction can be achieved in several ways (e.g. reducing the extent of green spaces), and sprawl may adopt numerous forms from clustered to diffuse development (e.g. Pejchar et al. 2007). Therefore, these diverse models of urbanisation should be properly evaluated for their effectiveness at protecting bird fauna. Although several studies indicate that compact design entails less impact than urban sprawl on bird fauna (Gagné and Fahrig 2010; Sushinsky et al. 2013, but see Lenth et al. 2006) and on some invertebrate taxa (Soga et al. 2014), the evidence is still scant.

Irrespective of the urbanisation model, landscape-level (e.g. size and connectivity of habitat patches, Donnelly and Marzluff 2006) and fine-scale factors

(e.g. decisions on plant composition, Stagoll et al. 2010) will be critical in retaining part of the bird fauna previous to the development or to promote (or avoid) the establishment of a new one. Traditionally, conservation strategies have been focused on remnants of more natural habitats, public green spaces and private gardens and to a lesser degree on derelict land (see Meffert 2016). It is time to pay attention to buildings which may impact negatively on bird fauna through collisions (Hager et al. 2008; Sheppard 2011) and conversely may provide nesting and feeding opportunities through green walls and roofs (Baumann 2006; Chiquet et al. 2013).

In short, the influence of the different aspects of urban design on urban bird fauna should be the object of an increasing research effort. Because urban areas may differ markedly not only in broad design (compact versus sprawl) but also along many environmental features (provisioning of green spaces, management, etc.), thus the value of future work would be enhanced through comparative research between different towns and cities (Hahs et al. 2009).

24.3.2   Is a Specific Framework to Urban Bird Conservation Needed?

The long-standing consideration of urban settings as a marginal habitat for wildlife where some of the most thriving birds are considered pests has entailed two undesirable consequences. From one side, bird conservation programmes in urban areas have been a largely neglected issue in most countries (Fergus et al. 2013). To the other side, we mostly lack a critical examination about (i) the application in urban areas of generic conservation criteria and strategies and (ii) the incardination of urban conservation into a wider conservation context. As an example, we will focus on bird density and abundance in the below text since it is a common conservation metric.

It is generally assumed that there is a positive relationship between avian density and demographic parameters (Bock and Jones 2004) in such a way that the probability of population persistence is enhanced in habitat patches showing a greater abundance of birds. Thus, it follows that conservation efforts should be addressed to increase abundance of scarcer species. This strategy poses an immediate problem of allocation effort in urban areas as far as these usually hold: (i) a large number[1] of low-density species which are common in the surrounding of nonurban habitats and (ii) a few high-density species very associated to urban areas. Should we spend part of the usually meagre conservation budgets in bird species common outside the city? Or should we focus on relatively uncommon species at both city and regional levels like the peregrine falcon *Falco peregrinus* in the UK (Drewitt 2014) and the lesser kestrel *Falco naumanni* in many Spanish regions

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[1]Note that species richness in urban areas heavily depends on the definition of what is "urban".

(Ortego 2010)? Further, wouldn't it be a good strategy to also concentrate efforts in representative, abundant species in cities? These species may be relevant to biodiversity conservation in wider geographical contexts (see Gaston and Fuller 2007) since they may fulfil a role in the urban ecosystem (for instance, rock doves as prey for urban raptors) and some of them are declining in urban areas (e.g. the house sparrow *Passer domesticus*; see De Laet and Summers-Smith 2007).

These decisions do however involve additional trade-offs. If (see Sect. 24.3.3) public awareness of biodiversity problems requires a daily contact with nature, then a diverse urban avian environment would be a requisite; on the other hand, a daily contact will not occur with rare species but with the common ones (e.g. rock dove) whose abundance is often blamed by people as a source of nuisance. Therefore, it would be necessary to encourage the appreciation of these species (Dunn et al. 2006).

Previous paragraphs are based on the premise that population size or density reflects the accurate quality of a habitat. Nevertheless, a negative or neutral relationship between abundance and reproductive rate may occur (van Horne 1983; Skagen and Yackel Adams 2011), thus producing ecological traps, i.e. environments selected by birds on the basis of cues that correlated formerly with habitat quality (Schlaepefer et al. 2002; Robertson and Hutto 2006). In this context, bird abundance may be a misleading parameter for conservation evaluation.

There are some suggestions that density is negatively related to reproductive success more often in areas of human disturbance (Bock and Jones 2004), thus constituting ecological traps. Some authors have found evidence that urban areas constitute ecological traps for birds (Strasser and Heath 2013; Bonnington et al. 2015) and some did not find any ecological traps (Leston and Rodewald 2006; Stracey and Robinson 2012). A deeper insight in this phenomenon (which could occur through adequate monitoring of breeding parameters; see Sect. 24.2.5) would be critical to obtain a realistic appraisal of what can bring urban areas to bird conservation. Importantly, such contribution should be evaluated in a wider context than cities. As populations do not occur in isolation, a potential negative effect of urban areas could threaten regional populations through source–sink dynamics. For instance, urban areas may offer an abundant and predictable source of food (through, e.g. bird feeders) that may attract birds of the surrounding landscape when there is a shortage of natural feeding resources (e.g. McKenzie et al. 2007), but on the other side, bird feeders may provoke a range of consequences from diseases to alteration of migratory patterns (for a review, see Jones and Reynolds 2008) that may impact bird populations at different geographical levels. Currently, our knowledge of the extent and significance of these issues for regional populations of birds is at best limited.

In summary, the application of a common conservation metric in urban areas is subjected to some uncertainties that should be evaluated. Whether other conservation biology basic principles and applications require a specific adaptation to urban areas remains an open question.

24.3.3 Support of City Dwellers to Bird Conservation

In the above sections, we have explored some topics on bird conservation not only at city scale but at wider contexts from an ecological perspective. Nevertheless, a sociological approach is important for urban (and elsewhere) bird conservation (see Goddard et al. 2016). Many decisions about how much worldwide conservation and restoration investment is appropriate will depend on people whose conception and experience of wilderness are deeply shaped by their life in urban areas (McKinney 2002; Hedblom et al. 2016). Some authors (see Miller 2005a; Dunn et al. 2006 and references therein) have suggested that (i) a decreasing contact with nature as it occurs in cities will lead to less sympathetic attitude to nature conservation and (ii) to reverse that situation would be necessary of a proper urban design and management that enhance nature in cities. These assertions depict a reasonable and logical scenario. However, there are some points that need further investigation.

A first one concern is whether the support to nature conservation depends on contact with biologically rich environments. If so, people living in rural areas should be more supportive than urban dwellers, but this remains an open question (for contrasting views on the scant existing evidences, see Mehtälä and Vuorisalo 2005; Miller 2005b); one could suspect that the opposite thing may occur, because for urban dwellers nature conservation usually does not limit conventional standards of well-being and socioeconomic expectations as may occur in rural areas (e.g. supporting wolf conservation is probably harder when a wolf pack has killed your guarding sheep mastiff). Of course, geographical variation in cultural values, education and socioeconomics (to cite a few variables) adds complexity to the question.

Second, there is scant evidence on the relative support to biodiversity conservation of people inhabiting cities differing in their biodiversity potential (but see Luck et al. 2011). A first step would be comparing support to nature conservation in compact cities (where people experience nature mostly through public urban green spaces) and in sprawling cities where private gardens constitute a relevant feature of the urban landscape. Results should be interpreted with caution: a hypothetical lesser support to nature conservation of compact city dwellers could be due to an untouched surrounding area perceived out of risk. Contrastingly, greater support to nature conservation of sprawling city dwellers may stem from a perception of land consumption due to development. In this last case, we would find the bitter paradox of people regretting the fate of a landscape that they contribute to degrade and eventually to destroy.

Third, an increasing experience of nature in cities could, paradoxically, diminish conservation support of wildland and rural areas. A comfortable (and usually less complex) experience of nature in public urban parks and private gardens could be regarded as enough satisfactory by urban dwellers who could consider unnecessary the more powerful but often effort-demanding experiences in wildland. This attitude in turn could lead to appealing but still little scientifically proved assumptions

on the compatibility of human activity and wildlife and to decreasing support to wildland protected areas (Battisti and Gippoliti 2004). Such hypothetical scenario cannot be ruled out automatically.

Fourth, irrespective of urban design, any enhancement of nature in cities will be useless in the absence of educational and participatory schemes that allow citizens to discover, have access to, understand and protect nature in urban settings and elsewhere. There are many interesting examples across the world (see, e.g. Blaustein 2013).

24.4 Conclusions

Across this chapter, we have pointed out some gaps in our knowledge of urban bird ecology and conservation, a circumstance that in no way eclipses the remarkable advance that the discipline has experienced in the last three decades. Nevertheless even such advance pales in comparison with the magnitude, pace and complexity of urbanisation phenomena worldwide. Nearly 2000 years ago, Greek sophist Philostratus wrote: "*Because gods perceive future things, men what is happening now, but wise men perceive approaching things*" (Philostratus, Life of Apollonius of Tyana). As scientists (i.e. learned women and men), we should make all effort through rigorous and collaborative research to anticipate urbanisation effects and use such knowledge to promote bird conservation in cities and in the surrounding land. Time presses.

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Marcus Hedblom Marcus received his PhD in 2007 concerning birds and butterflies in urban and peri-urban habitats. He has since then worked as a nature conservation strategist in the fourth largest city in Sweden (Uppsala), made a postdoc at Gothenburg University and worked as a project leader at the national monitoring program for biodiversity (NILS) at the Swedish University of Agricultural Sciences (SLU). He is presently involved in numerous transdisciplinary research projects concerning urban ecosystem services and leader of a research group studying human stress reduction from natural sounds in cities at SLU. Marcus is an associate editor of the Journal Urban Ecosystems and founder of the Swedish Think tank Green City.

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