Assessing the Ecological Significance of Linkage and Connectivity for Avian Populations in Urban Areas

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Abstract

As urbanisation continues to fragment and degrade habitats there is a need to ensure that cities are managed to sustain ecosystem function and high biodiversity. Ecological theories suggest that areas with higher levels of functional connectivity sustain a more diverse avian population. By identifying the key habitat features that dictate the distribution and abundance of avian populations it is possible to inform planning policy to maximise biodiversity. Bird species presence and abundance across an urban gradient in Birmingham (UK) was surveyed at 70 sites over three sampling periods (between 2009 and 2010), in combination with a tree survey and digital analysis of land use. Functional connectivity was shown to increase the abundance of bird species and to ameliorate the impacts of urban development. Bird species were found to vary with their associations with vegetation structure and a proxy for invertebrate productivity. There was clear evidence for increasing native tree species in the urban matrix to support more bird species. Ringing data collected between 2008 and 2011 were used to examine bird movements through the city and the influence of habitat factors such as connectivity and built space in the matrix. Bird movements between ringing sites demonstrated the permeability of the city and the importance of connectivity in the landscape. This work showed that the composition of the matrix influences bird occupancy and turnover of sites. The novel findings presented in this thesis on the influence of the urban landscape on urban avian ecology should make an important contribution to urban conservation methods.

For *my* urban birds; Maggie, Pi and Hansel

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Chapter 1. Introduction

1.1 Urbanisation

The human population is increasing and the proportion of people migrating into urban areas is rising. It is estimated that 58.0% of the population will reside in urban areas by 2025 and 67.2% by 2050 (United Nations, 2011) causing an intensification of land-use that threatens to compromise the quality of the urban environment for both people and biodiversity (Tratalos et al., 2007a).

Humans modify their environment to a great extent (Vitousek et al., 1997) and consequently the spatial pattern of land use in cities reflects human processes and influences the ecology of urban environments (Zhang et al., 2004). Cities are characterised by highly modified landscapes comprising possibly the most complex mosaic of relict habitats, designed spaces and multiple land uses of any landscape (Andersson, 2006). Continued development is leading to urban sprawl (Marzluff, 2001, Sadler et al., 2010) and the 'densification' of cities (Dallimer et al., 2011) potentially leading to the impairment of ecosystem function in the urban landscape, but few data currently exist to indicate how much densification can be withstood (Hale et al. 2012).

1.2 The impacts of an urban environment

The most pervasive issues relating to urbanisation are loss of habitat, deterioration of habitat quality, and increasing fragmentation of the remaining habitat (Hanski, 1999, Tratalos et al., 2007b). Through these processes, urbanisation results in an environment that is compositionally more heterogeneous (McDonnell and Pickett, 1990, Young and Jarvis, 2001, Sadler et al., 2006), geometrically more complex (Hale et al., 2012), and ecologically more fragmented (Luck and Wu, 2002, Zhang et al., 2004, Andersson, 2006) potentially resulting in reduced connectivity and, therefore, restricted dispersal potential for mobile taxa such as birds. Urbanisation has been suggested to be the most important driver of extinction during this century (Marzluff et al., 2001, Goddard et al., 2010) and consequently conservation of biodiversity in urban areas has become a priority (Marzluff, 2001, Loss et al., 2009, Yu et al., 2012).

Urban environments are characterised by features such as artificial light at night, altered ambient noise primarily from transport (typically loud and low) (Slabbekoorn and Ripmeester, 2008), additional anthropogenic food (Jones and Reynolds, 2008, Robb et al., 2008, Rolshausen et al., 2009), warmer microclimate (heat island effect), higher ozone levels, increased precipitation, modified

hydrology, altered ecological processes such as soil functionality, and increased numbers of exotic species (Pickett et al., 2001). These alterations in the ecological characteristics of the urban landscape can lead to a host of impacts on wildlife. In birds there have been measured changes in the timing of reproduction (Partecke et al., 2004), in song (Slabbekoorn and Ripmeester, 2008, Mockford and Marshall, 2009), in avian morphology and body size (Grégoire, 2003, Evans et al., 2009a), intensity of carotenoid-based plumage pigmentation reflecting oxidative stress (Isaksson et al., 2005, Isaksson and Andersson, 2007), increased predation from domestic pets (Sims et al., 2008), increased baseline corticosterone levels (Bonier et al., 2007, Schoech et al., 2007) and higher breeding densities (Pickett et al., 2001). Chamberlain et al. (2009) carried out a review of productivity of passerine species in urban areas and showed that the majority of species exhibited earlier lay dates, lower clutch size, lower nestling weight and lower fledging success in urban landscapes. It was suggested that food availability was a significant influence upon these demographic parameters. These changes demonstrate the importance of understanding the effects that urban landscapes can have on avian biology, enabling mitigation strategies to be put in place.

1.3 Importance of urban conservation

With the growth of the human population and its move into urban areas, urban ecology has become more important and relevant. There is a widening gap between humans and the natural world due to the increased habitation of cities (Miller, 2005). The modified human environment means that people have less contact with nature increasing the likelihood that they will have less interest in protecting it (Miller, 2005). Alternatively, the loss of an interaction with nature leads to a heightened appreciation of it, leading to a greater likelihood of a desire to conserve wildlife (Jones, 2010). Both arguments have been put forward, but importantly urban habitats are those that a large number of people interact with and therefore it is important that they are understood, protected and improved for biodiversity.

It is important that where people live should enhance health (both physical and psychological) and well being, and there is evidence to suggest that urban areas with higher biodiversity and increased green space provision do just that (Miller, 2005, Tzoulas et al., 2007, Sadler et al., 2010). Amongst other things, it has been found that people who are exposed to natural environments recover more quickly from stress, children have enhanced intellectual and emotional development (Miller, 2005), and there are psychological benefits increase with higher biodiversity of urban green spaces (Fuller et al., 2007). Such evidence justifies biodiversity protection, in addition to the value of biodiversity in its own right.

Ecosystem services are the benefits that humans gain from ecosystems (POST, 2007, Gaston, 2010, Gaston et al., 2010) and they unify economics and conservation biology (McDonald and Marcotullio, 2011). These services are grouped into:

- Supporting services that underpin the other services. They include nutrient cycling, soil formation and photosynthesis
- Provisioning services such as food, fuel, pharmaceuticals and water
- Regulating services such as climate regulation, water purification, waste treatment and flood protection
- Cultural services such as education, recreation, ecotourism and aesthetic value.

The Millennium Ecosystem Assessment (MA) was a project initiated by the United Nations Environment Programme (UNEP) in 2001 to assess how human-made changes to ecosystems affected human well-being (POST, 2007). Due to the extent of modification of the environment in urban areas, it is difficult to detect the provision of several ecosystem services (POST, 2007). Services such as climate regulation and biodiversity potential are influenced by the availability and type of vegetated cover. Increased densification of cities may reduce and change the distribution of such cover and may have undesirable effects on these services (Tratalos et al., 2007b, McDonald and Marcotullio, 2011). On the flip side, due to intensification of agricultural techniques, some urban areas may in fact provide wildlife havens due to the provision of extensive green space and habitat heterogeneity (Gregory and Baillie, 1998, Peach et al., 2004a, Gaston et al., 2010).

1.4 Fragmentation

Human-driven expansion and intensification of land use, such as that found during urbanisation, are the most prominent forces fragmenting green spaces (Andrén, 1994, Beier and Noss, 1998, Marzluff, 2001, Young and Jarvis, 2001), resulting in the loss of habitat, division of contiguous habitat, and isolation producing habitat patches of varying quality, surrounded by a matrix of habitats unlike the original (Andrén, 1994, Young and Jarvis, 2001).

A gradient approach is a useful method for developing an understanding of interactions between urban development and the structure and function of ecological systems (McDonnell and Pickett, 1990, Alberti et al., 2001). The urban gradient is complex and indirect (McDonnell and Hahs, 2008) with 'peaks' and 'troughs' in the levels of development (Alberti et al., 2001). For example the city of Birmingham, UK, which is the study site for this research, has gone through cycles of development that have produced areas with varying densities of development and sealed land-cover across the

city (Figure 2.1). Studies, however, often use a transect approach, measures of distance from the centre to quantify the level of urbanisation (e.g. Pennington and Blair, 2011, Dallimer et al., 2012) or a qualitative description of level of urbanisation (e.g. Blair, 1996, Reale and Blair, 2005, Blair and Johnson, 2008) and they often lack replicates of sites to represent each urbanisation type (e.g. Blair, 1996, Reale and Blair, 2005, Blair and Johnson, 2008, Chapman and Reich, 2007). A more representative gradient is one that describes urban pattern metrics such as percent land by land-cover or land-use type (Alberti et al., 2001) and is ecologically relevant to the taxa in question (McDonnell and Hahs, 2008). Additionally broader descriptions of urbanisation are of value as they are possible to apply to other urban areas. Until now, no studies have used a gradient approach where the land use and land cover have been quantified for birds in a British urban landscape.

1.5 Dispersal disruption

Through habitat destruction and increasing fragmentation, ecological barriers are being created affecting functional connectivity, increasing heterogeneity and, therefore, potentially dispersal. Connectivity is defined as the degree to which the landscape facilitates or impedes movement of individuals between resource patches (Taylor et al., 1993) and is important to maintain ecosystem function. The extent to which animals move through a landscape is dependent on the species' use, ability to move, risk of mortality, movement rate among habitat patches and features of the landscape (With et al., 1997, Tischendorf and Fahrig, 2000). With fragmentation often comes a loss of connectivity.

Reduced dispersal within urban or between urban and rural environments has been shown to lead to phenotypic and behavioural intraspecific divergence (e.g. Slabbekoorn and Peet, 2003, Isaksson et al., 2005, Partecke et al., 2006, Partecke and Gwinner, 2007). Behavioural divergence of a sexual signal such as song in Great Tits (*Parus major*) (Mockford and Marshall, 2009) could lead to or show existence of genetic divergence within the species. Reducing recognition of potential mates could effectively lead to assortative mating (e.g. Bearhop et al., 2005) and this, combined with potential geographic and ecological isolation, could reduce gene flow and reduce the genetic variation of a population. It has been suggested that the isolation of urban populations needs to be reasonably pronounced before genetic differentiation can be fixed (Johnston, 2001, Rolshausen et al., 2009). However, it has also been shown that divergence can also occur over a small spatial scale with continued gene flow (Blondel et al., 1999, Garant et al., 2005, Postma and van Norrdwijk, 2005, Senar et al., 2006).

In a fragmented environment, as found in urban areas (Luck and Wu, 2002, Zhang et al., 2004, Tratalos et al., 2007b), the three-dimensional structure of vegetation is potentially highly influential on bird assemblages and abundance, providing habitat for more birds which are sensitive to fragmentation (Goldstein et al., 1986). One of the most important and influential components of habitat structure is spatial heterogeneity or patchiness (Wiens, 1976), which includes both the characteristics of vegetation and its variation in space (Rotenberry and Wiens, 1980) within habitat patches and throughout the matrix. The matrix is an important feature of the urban landscape (Ricketts, 2001, Kupfer et al., 2006, Laurance, 2008, Prevedello and Vieira, 2010), as it can allow movement and provide alternative habitat. Abundance, movements, occupancy and turnover of birds can all be influenced by habitat and matrix structure, and vegetation composition. However until now there have been no studies that link these ecological parameters for birds to the environment in an urban context.

1.6 Study aims and objectives

The aims of this research are to understand the impact of landscape structure and connectivity on bird populations in urban environments using Birmingham, UK, as a case study and to assess the nature and permeability of the landscape matrix for bird movements.

The key objectives are to:

1. assess the abundance and distribution of birds across an urban gradient
2. model the connectivity of landscape for birds in Birmingham in a Geographic Information System (GIS)
3. assess the influence of urban landscape connectivity on bird abundance
4. quantify the influence of vegetation structure, composition and insect diversity on British urban bird abundance and distributions
5. Investigate whether there are seasonal changes in the way bird species respond to the urban landscape
6. quantify species-specific movements in an urban environment
7. investigate the significance of landscape connectivity and habitat features on the movement of urban birds
8. assess the influence of the landscape matrix on the occupancy and turnover of birds.

1.7 Thesis structure

Extensive bird surveys were carried out across 70 sites in Birmingham addressing the first objective to assess the abundance and distribution of birds across an urban gradient. In Chapter 2 these survey data are coupled with connectivity metrics of Birmingham produced in a GIS to investigate the effect of the level of connectivity of the landscape on avian abundance across an urban gradient addressing objectives 2 and 3.

In Chapter 3 the bird survey data is used to attend to objective 4 with vegetation physiognomy data across Birmingham from a GIS, tree survey data and literature-derived estimates of invertebrate productivity to investigate the influence of factors such as vegetation distribution, height and productivity of vegetative cover on bird species' distributions.

Extensive bird ringing was carried out across four years at 26 sites across Birmingham and these data are analysed in order to consider bird movement in an urban landscape and consequently focussing on objectives 6, 7 and 8. In Chapter 4these data are used along with environmental parameters derived from a GIS to focus on green space connectivity *via* an examination of bird movement through the cityscape.

In Chapter 5 the bird ringing data are used to investigate the influence of the composition of the matrix (the level of connected habitat and built space) on the occupancy and turnover of the ringing sites addressing objective 8.

In Chapter 6 a summary of the study's findings is presented with a discussion of the limitations of the study and suggestions of avenues for future research that would further illuminate influential factors on bird distributions and movements in an urban environment.

Chapter 2.   The importance of connectivity for birds in an urban environment

2.1 Introduction

2.1.1 Urbanisation

Urbanisation is increasing at a dramatic rate, to accommodate the growing human population and their activities (United Nations, 2011). Urban landscapes have become densified and greenspaces lost (Dallimer et al., 2011). Urban landscapes thus now often consist of a series of fragmented habitat patches of varying quality which are relics of previous, more widespread habitat (Young and Jarvis, 2001).

Human-driven expansion and intensification of land use, such as that found during urbanisation, are the most prominent forces fragmenting green spaces (Andrén, 1994, Beier and Noss, 1998, Marzluff, 2001, Young and Jarvis, 2001) leading to the loss of habitat, division of contiguous habitat, and isolation resulting in patches surrounded by a matrix of habitats unlike the original (Andrén, 1994, Young and Jarvis, 2001). Many studies have shown that habitat fragmentation leads to a decline in biodiversity and negatively affects species' persistence within habitat patches (e.g. Andrén, 1994, Hanski, 1999, Trzcinski et al., 1999). This is due to an increase in risk of mortality whilst moving between patches, lower recolonisation rates of empty patches, and reduced local population sizes resulting in increased susceptibility to extinction (Trzcinski et al., 1999, Marzluff and Ewing, 2001). In urban areas habitat fragmentation is exacerbated by multiple land uses, coupled with long-term changes in land use, causing widespread isolation and reduced levels of connectivity (Hale et al. 2012).

2.1.2 Structural versus functional connectivity

Connectivity is known to be important to maintain ecosystem function and can be defined as the degree to which the landscape facilitates or impedes movement of individuals between resource patches (Taylor et al., 1993). The extent to which animals move through a landscape is dependent on the species' use, ability to move, risk of mortality, movement rate among habitat patches and the features of the landscape (With et al., 1997, Tischendorf and Fahrig, 2000). Therefore, connectivity

should be described in relation to individual species rather than broad taxon groups. This species-centric connectivity is referred to as functional connectivity (Tischendorf and Fahrig, 2000). Structural connectivity, on the other hand, refers to habitat contiguity and is measured by analysing the landscape structure independent of any attributes of the focal organism (Tischendorf and Fahrig, 2000). Functional connectivity is thought to be a key property enhancing population persistence and species' occupancy in complex landscapes (Marzluff and Ewing, 2001, FitzGibbon et al., 2007) and increasingly, its importance is being recognised in studies of habitat fragmentation and the effects on wildlife populations (FitzGibbon et al., 2007).

The same landscape may have varying levels of connectivity dependent on the movement attributes of the focal organism. Structurally connected habitats may not be functionally connected if habitat features do not support movement. Likewise, non-contiguous habitats may be functionally connected if an animal is able to cross the matrix between habitat patches (Tischendorf and Fahrig, 2000, FitzGibbon et al., 2007). Species' responses to habitats are complex and throughout the year requirements may change when birds are establishing and maintaining territories, mate searching, nest building, foraging and provisioning young, or foraging and dispersing during the winter, for example (Simms, 1978, Perrins, 1979). These changes in requirements and behaviour are likely to have an impact on how the focal organism responds to the landscape and the level of connectivity it supplies.

2.1.3 The role of the matrix

The theory of metapopulation dynamics that was first proposed by Levins (1969) and elaborated into the current form by Hanski (1998), and island biogeography (MacArthur and Wilson, 1963) assume that sub-populations living in habitat patches are relatively isolated from each other (Andrén, 1994, Hanski, 1999). However, these assumptions are likely be violated in an urban environment where the landscape between the habitat patches (i.e. the matrix; Ricketts, 2001), may provide more connectivity than is immediately apparent (Prugh et al., 2008). Theories describing spatially structured populations often oversimplify or ignore the matrix (e.g. Ricketts, 2001, Kuefler et al., 2010) .

A landscape is not a binary mosaic of habitat and non-habitat but is, instead, grades of habitat that may be used for different functions such as foraging or nesting and to different degrees (With et al., 1997). Urban landscapes are not simply habitat and non-suitable matrix (Ricketts, 2001) but a gradient that varies in its role as a barrier or conduit for movement (Ricketts, 2001, Kuefler et al., 2010, Eycott et al., 2012). A habitat patch is a part of a landscape mosaic and any species found there

will not only be affected by the features of that patch (e.g. size, isolation) but also by the features of the surrounding matrix (Andrén, 1994, Castellon and Sieving, 2006). Functional connectivity incorporates the combined effects of matrix structure and its influence of movement on a species (FitzGibbon et al., 2007).

Where little habitat is available, such as in an urban landscape, it might be predicted that connectivity should be more important than in areas where plenty of habitat is available (Trzcinski et al., 1999, Martensen et al., 2008). However, where the taxon in question is mobile, as in birds, the impacts of isolation may only be evident in landscapes with very fragmented habitat and high levels of patch isolation, when the landscape consists of only 10-30% of the original habitat (Andrén, 1994).

There has been little work on fragmentation in urban habitats (FitzGibbon et al., 2007) and is currently very little evidence that connectivity in urban landscapes is important for birds. However there is evidence that connectivity is important for volant non-avian species such as bats in urban areas (Hale et al., 2012) suggesting that similar results may be found for birds. .

Many previous connectivity studies on birds have concentrated on translocation experiments in tropical systems where forest-dwelling birds are forced to choose an exposed or covered route back to their territories. Castellón and Sieving (2006) studied the Chucao Tapaculo (*Scelorchilus rubecula*); an endemic forest understory species in Chile. They showed that birds relocated to open habitat took much longer to disperse than those placed in treatments with adjoining corridors or surrounded by dense shrubs, where connectivity was enhanced. In a similar study, Gillies and St. Clair (2008) translocated and radio-tagged Barred Antshrikes (*Thamnophilus doliatus*), a forest specialist species, and Rufous-naped Wrens (*Campylorhynchus rufinucha*), a forest generalist species, from their territories in tropical dry forest of Costa Rica. The forest specialist was found to use wooded corridors for movement to a greater extent than the forest generalist. In both of these examples the species evolved in an undisturbed, contiguous habitat, and consequently are most likely to be vulnerable to habitat fragmentation (Marzluff and Ewing, 2001, Hashimoto, 2007).

These studies in a non-urban landscape cannot be easily applied to an urban area given the different habitat composition and matrices (FitzGibbon et al., 2007). Functional connectivity rather than connectivity based on Euclidean distances i.e. structural connectivity, is much more important due to the complexity of the matrix (FitzGibbon et al., 2007).

There have been a few studies directly investigating the role of connectivity in bird movements in the urbanised landscape. For example, Shanahan et al. (2011) assessed the importance of connectivity

and patch size in urban re-vegetation in Brisbane, Australia and found that connectivity positively influenced bird species' richness, and that connectivity in combination with patch area was important in increasing bird abundance. They measured connectivity of the vegetated patches using a multi-scale graph-theoretical approach, which produced measurements of total vegetated area connected to the study sites at different scales. This study focused on 20 sites with young stands of new vegetation, and only assessed urbanisation through human population density, rather than built space which is more appropriate in terms of the impacts on the landscape (McDonnell and Hahs, 2008). Questions also arise as to what landscape features act to enhance or reduce connectivity in urban areas. Fernández-Juricic (2000a) suggested that wooded streets were used by many bird species in Madrid, Spain, concluding that linear tree-lines could be utilised as corridors in urban areas. Their study, however, investigated a very restricted sample of the habitat available to urban birds, concentrating on only four parks and five wooded streets. Fernández-Juricic did not consider other urban vegetation, domestic gardens or the urban gradient as a context for considering the impact that linear vegetated features might have on bird movements. In a study in Calgary, Alberta, Canada, using an avian mobbing call as a lure, Tremblay and St. Clair (2009) showed that both anthropogenic and natural linear features such as roads, railway lines, transportation bridges across riparian corridors and rivers can impede bird movements, creating barriers to movement in the landscape. They suggested that managing vegetation adjacent to these features could mitigate the fragmenting effect of these liner features to movement.

Bolger et al. (2001) investigated the use of corridor-like structures by birds and small rodents in remnant strips of coastal sage scrub habitat, in dense residentially developed areas of San Diego County, California, USA. They found that the remnant strips of habitat and re-vegetated highway rights-of-way had the potential to be used as habitat linkages for native rodents and fragmentation-tolerant species of birds, and that habitat remnants only were suitable for fragmentation-sensitive bird species. This study further demonstrated the importance of assessing connectivity in a functional way, addressing the landscape on a species by species basis.

Predicting the spatial distribution of wildlife populations is important when developing management and conservation strategies (Rhodes et al., 2009), and research has shown that landscape structure and composition are influential factors in spatial distributions (Bergen et al., 2007, Whittaker and Fernández-Palacios, 2007, Laurance, 2008), dependent on the landscape and species in question. Understanding how birds use the whole landscape including the matrix and how the structure

influences permeability to animal movement is key to managing and conserving urban landscapes (Castellon and Sieving, 2006).

2.1.4 Aims

To date studies have not focused on the significance of the landscape matrix between the habitat patches nor the complexity of the urban landscape (e.g. Fernández-Juricic, 2000, Shanahan et al., 2011). The landscape is often examined as a series of homogenous pixels or grids, rather than in fine detail (Young and Jarvis, 2001) which loses clarity. In this study the landscape has been analysed at a fine scale to capture its complexity using a similar method to that employed by Hale et al. (2012). A focus on the role of all accessible vegetation to birds was taken, rather than just on linear features. The aims of the study were to:

i)   Assess whether urban landscape connectivity influences bird species' abundance;

ii)   Assess whether tree-lines are a good surrogate for functional connectivity for bird species in an urban context;

iii)   Consider whether there are seasonal differences in the response of birds to connectivity in the urban landscape.

2.2 Methods

2.2.1 Study site

Birmingham, UK, has a population of ~ 1 million people (2010) and is a highly urbanised region of the UK. Birmingham was a centre of the industrial revolution and has since undergone repeated development cycles and consequently distinct zones representing pre- and post-war regeneration can be identified. Within the study area there are high levels of sealed land-cover, canals, railways, residential areas of varying housing density, industrial zones, parks, nature reserves and agricultural land on the urban fringe (Hale et al., 2012).

Green space accounts for 14% of the land cover in urban spaces in the UK but some cities are greener than others. Birmingham has 33.7% green space (Sadler et al., 2010) and therefore is comparable to Leicester with 25% (Comber et al., 2008), Greater Manchester which has 32% (Gill et al., 2008), 30% of Greater London (Wilby and Perry, 2006) and Sheffield with 45% (Fuller and Gaston, 2009). What is more, Birmingham is comparable to cities across Europe (Table 2.1) making Birmingham a good case study and a relevant study site.

Table 2.1 Percentage of green area in European cities ordered by the amount of green area found in the city. Birmingham is highlighted in blue. (Figures collated from EEA, 2002, Fuller and Gaston, 2009 and Sadler et al., 2010).

City	Green Area (%)
Milan	1.2
Reggio di Calabria	1.9
Iraklion	7.4
Dublin	7.7
Lyon	11.1
Brussels	12.2
Nicosia	12.9
Sunderland	13.1
Ruhrgebriet	13.5
Porto	14.6
Prague	15.2
Copenhagen	18.4
Dresden	24.0
Leicester	25.0
Munich	25.2
Venice	28.5
Vienna	28.5
Greater London	30.0
Setubal	31.9
Greater Manchester	32.0
Grenoble	32.3
Birmingham	33.7
Bratislava	33.8
Palermo	36.8
Algarve	39.4
Bilbao	44.7
Sheffield	45.0
Ferol	46.0
Helsinki	46.3
Marseille	48.3
Tallinn	62.5

The landscape of the study area within Birmingham, was classified into 1 km^2 pixel urban land classes by Owen et al. (2006). Owen et al. used a Principal Component Analysis (PCA) to reduce dimensionality of the input database (spatial land-cover data from Centre for Ecology and Hydrology and UK Ordnance Survey) and extract any dominant relationships between the land-use variables. This was followed by a cluster analysis to aggregate the most closely related 1km^2 pixels into one of eight urban land-cover classes. These urban classes were used to stratify the sample of survey sites along an urbanisation gradient (Figure 2.1).

12
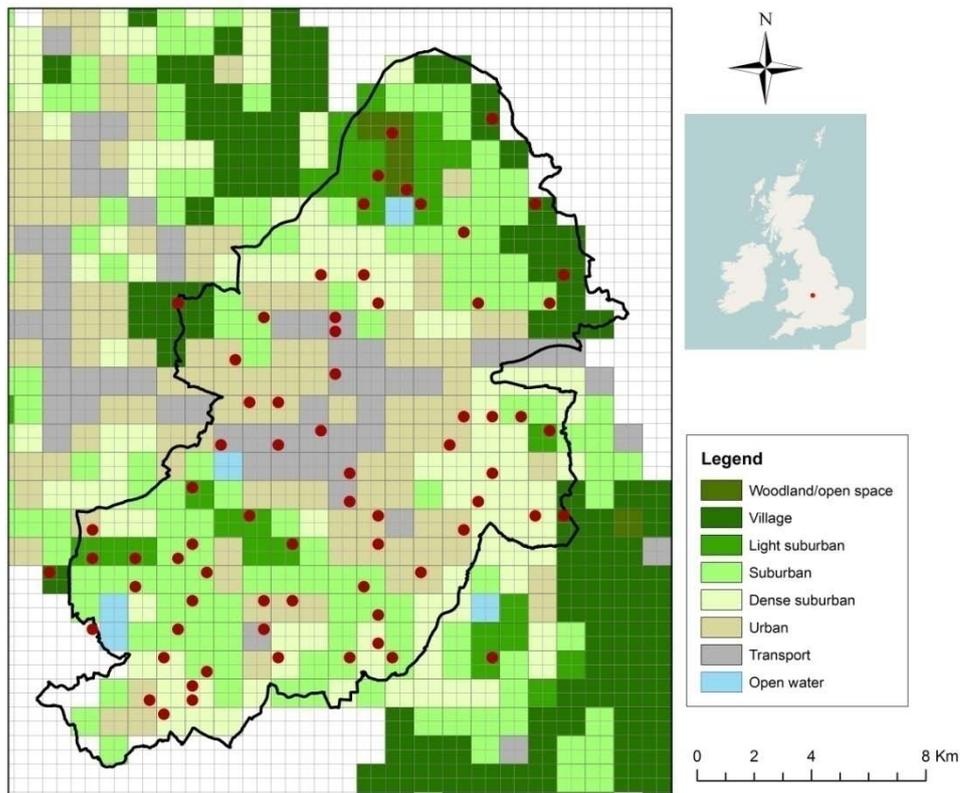
Figure 2.1 Study sites across the urban gradient in Birmingham, UK. Location of Birmingham in the UK (top right) and the study area within the city of Birmingham with the local authority border shown (main image). The 1 km^2 grid of urban land classes is shown (after Owen et al., 2006) by the green gradient, with details described in the legend to the right of the main image. The 500 m^2 pixel grid (in grey) that was used as a scale for site selection in this study is also displayed. 70 500 × 500 m field sites were selected (shown as red circles) in a stratified manner according to the urban land classes. These sites were surveyed for birds and the species' abundances were linked to habitat factors.

A 500 m^2 pixel grid and the Birmingham local authority boundary were laid over the Ordnance Survey maps in a GIS (ArcGIS 9.2, ESRI Redlands, USA) to aid site selection. Preliminary assessment of the candidate sites was carried out by satellite photography through Google Earth (Google, 2009) to evaluate land cover type and accessibility. Seventy 500 × 500 m sites were selected across the urban gradient, with a balanced design within each of the six land classes to allow a robust statistical analysis.

At each site two 500m transects were set up. These were as parallel to one another as the sites allowed to avoid double counting birds. Each transect line was divided into five equal 100 m lengths, making a total of ten sections, numbered 1 to 10.

2.2.2 Bird surveys

Comprehensive bird surveys were carried out at all 70 sites. Transect-based techniques were employed as they are known to assess bird numbers more accurately than point counts, which can

under sample (Nichols et al., 2000). Two summer surveys were carried out at all of the sites; 26 of the sites were surveyed by nine experienced volunteers. The first summer surveys (S1) were conducted between 28/04/2009 and 29/06/2009. The second summer surveys (S2) were conducted between 08/06/2009 and 17/09/2009. Winter surveys (S3) were carried out at all of the sites between 17/01/2010 and 10/02/2010, 17 of the sites were surveyed by six experienced volunteers.

Bird surveys were based on the British Trust of Ornithology's (BTO) Breeding Bird Survey (BBS) (BTO, 2009). All surveys followed the same procedure, and the summer visits were at least four weeks apart. The first summer surveys started between 05:40 and 09:38 hrs GMT; the second summer surveys started between 05:30 and 09:50 hrs GMT. Where possible, surveys started at the same time on the pairs of summer visits. The winter surveys started between 07:45 and 12:53 hrs GMT.

All birds seen or heard, except those that could be identified as juveniles, were recorded. Effort was made not to record the same bird twice. The sex and activity of birds were not recorded. Birds were recorded in the appropriate section of the transect and distance either side of and at right angles to, the transect line was recorded in a categorical manner:

1. Within 25 m
2. Between 25 and 100 m
3. More than 100 m including birds outside the 500 m × 500 m square boundary
F. Birds in flight only, at any distance.

Skylarks (*Alauda arvensis*) in display flight and hovering Kestrels (*Falco tinnunculus*) were recorded in the relevant distance category. Aerial-feeding Swifts (*Apus apus*), Barn Swallows (*Hirundo rustica*) and Common House Martins (*Delichon urbica*) were recorded in the flight category, unless they were seen to land or fly into a nest site. Transects were walked at a slow, methodical and consistent pace with no long stops with an approximate time of 25 minutes for 500 m.

Bird surveys were not carried out in persistent heavy rain, very poor visibility or strong wind. Weather conditions were recorded in a coded system through selecting the single category that best represented the overall conditions per transect (Table 2.2).

Table 2.2 Table of weather conditions including cloud cover, rain, wind and visibility and associated score of 1-3 to be recorded for bird surveys. Bird surveys were not carried out in heavy rain, very poor visibility or strong wind.

Code	Cloud cover	Rain	Wind	Visibility
1	0-33%	None	Calm	Good
2	34-66%	Drizzle	Light	Moderate
3	67-100%	Showers	Breezy	Poor

The sites were also surveyed for the presence of tree species during the months of July in 2009 and July and August in 2010. Tree species were recorded as present or absent per 100 m transect section.

Resident passerines were selected for this study due to their association with vegetative cover (Hinsley et al., 1995b) and the ability to examine their response to the habitat across the seasons. Species data were only included in the analysis if they had counts of a minimum of ten individuals per season, for each of the three seasons to allow a robust statistical analysis (Table 2.3).

Table 2.3 Resident passerine species used in an investigation of the importance of connectivity in an urban landscape. Each species is listed with associated total counts across all survey sites for each season.

Bird species	Total count in Season 1	Total count in Season 2	Total count in Season 3
Coal Tit	44	31	22
Common Blackbird	672	637	250
Common Chaffinch	229	200	87
Common Starling	736	555	968
Dunnock	83	129	94
Eurasian Blue Tit	285	339	546
Eurasian Bullfinch	21	29	41
Eurasian Wren	326	355	56
European Goldfinch	120	150	140
European Greenfinch	158	214	104
European Robin	449	273	382
Great Tit	216	226	507
House Sparrow	423	527	409
Long-tailed Tit	70	75	220
Mistle Thrush	38	45	57
Eurasian Nuthatch	11	22	16
Song Thrush	81	67	16

2.2.3 Environmental variables

2.2.3.1 Vegetation layer

A signature file created from near-infrared and colour photography collected in 2007 (Bluesky International Ltd, Leicestershire, UK) was used to extract a raster layer representing vegetation at a 2 m pixel resolution. A tree dataset was generated by selecting areas of the described vegetation dataset at a height of ≥ 3m above the ground, according to photogrammetrically derived data collected in 2007 (Bluesky International Ltd, Leicestershire, UK).

To avoid higher levels of error in the dataset (e.g. due to inclusion of non-vegetation land-cover), 3 m was set at the lower limit. A mask of buildings expanded by 4 m in each direction was applied to remove vegetation within 4 m of a building's edge. This ensured that vegetated roofs were not classified as trees. Vehicles, possibly with algal or moss growth on the roof, were often detected with the near-infrared photography and therefore showed up as vegetation on motorways. Motorways and all of the 70 500 × 500 m study sites were manually inspected to compare the digital tree layer with the aerial photography (Bluesky International Ltd, Leicestershire, UK).Mis-classified and erroneous pixels were removed at this point. A mask was not applied to the motorways in order to retain central reservation and embankment trees, as these are likely to aid gap-crossing (pers. obs.) but instead were manually inspected for errors. During this process it was noted that many errors were one pixel (2 × 2 m) in size. A cleaning process was then carried out where all stand-alone pixels were removed from the vegetation dataset. This process removed any small, undetected errors but is also likely to have removed some saplings from the vegetation dataset. However, these are unlikely to have provided many resources in comparison with vegetation retained for the study.

2.2.3.2 Connectivity metrics

In order to investigate passerine use of the landscape, a proxy measure of functional connectivity was developed based on previous passerine gap-crossing studies. There are no gap-crossing studies of British birds in an urban context on which to draw, and so the most similar studies were used as a point of reference. Bélisle and Desrochers (2002) showed that birds rarely ventured more than 25 m from forest edges in a gap-crossing experiment in an agricultural land-dominated landscape with fragmented woodland near Québec City, Québec, Canada. Desrochers and Hannon (1997) investigated gap-crossing decisions by forest songbirds during the post-fledging dispersal period in both a rural and a forested landscape also near Québec City. These authors showed that birds preferred using wooded corridors rather than open areas, and although gaps less than 30 m had little overall impact on bird movements, individuals were three times less likely to cross 70 m gaps and

about eight times less likely to cross 100 m gaps. St Clair et al. (1998) showed that chickadees (*Poecile* spp.) were unwilling to cross gaps of more than 50 m when they had forested alternatives, although they crossed gaps as large as 200 m when there was no other option. In a rare urban gap-crossing study based in Calgary, Tremblay and St. Clair (2009) used playback (the playing of recordings of alarm or mobbing calls of conspecifics from an audio system in order to attract animals) and discovered that as gaps in vegetation exceeded 30 m, the likelihood of movement decreased dramatically. Gaps of 45 m resulted in birds being half as likely to cross gaps as they were to move the same distance in continuous tree cover.

In a study examining gap-crossing decisions of woodland songbirds in coniferous plantation with patches of oak (*Quercus* spp.) in Scotland, Creegan and Osborne (2005) observed that when playback was not being used, Common Chaffinches (*Fringilla coelebs*) crossed gaps up to 120 m wide. Fewer than a quarter of experiments had observed crossings for gaps of up to 10 m in width for European Robins (*Erithacus rubecula*) and Coal Tits (*Periparus ater*). The maximum gap-crossing distances that were observed for both of these species were less than 50 m. Gap-crossing activity was not observed for Goldcrests (*Regulus regulus*). When playback was used the distances crossed increased substantially, where Goldcrests were seen crossing gaps of 46 m, European Robins 60 m, Coal Tits 92 m and Common Chaffinches gaps of 150 m. These studies demonstrate the impact of playback on decision making in birds, where the size of gaps crossed can increase significantly (Creegan and Osborne, 2005). Although alarm calling and mobbing responses occur naturally, and the use of playback experiments can allow detailed observations on specific movements, they are likely to have less relevance to dispersal or daily movement behaviour (Castellon and Sieving, 2006).

On the balance of evidence 30 m was selected as a conservative estimate of natural gap-crossing behaviour (without playback) thresholds for passerine species and a good estimate of a limit to functional connectivity (Tischendorf and Fahrig, 2000). The tree networks were buffered (expanded digitally from the edge of the object) by 15 m consequently encompassing all gaps ≤ 30 m and creating a connectivity mask (Figure 2.2) that captured the structural connectivity of the landscape surrounding the site.

Figure 2.2 A study site in Birmingham, UK, showing the original vegetation layer and connectivity mask. The vegetation layer (shown in dark green) was expanded by 15m in each direction, therefore encompassing all gaps ≤30m to create the connectivity mask (shown in paler green).The Ordnance Survey (Ordnance Survey, 2008) line map is shown in grey. The connectivity mask was used in the analysis of bird distributions across the urban gradient in Birmingham.

2.2.3.3 LULC data extraction

Land use and land cover (LULC) data were derived from OS Mastermap (OSM) (Ordnance Survey, 2008) which is a high-resolution parcel-based GIS dataset and was used to extract a range of environmental variables. OSM polygon data were converted into a 2 m pixel resolution raster and captured in a GIS (ArcGIS 9.2, ESRI Redlands, USA) (Figure 2.3).

Figure 2.3 Land use and land cover dataset. Aerial photograph of an area of Birmingham (image on the right) and the same area displayed showing the land use and land cover (LULC) data (image on the left) from OS Mastermap (OSM) (Ordnance Survey, 2008) which was used to extract a range of environmental variables for analysis examining bird species' abundances across an urban gradient.

Two approaches were taken to extract LULC summary data for the landscape surrounding each survey site. First, a 500 m radius buffer was constructed around the site centre using the GIS as it is a fair estimate of breeding home range and territory of most of the study species (Perrins, 1979, Snow, 1988, Davies, 1992, Cramp et al., 1993, Cramp et al., 1994, Naef-Daenzer, 1994). Complete summaries of the underlying landscape were extracted using this buffer with the Thematic Raster Summary tool in Hawth's Tools (Beyer, 2004). This approach assumes that all of the habitat in the landscape is potentially relevant or available to the species concerned.

The second approach was to restrict the landscape analysis to areas within 15 m of tree-lines by using the connectivity mask. This then provided the available habitat and land cover available to birds if the assumption is held that they are likely to move 15 m from cover (e.g. Newton, 1972, Desrochers and Fortin, 2000, Bélisle and Desrochers, 2002, Desrochers et al., 2002). This has proven to be a strong surrogate for functional connectivity for bat species that utilise tree-lines (Hale et al., 2012). LULC summaries were again extracted from the 500 m radius buffer around each site centre, but this time the available data were limited to the areas of the connectivity mask intersected by the 25 m buffer around the survey transects (Figure 2.4) to ensure that only the vegetation functionally connected to the survey area, and therefore relevant to the birds surveyed, was included in analysis.
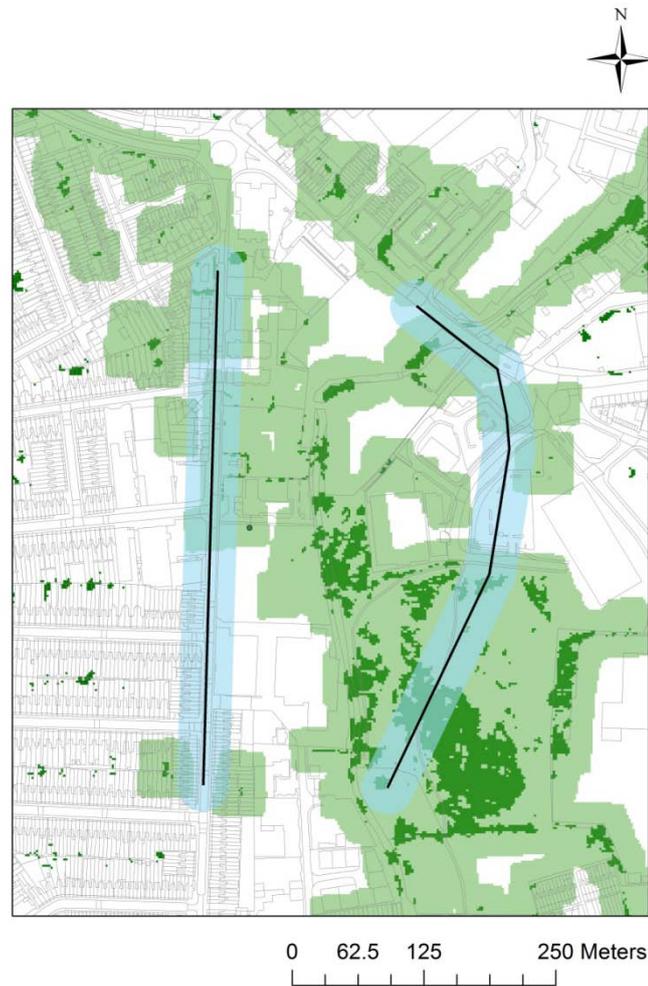
Figure 2.4 A survey site with survey transects and method to extract landscape data. Map displaying Ordnance Survey (Ordnance Survey, 2008) line map at an example study site in Birmingham, UK. Two 500 m transects (shown as black lines) were surveyed at each site were. In a GIS these were buffered at 25 m to gain a summary of land use and land cover at the study site and the influence on bird distribution across an urban gradient**.** The original tree layer (shown in dark green) was buffered by 15 m in order to incorporate all gaps of 30 m and less creating a connectivity mask (shown in light green). The connectivity mask was then re-selected where it intersected the area 25 m around the transects (shown in light blue), to ensure only the vegetation connected to the survey area, and therefore relevant to the birds surveyed, was included in analysis.

Total area of connected tree cover for each site was not used as most of the tree network in Birmingham is connected (Figure 2.5) and this would not provide a realistic view of natural use. Birds do not use all landscape that is available to them, solely because it is available for use; they restrict their movements and use of the landscape to their energetic and resource requirements (MacArthur and Pianka, 1966).
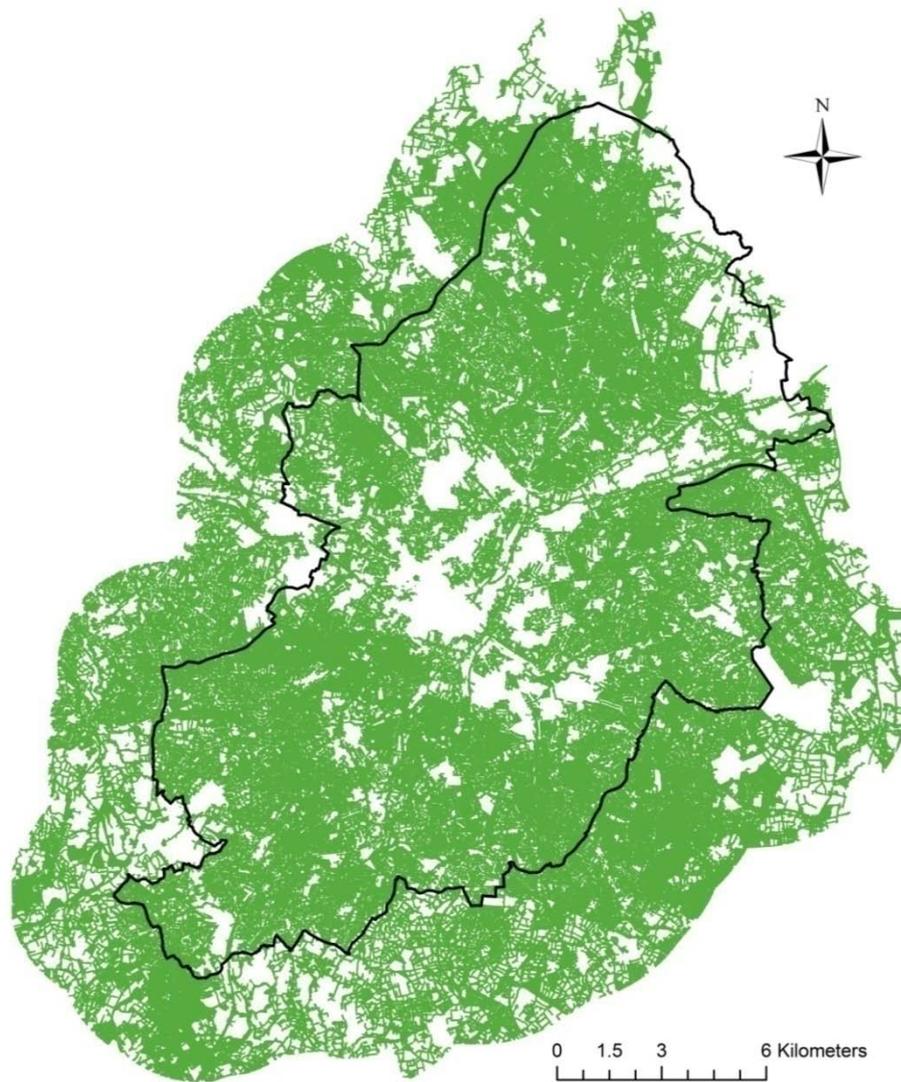
Figure 2.5 Map demonstrating the connectivity for passerine birds in Birmingham, UK. The local authority boundary of Birmingham is shown in black and the connected tree network is shown in green. The original vegetation layer (described in section 2.2.3) was expanded by 15m in each direction encompassing all gaps ≤30m and creating a connectivity mask, reflecting natural gap crossing behaviour of passerine species. Connectivity clearly drops off in the North-East of the city where agricultural practises are dominant in the landscape. 'Holes' in the connectivity mask are also seen in areas with high levels of built land cover, such as the city centre, and the airport in the East.

In order to have a measure of change in the landscape at a set of distances away from the centre of the site each site was buffered from the centre point at 250, 500, 750, 1000 and 1500 m creating circles of the diameters stated. (Figure 2.6).
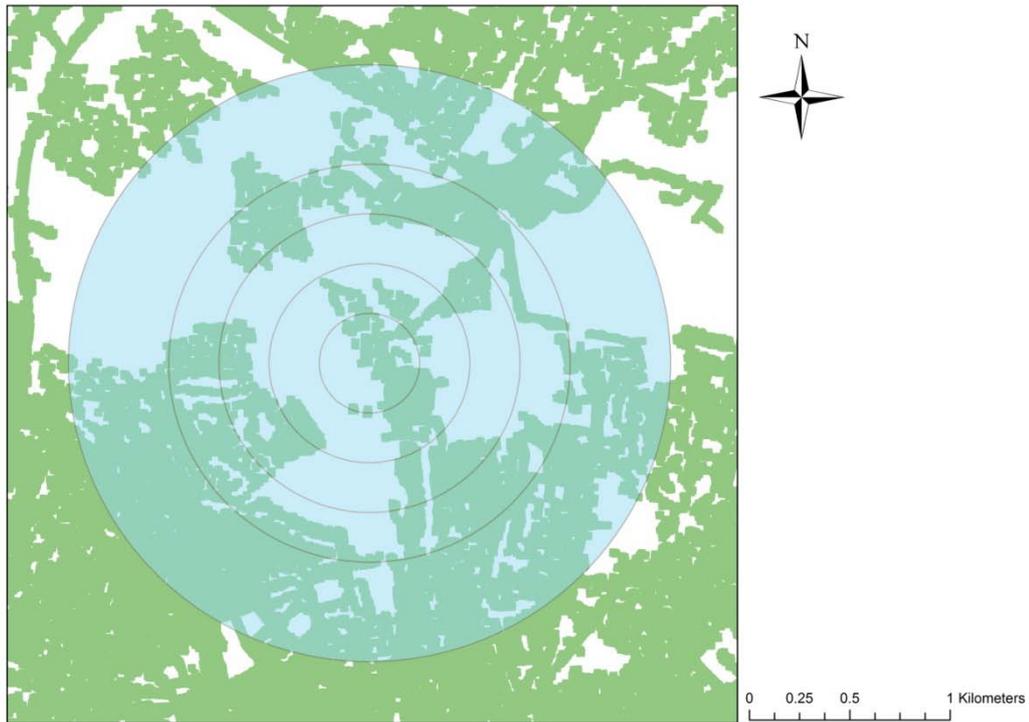
Figure 2.6 A survey site with data extraction method. Buffers from the centre point of a survey site at 250, 500, 750, 1000 and 1500 m (shown in blue) overlaid on the connectivity mask (shown in green)

The summarised land cover was extracted for each of the buffers at each of the sites. In order to compare land cover at these different distances, the area was calculated for the differenced circles i.e. concentric rings. The differences between the concentric rings were calculated, thereby creating an area value for a ring (e.g. 500 m circle area - 250 m circle area = 500 m ring). The land cover per m^2 was calculated for the 250 m and each distance ring, and these values were plotted with a least squares regression for each site. The gradient of the regression line was used as a value of change of land cover of distance from each site.

2.2.3.4 Environmental variables for analysis

LULC summary data and connectivity measures from the extraction methods described were then used to create response variables for statistical analysis where habitat factors were inspected for associations with bird species' abundance (Table 2.4).

Table 2.4 Details of the variables generated for statistical analysis from the survey work, GIS and literature review as described above. The name of the variable used in the statistical models is listed on the left and details of the generation method and how it relates to the environment is described on the right.

Variable	Details
btrees	Fixed effect. The actual tree cover≥3m buffered by 15m and inter secting the survey transects per m^2 within the 500m buffer from the centre of each survey site.
tgrad	Fixed effect. The gradient of a least squares regression of buffered tree cover per m^2 from 250m to 1500m, the value represents a measure of change away from the site in available tree cover.
built	Fixed effect; built land cover. The total land cover that can be categorised as built including buildings, roads, pavements, etc per m^2 within the 500m buffer from the centre of each survey site. The LULC data were collated from data extracted with the thematic raster summary tool in Hawth's Analysis Tools for ArcGIS (ArcGIS 9.2, ESRI Redlands, USA)
bgrad	Fixed effect. The gradient of a least squares regression of built space per m^2 within the connected network from 250 m to 1500 m, the value represents a measure of change away from the site in built space within the connected network.
season	Random effect. Used in the GLMMs to indicate a seasonal difference in response to the environment. Season 1=a, Season 2=b and Season 3=c.

From the LULC data a category of built space was created by combining buildings, roads, railway and so on and used to create the variable built. The availability of connected habitat is represented by the variable btrees, and a measure of change in available connected habitat away from the study sites beyond 500 m is represented by tgrad. Similarly a change in built land cover is represented by bgrad.

2.2.4 Statistical Analysis

Prior to analysis the data were screened using a range of exploration techniques (Zuur et al., 2010). Cleveland dot plots were used to confirm that there were no outliers. Co-linearity was examined using pairplots, and variance inflation factors were calculated to assess co-linearity amongst explanatory variables. All values were ≤2 and, therefore, it can be concluded that no co-linearity existed between the explanatory variables (Zuur et al., 2009). Histograms of the count data were created to examine the distribution of counts, and it was clear that zero-inflation occurred for most of the species (Figure 2.7).
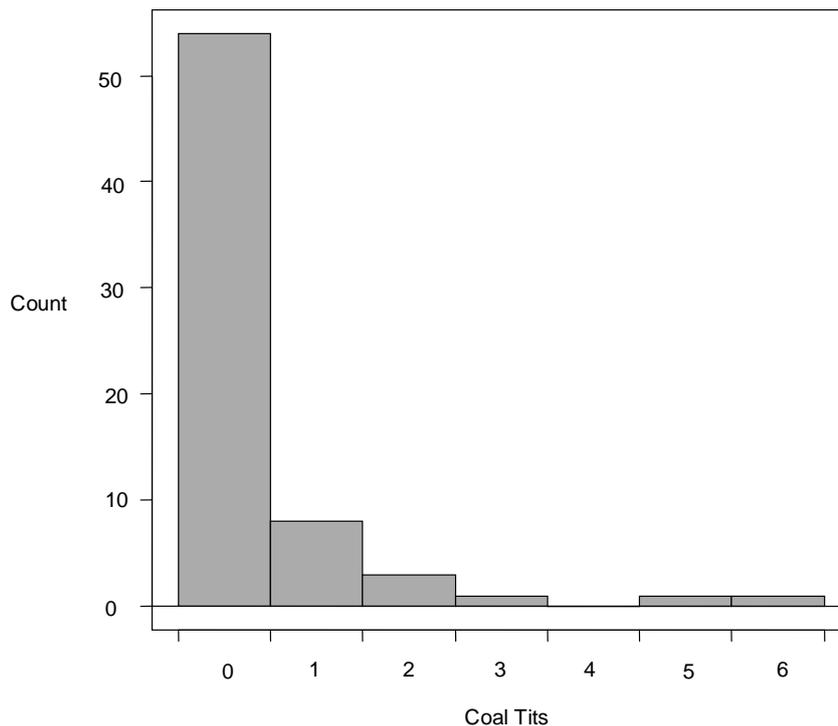
Figure 2.7 Histogram demonstrating zero-inflation. An example using Coal Tit counts from Season 1, the occasions that no Coal Tits were counted number at over 50, and the next category of one Coal Tit counted is below 10 occasions. Histograms like this led to a zero-inflated analysis approach being taken.

Associations between avian species abundance and habitat characteristics were modelled using general linear mixed models (GLMMs) and zero-inflated negative binomial general linear models (GLMs) in R (R Core Development Team, 2011). GLMMs were run with the package lme4 (Bates et al., 2011) and zero-inflated negative binomial GLMs were run with the package pscl (Zeileis et al., 2008). Seventeen bird species were modelled separately. Since this study examined a range of bird species and their response to the urban environment, a single-species modelling approach is valid and appropriate. Bird species differ in their ecology and, consequently, respond to the landscape differently (Young and Jarvis, 2001, Hashimoto, 2007), therefore, separate hypotheses were applied to each species in this study.

GLMMs were run for all 17 species and the standardised residuals were plotted against the fitted values and inspected for heteroscedasticity. Where a cone distribution was seen the model was rejected (Crawley, 2007, Zuur et al., 2009) and a zero-inflated negative binomial GLM was used. In total 391 models were run. The best-fit models were selected through AIC (Akaike's Information Criterion) and backward selection with stepAIC (Burnham and Anderson, 2002, Crawley, 2007).

Spline (cross-)correlograms (package ncf; Bjornstad, 2009) using the residuals of the models were used to look for spatial autocorrelation (Zuur et al., 2009). Spline (cross-)correlograms estimate spatial dependence as a continuous function of distance (Bjornstad and Falck, 2001). All GLMMs were found to have none (e.g. see Figure 2.8). Where spline correlograms indicated a level of spatial autocorrelation, the models were rejected from this study (Zeileis et al., 2008).
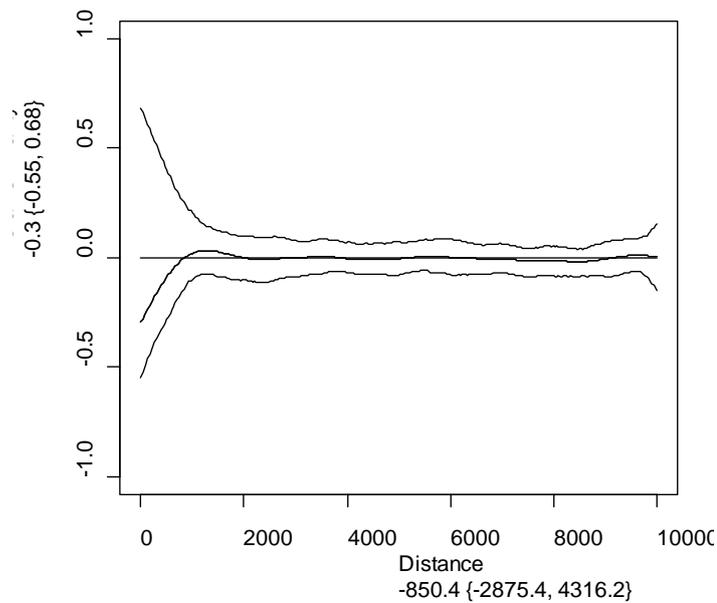
Figure 2.8 Spline correlogram, with 95% pointwise bootstrap confidence intervals, of residuals of the best-fit GLMM model for Great Tit demonstrating a lack of spatial autocorrelation.

2.3 Results

2.3.1 Urban gradient within the study sites

The study sites represent a gradient of grey space (Figure 2.9) and tree cover (Figure 2.10) within the urbanised landscape and, therefore, represent a range of environmental conditions to which moving birds are exposed.
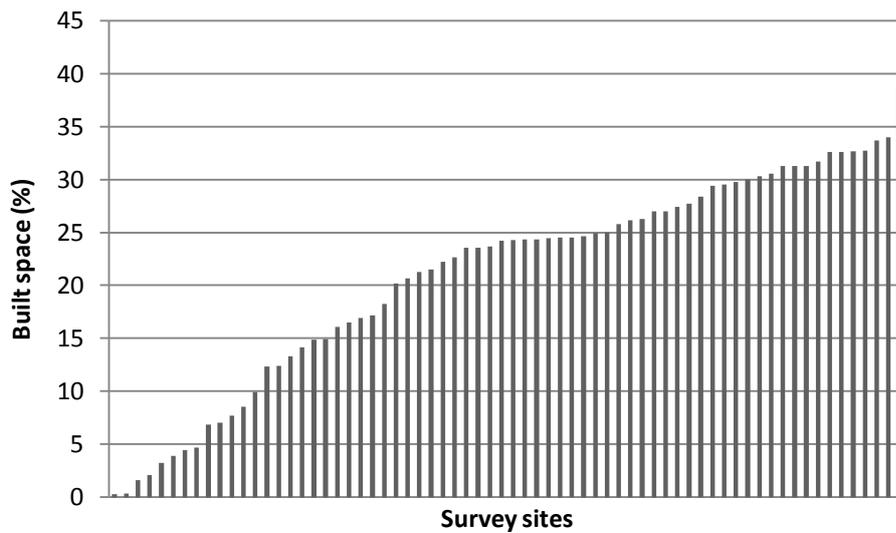
Figure 2.9 The built land cover (%) at the 70 survey sites across Birmingham, demonstrating an urban gradient
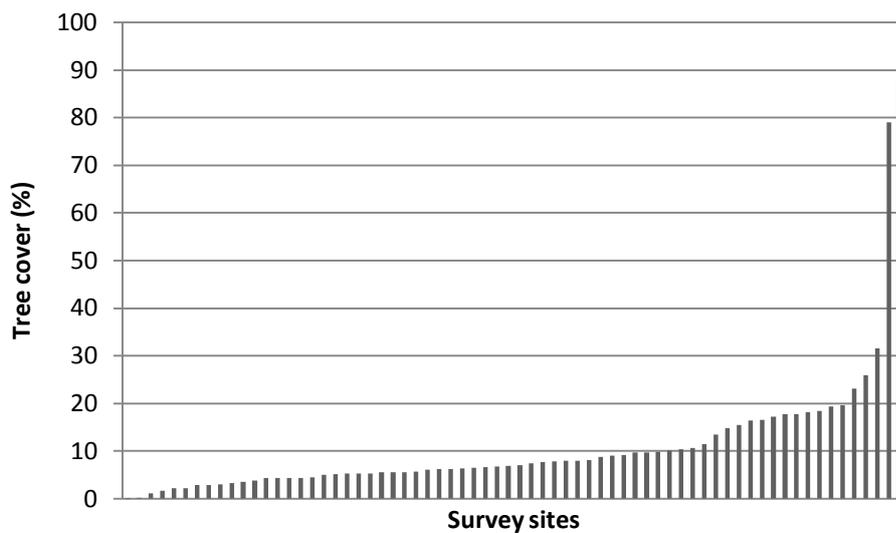
Figure 2.10 The tree cover (%) at the 70 survey sites across Birmingham, demonstrating a gradient of habitat

The extremes of these environmental gradients are demonstrated by Figure 2.11. It is interesting to note that the site at the lower end of both the built gradient and the tree cover gradient is in fact the same site in agricultural land.

Figure 2.11 Aerial photographs of sites at each end of the gradient. The top left image is of the site with least built cover per m^2, the top right image is of the most built space per m^2. Bottom left is the site with the least tree cover per m^2, the bottom right image is of the most tree cover per m^2. Note that both the site with the least tree cover and built space are the same site.

2.3.2 Connectivity characteristics of Birmingham

The map of Birmingham (Figure 2.5) demonstrates the connectivity of Birmingham for passerines, with the city centre and the airport as obvious gaps in the tree network. If the functionally connected trees (based on the 30 m gap-crossing ability of birds) are used as a basis for assessing habitat

distribution; the city does not appear to have clear 'islands' of habitat connected by corridors but a more or less continuous availability of vegetative cover, with 'holes' in more built up areas.

The rural areas have a considerable drop-off in connectivity, where trees are fewer due to agricultural intensification. This can be seen to the north-east of the city boundaries in Figure 2.12.

Figure 2.12 Aerial photograph of arable agricultural land to the North East of Birmingham demonstrating the drop-off in connectivity (shown in green)

2.3.3 The influence of a connected landscape on bird populations

The best-fit models regularly show an increase in the amount of connected habitat as a significant factor influencing bird distribution. Of the best-fit models, 89% contain btrees, the variable representing amount of connected habitat. Of those models where amount of connected habitat was a variable, it was a significant factor in influencing the distribution of the bird species in question in 53% of the models.

All 17 species of birds were positively influenced by an increase in connected habitat in at least one season and was shown to be a significant variable in the best-fit models for 13 of the species modelled in this study.

A summary of the results of the best-fit GLMM models for each species analysed is presented in Table 2.5. A summary of the results of the best-fit models for each species analysed with a zero-inflated general linear model is presented in Table 2.6 for surveys carried out in Season 1, Table 2.7 for Season 2 and in Table 2.8 for surveys in Season 3. Not all species are shown for each of the three seasons as some models were rejected due to spatial autocorrelation. The significant factors are presented along with the *p*-values. Where the best fit model is displayed as ~ 1, this indicates that a null model was found as the best fit for that species, indicating that no landscape variable could explain the distribution.

Table 2.5 Summaries of the best-fit General Linear Mixed Models for species with few enough zeros counts that zero-inflation was not required. The best-fit model is displayed for each of the species modelled, with interactions and the associated significant factors and *p*-value. Birds were surveyed across 70 sites in Birmingham.

Species	Model	Significant factors	*p*-value
Common Blackbird	btrees*bgrad*tgrad*season+(1|site)+(1|season)	bgrad	0.007
		tgrad	0.002
		btrees:bgrad	0.005
		btrees:tgrad	0.002
		bgrad:tgrad	0.002
		tgrad:season[T.c]	0.03
		btrees:bgrad:tgrad	0.002
		btrees:tgrad:season[T.c]	0.04
		bgrad:tgrad:season[T.b]	0.02
		btrees:bgrad:tgrad:season[T.b]	0.02
Eurasian Blue Tit	season*btrees*built+(1|site)+(1|season)	season[T.c]:btrees	0.03
Great Tit	btrees*tgrad*built*season+(1|site)+(1|season)	tgrad	0.03
		built	0.02
		btrees:tgrad	0.04
European Robin	btrees*bgrad*season+(1|site)+(1|season)	btrees	0.002

Table 2.6 Summaries of the best-fit zero-inflated general linear models for each species in Season 1 (S1) (between 28/04/2009 and 29/06/2009) surveys species counts. The best-fit model is displayed for each of the species modelled, with interactions and the associated significant factors and *p*-value. Where a hyphen appears there is no associated *p*-value. ~ 1 indicates a null model, glm.nb indicates that a negative binomial model was a better fit than a zero-inflated model. Birds were surveyed across 70 sites in Birmingham.

Species	Best-fit model	Significant factors	*p*-value
Eurasian Bullfinch	~ 1		-
Dunnock	zeroinfl(D~btrees*built|btrees+built, dist="negbin", EM=TRUE)	none	-
European Goldfinch	zeroinfl(GO~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	none	-
European Greenfinch	zeroinfl(GR~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	none	-
Long-tailed Tit	zeroinfl(LT~btrees + tgrad + built, dist="negbin", EM=TRUE)	btrees	0.008
Mistle Thrush	~ 1		-
Nuthatch	zeroinfl(NH~btrees*tgrad|btrees, dist="negbin", EM=TRUE)	none	-
Common Starling	zeroinfl(SG~btrees+built|btrees+built, dist="negbin", EM=TRUE)	None	-
Song Thrush	zeroinfl(ST~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	tgrad	0.008
		bgrad	0.03
		built	0.002
		btrees:tgrad	0.01
		bgrad:built	0.01
Eurasian Wren	glm.nb(WR~btrees + tgrad + built + btrees:tgrad)	btrees	<0.001
		tgrad	0.003
		built	<0.001
		btrees:tgrad	0.002

Table 2.7 Summaries of the best-fit zero-inflated general linear models for each species in Season 2 (S2) (between 08/06/2009 and 17/09/2009) surveys species counts. The best-fit model is displayed for each of the species modelled, with interactions and the associated significant factors and *p*-value. Where a hyphen appears there is no associated *p*-value. Birds were surveyed across 70 sites in Birmingham.

Species	Best-fit model	Significant factors	*p*-value
Eurasian Bullfinch	zeroinfl(BF~btrees + tgrad + bgrad + built + btrees:tgrad, dist="negbin", EM=TRUE)	btrees	<0.001
		tgrad	<0.001
		bgrad	<0.001
		built	0.02
		btrees:tgrad	<0.001
Common Chaffinch	zeroinfl(CH~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	btrees	<0.001
		built	0.004
		Log(theta)	0.03
Coal Tit	zeroinfl(CT~btrees+built|btrees+built, dist="negbin", EM=TRUE)	none	-
Dunnock	zeroinfl(D~btrees*tgrad|btrees, dist="negbin", EM=TRUE)	None	-
House Sparrow	zeroinfl(HS~btrees+built|btrees+built, dist="negbin", EM=TRUE)	None	-
		ZI binomial btrees	0.02
		ZI binomial built	0.03
Long-tailed Tit	zeroinfl(LT~btrees + tgrad + built + btrees:tgrad, dist="negbin", EM=TRUE)	tgrad	<0.001
		btrees:tgrad	<0.001
Mistle Thrush	zeroinfl(M~btrees + tgrad + bgrad + built + btrees:tgrad, dist="negbin", EM=TRUE)	built	0.01
Nuthatch	zeroinfl(NH~built, dist="negbin", EM=TRUE)	none	-
		ZI binomial built	0.03
Common Starling	zeroinfl(SG~btrees+built|btrees+built, dist="negbin", EM=TRUE)	Log(theta)	0.002
		ZI binomial built	0.04
		ZI binomial btrees	0.03
Song Thrush	zeroinfl(ST~btrees+tgrad+bgrad+built|btrees+built, dist="negbin", EM=TRUE)	bgrad	0.006
		built	<0.001
Eurasian Wren	zeroinfl(WR~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	tgrad	0.03
		btrees:tgrad	0.04
		Log(theta)	<0.001

Table 2.8 Summaries of the best-fit zero-inflated general linear models for each species in Season 3 (S3) (between 17/01/2010 and 10/02/2010) surveys species counts. The best-fit model is displayed for each of the species modelled, with interactions and the associated significant factors and *p*-value. Where a hyphen appears there is no associated *p*-value. . ~ 1 indicates a null model, glm.nb indicates that a negative binomial model was a better fit than a zero-inflated model. Birds were surveyed across 70 sites in Birmingham.

Species	Best-fit model	Significant factors	*p*-value
Common Chaffinch	zeroinfl(CH~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	none	-
Coal Tit	zeroinfl(CT~btrees+built|btrees+built, dist="negbin", EM=TRUE)	none	-
Dunnock	~ 1		-
European Goldfinch	zeroinfl(GO~btrees + tgrad + bgrad + btrees:tgrad, dist="negbin", EM=TRUE)	tgrad	0.005
		btrees:tgrad	0.004
European Greenfinch	zeroinfl(GR~btrees, dist="negbin", EM=TRUE)	Log(theta)	<0.001
House Sparrow	zeroinfl(HS~tgrad + bgrad + built + bgrad:built, dist="negbin", EM=TRUE)	Log(theta)	0.005
Long-tailed Tit	zeroinfl(LT~btrees*tgrad+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	Log(theta)	0.002
		ZI binomial btrees	0.03
		ZI binomial built	0.02
Mistle Thrush	zeroinfl(M~btrees+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	btrees	0.01
Common Starling	zeroinfl(SG~btrees*tgrad+built|btrees+built, dist="negbin", EM=TRUE)	Log(theta)	0.004
Song Thrush	zeroinfl(ST~btrees+bgrad*built|btrees+built, dist="negbin", EM=TRUE)	none	-
Eurasian Wren	glm.nb(WR~btrees)	btrees	0.001

2.3.4 Does a connected landscape ameliorate urbanisation?

An increase in built space had a significant influence increasing the abundance of Eurasian Bullfinches (*Pyrrhula pyrrhula*) ($p < 0.05$), House Sparrows (*Passer domesticus*) ($p < 0.05$), and Common Starlings (*Sturnus vulgaris*) ($p < 0.05$), in combination with an increase in connected habitat (Eurasian Bullfinch: $p < 0.001$, House Sparrow: $p < 0.05$, Common Starling: $p < 0.05$) in Season 2 (Table 2.7).

2.3.5 Seasonal differences in the response of birds to the landscape

Weather data suggested that summer 2009 was a relatively average weather year; 0.7°C above the 1971-2000 average, sunshine totals were within +/- 10% of the 1971-2000 average and rainfall was above normal but very similar to 2008 and 2007. Winter 2009/2010 was colder than average which was likely to lead to higher bird activity (Met Office, 2010).

The best-fit model for Eurasian Blue Tits (*Cyanistes caeruleus*) showed that a positive trend in connected habitat in the Season 3 (indicated as [T.c] in the significant factors in Table 2.8) increased their abundance ($p < 0.05$). No other factors showed a significant influence on this species' distribution.

Within the individually modelled species using zero-inflated GLMs, there were best-fit models with significant factors to explain the distribution of Long-tailed Tits (*Aegithalos caudatus*), Song Thrushes (*Turdus philomelos*) and Eurasian Wrens (*Troglodytes troglodytes*) across all three surveys. Numbers of Long-tailed Tits showed a consistent significant, positive trend with the amount of connected habitat across all three sampled surveys. In Season 2 (Table 2.7) there was also a highly significant interaction with Long-tailed Tit numbers and a decrease in the amount of connected habitat beyond 500 m from the site ($p < 0.001$). In Season 3 a decrease in the amount of built space beyond 500 m was highly significant ($p < 0.05$) in increasing their abundance (Table 2.8). Built space was a variable in all the best-fit models for Long-tailed Tit but it had a significant influence in increasing their abundance in Season 3 (Table 2.8).

A negative trend in the amount of built space was shown to be a significant factor in increasing the abundance of Song Thrushes in both Season 1 ($p < 0.005$) (Table 2.6) and Season 2 ($p < 0.001$) (Table 2.7). An interaction of built space and a change in built space away from the site was shown in both surveys, but in Season 1 the trend in change from the site was positive ($p = 0.01$) but negative in Season 2 ($p = 0.005$). In Season 1 an increase in Song Thrush numbers was found with an increase in available connected habitat within 500 m and a decrease in the amount of connected habitat beyond 500 m from the site ($p < 0.01$) (Table 2.6).

Eurasian Wrens showed a consistent response to the environment across the three sampled surveys, where an increase in connected habitat increased abundance. In both Seasons 1 and 2 an interaction was found between a positive trend in the amount of connected habitat and a decrease in available connected habitat beyond 500 m from the site (S1: $p < 0.005$, S2: $p < 0.05$) (Tables 2.6 and 2.7). A decrease in the amount of built space was also shown to be a significant factor in increasing numbers of Eurasian Wrens in Season 1 ($p < 0.001$) (Table 2.6).

2.3.6 Responses to the environment on different scales in different seasons

The best-fit GLMM model for the Common Blackbird (*Turdus merula*) (Table 2.5) demonstrated seasonal changes in response to the environment. In Season 1 (indicated as [T.b] in the significant factors in Table 2.5) there was an increase in Common Blackbird numbers when there was less

available connected habitat beyond 500 m from the site ($p < 0.05$), and in Season 3 (indicated as [T.c] in the significant factors in Table 2.5) this became the case with an increase in available connected habitat beyond 500 m from the site.

A significant positive trend in the interaction between the amount of connected habitat within 500 m of the site and an increase in available connected habitat beyond 500 m from the site ($p < 0.005$) was shown to increase the abundance of European Goldfinches (*Carduelis carduelis*) in Season 3. A change in the amount of available connected habitat beyond 500 m from the site did not influence the distribution of European Goldfinches in the other surveys.

For a summary of the main responses of all the bird species to the environmental factors see Table 2.9.

Table 2.9. Summary of the significant environmental factors which led to either an increase or decrease in numbers for the best-fit model each bird species across all three surveys. An upwards arrow (green cells) indicates increased numbers of birds, a downward arrow (red cells) indicates decreased numbers of birds. Species with no arrows in cells had no significant factors influencing abundance in the best-fit models. Birds were surveyed across 70 sites in Birmingham.

Species	Connected habitat (btrees)	Change in connected habitat over distance (tgrad)	Change in built space over distance (bgrad)	Built space
Coal Tit				
Common Blackbird	↑	↑	↓	↑
Common Chaffinch	↑			↓
Common Starling	↑			↑
Dunnock				
Eurasian Blue Tit	↑			
Eurasian Bullfinch	↑	↓	↑	↑
Eurasian Wren	↑	↓		
European Goldfinch	↑	↓		↓
European Greenfinch				
European Robin				
Great Tit				
House Sparrow	↑			↑
Long-tailed Tit	↑	↓		↓
Mistle Thrush	↑			↑
Nuthatch				↓
Song Thrush	↑		↑ ↓	↓

2.4 Discussion

These findings demonstrate that connectivity is an influential feature of the urban environment for all of the bird species investigated. More connected habitat at a site was related to a higher abundance of the passerine species investigated in at least one of the survey periods. Functionally connected habitat enabled birds to maintain populations in areas of high levels of built space. Each species responded to the environment differently reflecting their varying ecology (Trzcinski et al., 1999) with some demonstrating clear seasonal differences.

2.4.1 The influence of a connected landscape on bird populations

When 30 m is used as a key drop-off in gap-crossing behaviour, Birmingham can be shown to be a connected landscape for birds. Areas which are highly urban, such as the city centre, were less connected (Figure 2.5), and there was also a drop-off in levels of connectivity in the agricultural areas around the city (Figure 2.12). These areas had the lowest counts of birds demonstrating the impact that anthropogenic fragmentation from agriculture and urbanisation (Trzcinski et al., 1999, Marzluff and Ewing, 2001, FitzGibbon et al., 2007) can have on bird abundance.

Connectivity was a key feature of the best-fit models in at least one survey for every bird species which demonstrates its importance in influencing the distribution of birds across the urban landscape. This agrees with Fernández-Juricic (2000a) who suggested that tree-lines are linear features that enhance connectivity for birds. There was a lack of evidence of habitat islands linked by corridors (Hess and Fischer, 2001), but rather a contiguous, albeit patchy, level of connectivity across habitat patches and matrix alike. This demonstrates that the matrix plays an important part in the functional connectivity of the landscape (Ricketts, 2001, Kuefler et al., 2010) supported by the increased abundance of birds in areas with higher availability of connected habitat. This suggests that the increased levels of connectivity allow movement of birds and provide the resources they require.

The importance of connectivity at this scale suggests that the findings of Tremblay and St. Clair (2009) in a Canadian city are a good basis for gap-crossing behaviour of birds in a British city and that the size of naturally crossed gaps (with no translocation or playback) of British birds in a forested area as described by Creegan and Osborne (2005), are a reasonable 'model' for an urbanised habitat.

2.4.2 Does a connected landscape ameliorate urbanisation?

Some bird species showed an increase in numbers in association with an increase in built space as long there is functionally connected habitat available. House Sparrows and Common Starlings are traditionally urban specialists and nest and roost in buildings (Feare, 1996, Summers-Smith, 2003) but both are a Red-listed declining species (Gregory et al., 2002). Both responded positively to an increase in built space and also with an increase in connectivity in Season 2 (i.e. in late summer). Common Starlings primarily forage on the ground for invertebrates and seeds, but they will also forage in trees for caterpillars and fruit (Feare, 1984, Feare, 1996) which might explain the importance of trees and green space in their distribution. House Sparrows feed on seeds throughout the year and provision young with invertebrates (Summers-Smith, 2003). The connected available habitat would provide these resources (see Chapter 2), as well as cover for movement and predation

avoidance. With the loss of nest spaces in buildings due to more efficient designs of modern builds and renovations leaving fewer available and safe nesting holes, thick vegetation may also offer alternative nesting sites along with foraging options (Summers-Smith, 2003).

The Eurasian Bullfinch also increased in numbers with an increase in built space but with an interaction with more connected available habitat. Bullfinches are in decline (Gregory et al., 2002) but the causes are not fully understood. It is thought that habitat loss, reduction in woodland management and increased pressure from deer leading to a loss of understory and associated food resources, could be reducing their numbers (Fuller et al., 2005). Hinsley et al. (1995b) suggested that hedgerows could be used by the species for travel and cover between woods as Eurasian Bullfinches are generally reluctant to break cover. In the urban environment functionally connected vegetative cover, as measured in this study, may provide the same function, while also providing potential nesting habitat (Hinsley et al., 1995b).

Studies such as Hinsley et al. (1995), Gregory and Baillie (1998), and Marshall et al. (2006) across different landscape types have shown that Common Blackbirds are found less in open areas but, instead, they are associated with vegetative cover such as woodland edges, hedges and copses. This corresponds with the finding in this study that an increase in available connected habitat was shown to increase numbers of Common Blackbirds. Such vegetative cover is likely to provide nesting cover and foraging resources (Simms, 1978).

2.4.3 Seasonal differences in the response of birds to the landscape

One might expect birds to change their behaviour and response to the landscape between seasons. In spring and early summer they establish and defend territories, breeding and provisioning young (Simms, 1978, Perrins, 1979). In the later summer young fledge and adults often continue to provision fledglings outside of the nest, and then the juveniles disperse. These changes in behaviour may be reflected in the findings that most species were found to change their habitat use and associations across the seasons

Common Blackbirds responded to the landscape at different scales according to the season. During the summer the landscape within 500 m was more influential on their distribution. The dates of the early summer survey corresponded to the period where a territory is held and young are being raised and then fledged (Robinson, 2005) which is when they would be foraging in the immediate area and not roaming far from the nest site. During the winter survey period they were shown to be influenced by the landscape on a larger scale, reflecting their requirement to forage more widely to

find sufficient food (Andrén, 1994). An expansion in habitat ranges in the non-breeding season was also found in four passerine species; Bush Warbler (*Cettia diphone*), Long-tailed Tit, Varied Tit (*Cyanistes varius*), and Masked Grosbeak (*Eophona personata*) in a study carried out in Kyoto, Japan (Hashimoto, 2007).

During the breeding season the home ranges of Song Thrushes are relatively small (Peach et al., 2004a) and this was reflected in their response to the amount of connected environment on a smaller scale during Season 1, when an increase in available connected habitat within 500 m increased their numbers but the amount of connected habitat beyond 500 m was less important. However, an increase of built space beyond 500 m resulted in a decrease in Song Thrush numbers, indicating that built space in the environment is responded to on a large scale. The differences in the scale at which this species responds to the environment may reflect their sensitivity to urbanisation and land use changes, where built space, especially during the breeding season, is responded to beyond the territory and home range. This species has declined in agricultural areas, woodland, gardens and suburban landscapes (Gregory et al., 2002, Peach et al., 2004b). The loss of key habitats such as dense, species-rich vegetation for nesting, associated with damp soils to provide a supply of invertebrate prey for adults and to raise young, is believed to be a major contributor to their decline (Gruar et al., 2003, Peach et al., 2004b). The loss of these habitats may well be exacerbated in urban areas with an increase of sealed land cover (McKinney, 2002) and modified vegetation (Loram et al., 2008) leading to a lack of access to these key resources for reproduction and foraging.

An increase in connectivity of the landscape resulted in more Eurasian Blue Tits; a generalist species and urban exploiter. This was especially so in winter when there is less food and vegetation provides less cover due to the loss of leaves and a connected environment is more important for safe movement and efficient foraging activity. This coincides with Eurasian Blue Tits joining mixed feeding flocks during the autumn and winter (Székely et al., 1989). Mixed feeding flocks have a variety of benefits including reduced antagonistic interactions with competitors, an increased access to resources, and improved predator avoidance due to the benefit from 'safety in numbers' and the 'many eyes effect' resulting in the vigilance and alarm calls of other flock members (Hamilton, 1971, Roberts, 1996, Beauchamp, 2003, Harrison and Whitehouse, 2011). Improved foraging efficiency may be acquired in mixed species flocks through social learning, following successful foragers, and information exchange between individuals, for instance the success or failure of a bird that forages in a certain patch represents public information. There may also be a level of community memory

where experienced members of the flock lead less experienced or younger individuals to successful foraging patches (Harrison and Whitehouse, 2011).

Long-tailed Tits are strongly influenced by connectivity in the landscape, showing an increase in numbers where there is more connected habitat in all three surveys. Studies such as Hinsley et al. (1995) and Fuller et al. (2005) have shown the importance of woodland cover and hedgerows in the wider environment which are likely to be used as corridors, especially by foliage insectivores that glean insects from tree leaves. Hashimoto (2007) investigated stepping-stone corridors for birds in the Japanese urban landscape and also showed that Long-tailed Tits were influenced by connectivity. It was found in this study that they declined in numbers in areas with extensive built space, a pattern that becomes more pronounced in winter. This is likely to reflect their preference for travelling under natural cover (Hinsley et al., 1995b, Fuller et al., 2005) and the decreased availability of food that drive birds into areas with more available habitat. Long-tailed Tits are known to join mixed feeding flocks in the winter (Morse, 2008) as seen in Eurasian Blue Tits, further demonstrating the need for anti-predation strategies and increased foraging efficiency in colder months (Székely et al., 1989).

A consistent response to the environment across the seasons was found for Eurasian Wrens. Greater connectivity increased their abundance, which might be expected as they are known to use small woodlands and hedges (Hinsley et al., 1996, Marshall et al., 2006) for territory maintenance through singing, foraging for their invertebrate prey and breeding (Cramp et al., 1988). They were also shown to respond to the environment on a small scale in the summer, reflecting breeding and territory-holding behaviour (Cramp et al., 1988, Robinson, 2005).

2.4.4 Conclusions

With the increase in urbanisation and fragmentation of the environment animals can become limited in their movements which can affect immigration to habitat patches. This can have significant impacts on metapopulation viability (Hanski, 1998) and species diversity at local community levels (Van Dyck and Baguette, 2005, Whittaker and Fernández-Palacios, 2007) population size and distribution (Hinsley et al., 1995b), genetic diversity and biodiversity (Fahrig, 2003, Bonte et al., 2012).

This work has demonstrated the functional connectedness of Birmingham's urban environment and shown that it has a positive impact on avian numbers. Despite their mobility, birds still benefit from the foraging and nesting resources and protection from predators that a connected environment can provide. However for greater clarity, future work should address connectivity on a range of scales,

both through varying gap sizes between vegetative cover to reflect a range of gap-crossing abilities between species (Creegan and Osborne, 2005, Shanahan et al., 2011) and to address the impacts of extent of available connected habitat on different landscape scales (Hale et al., 2012).

Structural connectivity through trees within 30 m of one another clearly improves conditions for avian populations across the seasons, consequently suggesting functional connectivity in this urban landscape (Mills et al., 1991, Shanahan et al., 2011). Conservation of functional connectivity is central to long-term conservation of wildlife in urban landscapes (FitzGibbon et al., 2007). The majority of the species studied here showed a negative trend with an increase in built space, demonstrating that although connectivity provides some resilience to the impacts of urbanisation, large connected areas of habitat are valuable and preferable.

The urban landscape is complex (Andrén 1994) and cannot simply be seen as corridor and non-corridor. Instead, it is a matrix dotted with trees which combine to make tree-lines. This study provides evidence to reinforce the message that in order to support passerine species it is important that urban planners take the urban green infrastructure and matrix into consideration in planning decisions to ensure functional connectivity across the city and greater conservation returns (Prugh et al., 2008). Native tree species and vegetative cover should be incorporated into the landscape to provide cover and conduits for bird species (Lancaster and Rees, 1979, Beissinger and Osborne, 1982). Furthermore, the more similar the matrix is to the preferred habitat of a species, the more permeable the landscape is to that species (Prevedello and Vieira, 2010, Eycott et al., 2012).

In this age of climate change and urbanisation, the need for functional connectivity is becoming more acute as these changes drive shifts in species' ranges (Dawson, 1994, Huntley et al., 2007, Hale et al., 2012). Functional connectivity can support birds on a local basis, providing cover and foraging resources, as well as enhancing population persistence and species occupancy in complex landscapes (Marzluff and Ewing, 2001, FitzGibbon et al., 2007). This study showed that Birmingham's green infrastructure and connectivity contribute to increased numbers in passerine bird species. Through a comparison of sites with more or less connected habitat it was shown that populations of birds increase despite, in some cases, the amount built space being higher. This indicates that providing increased functionally connection through increased vegetation, regularly distributed through the urban landscape is likely to make avian populations resilient to future urban development.

Chapter 3. The effect of vegetation structure and productivity on birds across an urban gradient

3.1 Introduction

Habitat structure often strongly influences animal-habitat associations (MacArthur and MacArthur, 1961, Vierling et al., 2008) and in a fragmented environment, such as that found in urban areas (Luck and Wu, 2002, Zhang et al., 2004, Tratalos et al., 2007b), the three-dimensional structure of vegetation is potentially more influential on bird assemblages and abundance than in more contiguous environments, providing habitat for more bird species which are sensitive to fragmentation (Goldstein et al., 1986). One of the most important and influential components of habitat structure is spatial heterogeneity or patchiness (Wiens, 1976), which includes both the characteristics of vegetation and its variation in space (Rotenberry and Wiens, 1980).

The influence of vegetation on birds was first investigated at the beginning of the last century when Dunlavy (1935) studied and described the variation in bird distribution with vertical structure of vegetation. Subsequently, MacArthur and MacArthur (1961) developed a quantitative approach to analyse bird species' diversity in relation to latitude and habitat factors, including plant species' composition and foliage height profiles. They found that the height profile of vegetation (or vertical vegetation "structure") predicted bird species' distribution and that plant species composition played a subsidiary role. This was interpreted as an illustration of a positive relationship between potential niche space and vegetation structure diversity, and it initiated a long-running debate about the relative importance of plant species composition *versus* the structure of vegetation for the diversity and composition of bird assemblages (Fleishman and MacNally, 2006, Müller et al., 2010). In desert and shrub-steppe environments for example, plant species composition is highly significant in regulating breeding bird communities (Tomoff, 1974, Wiens and Rotenberry, 1981) whereas habitat structure has been found to be influential in species distribution in Eastern U.S. deciduous forest (Anderson and Shugart, 1974). Vegetation that is species rich and complex in structures enhances insect productivity (Mills et al., 1989).

3.1.1 Invertebrate productivity

Differences in prey abundance between tree species may lead to foraging preferences which can shape the distribution of birds (Gabbe et al., 2002). The structure of vegetation may provide birds with cues or 'sign stimuli' (Anderson and Shugart, 1974) to the potential availability and diversity of food, protection and nest sites suitable for reproduction (Wiens and Rotenberry, 1981).

Mills et al. (1989) found that breeding bird densities in native habitats in the USA correlated strongly with the volume of native vegetation and they suggested that this was due to a correlation between vegetation volume and the resources it provided for birds. This resource-based hypothesis was then applied to an urban context and it was found that the same relationship held, but that the native vegetation supported more birds than expected in comparison to the natural system. Mills et al. (1989) demonstrated the importance of vegetation structure and resource provision for birds in an urban context.

3.1.2 Study aims

This study examines whether there are specific characteristics of vegetation that influence bird distributions in a UK urban environment. Identifying tree species preferences of foraging birds in combination with structural features could potentially provide planners with key information to mitigate the effects of urbanisation and provide the highest quality habitat for the broadest assemblage of birds. Comparing the predictive power of plant species' composition and vegetation structure for bird assemblages was the main aim of both MacArthur and MacArthur (1961) and Müller et al. (2010). This study takes this one stage further by investigating whether it is vegetation structure, composition and associated invertebrate food provision or a combination of factors that influences British bird distributions across an urban gradient over two survey periods, when resources may vary with vegetation type, using a combination of survey and remote sensed data.

The study addresses the following aims:

i) To assess the effect of the three-dimensional structure of vegetation on the distribution of bird species in an urban environment, with a focus on vegetation height characteristics and distribution of patches

ii) To assess the impact of invertebrate prey diversity of vegetation on the distribution of birds

iii) To investigate whether there is a season-specific association between birds and vegetation

3.2 Methods

3.2.1 Study area

This study was carried out in Birmingham, UK, with sites selected in a stratified manner across the urban gradient as described in Chapter 2 (Figure 2.1).

3.2.2 Bird surveys

Comprehensive bird surveys were carried out at all 70 sites. As described in section 2.2.2, two summer surveys were carried out at all of the sites; 26 of the sites were surveyed by nine experienced volunteers. The first summer surveys were conducted between 28/04/2009 and 29/06/2009. The second summer surveys were conducted between 08/06/2009 and 17/09/2009. Winter surveys were carried out at all of the sites between 17/01/2010 and 10/02/2010, 17 of the sites were surveyed by six experienced volunteers.

3.2.3 Environmental variables

A methodological review of the literature for gap-crossing behaviour of passerine species (described in detail in section 2.2.3.2) suggested that 30 m was an approximate limit to natural gap-crossing (without playback) for passerines in the UK (Creegan and Osborne, 2005) and in an urban setting in Canada (Tremblay and St. Clair, 2009). The tree networks were buffered by 15 m consequently encompassing all gaps ≤30m and creating a connectivity mask (Figure 2.2) that captured the structural connectivity of the landscape surrounding the site.

3.2.3.1 Measuring vegetation structure

In recent years laser altimetry, commonly referred to as light detection and ranging (LiDAR), has been recognised as a methodological solution to measuring the physiognomy of vegetation in an ecological context (Lefsky et al., 2002, Bradbury et al., 2005, Hinsley et al., 2006, Goetz et al., 2007, Vierling et al., 2008, Müller et al., 2010). LiDAR is a remote sensing technique that can provide fine-grained information about the three-dimensional structure of habitats, measuring the topography of both plant canopies and sub-canopies, thereby providing high-resolution topographic maps and highly accurate estimates of vegetation height, cover and canopy structure (Lefsky et al., 2002, Vierling et al., 2008). Vegetation has high reflectance in the wavelength range (900-1064 nanometres) of lasers used in LiDAR devices for terrestrial applications, resulting in accurate vegetation measurements (Lefsky et al., 2002).

The vegetation layer was multiplied by differenced rectified LiDAR data, which provided the height of all vegetation (Figure 3.1) with an accuracy to within a metre. Heights of trees derived from LiDAR were ground truthed by James D. Hale, Alison J. Fairbrass and Tom J. Matthews.
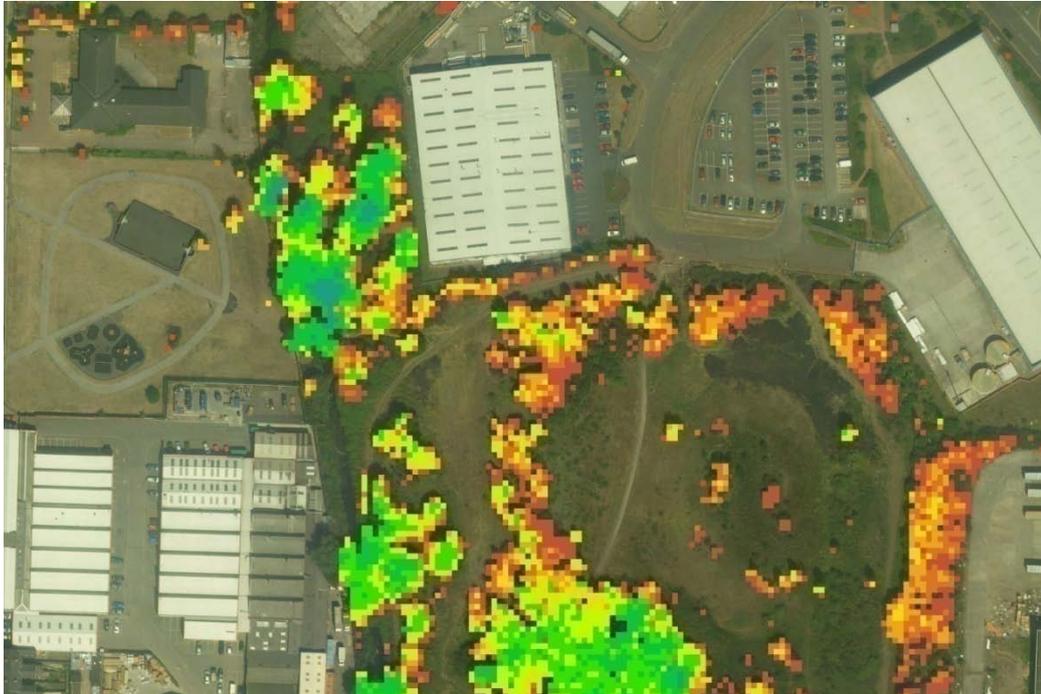
Figure 3.1 Aerial photograph of an area of Birmingham, UK, showing heat scaled vegetation height data. Red pixels show the lowest vegetation at 3 m and blue shows the highest which varied from site to site. The original vegetation layer was multiplied by differenced rectified LiDAR data which provided the height of the vegetation, this was then used to model the bird-habitat relationships.

As in Chapter 2, (section 2.2.3.3) two approaches were taken to extract LULC summary data for the landscape surrounding each survey site. First, a 500 m radius buffer was constructed around the site centre using the GIS as it is a fair estimate of breeding home range and territory of most of the study species (Perrins, 1979, Snow, 1988, Davies, 1992, Cramp et al., 1993, Cramp et al., 1994, Naef-Daenzer, 1994). Complete summaries of the underlying landscape were extracted using this buffer. This approach assumes that all of the habitat in the landscape is potentially relevant or available to the species concerned. The second approach was to restrict the landscape analysis to areas adjacent to tree-lines by using the connectivity mask. LULC summaries were again extracted from the 500 m radius buffer around each site centre, but this time the available data were limited to the areas of the connectivity mask intersected by the 25 m buffer around the survey transects.

3.2.3.2 Tree insect productivity
Over the 70 sites surveyed 58 tree species or tree families (where species could not be identified) were recorded. In order to have an effective method of analysing the impacts of tree species on the

distribution of bird species, it was necessary to group tree species into categories and create a score that quantified invertebrate productivity in a simple, yet robust, manner. This study focussed on the distribution of small passerine species, so focusing on insect productivity of tree species as an indicator, or 'sign stimulus' to a bird of a potentially good foraging site, is a justifiable approach (Anderson and Shugart, 1974, Wiens and Rotenberry, 1981, Greenberg and Bichier, 2005).

Observations on the numbers of insect species on trees in Britain were obtained from Southwood (1961), Southwood et al. (1982), Kennedy and Southwood (1984) These were used as a basis for categorising the trees surveyed in Birmingham. When plotted four categories of trees were apparent as characterised by steps in the numbers of insect species they support (Figure 3.2).
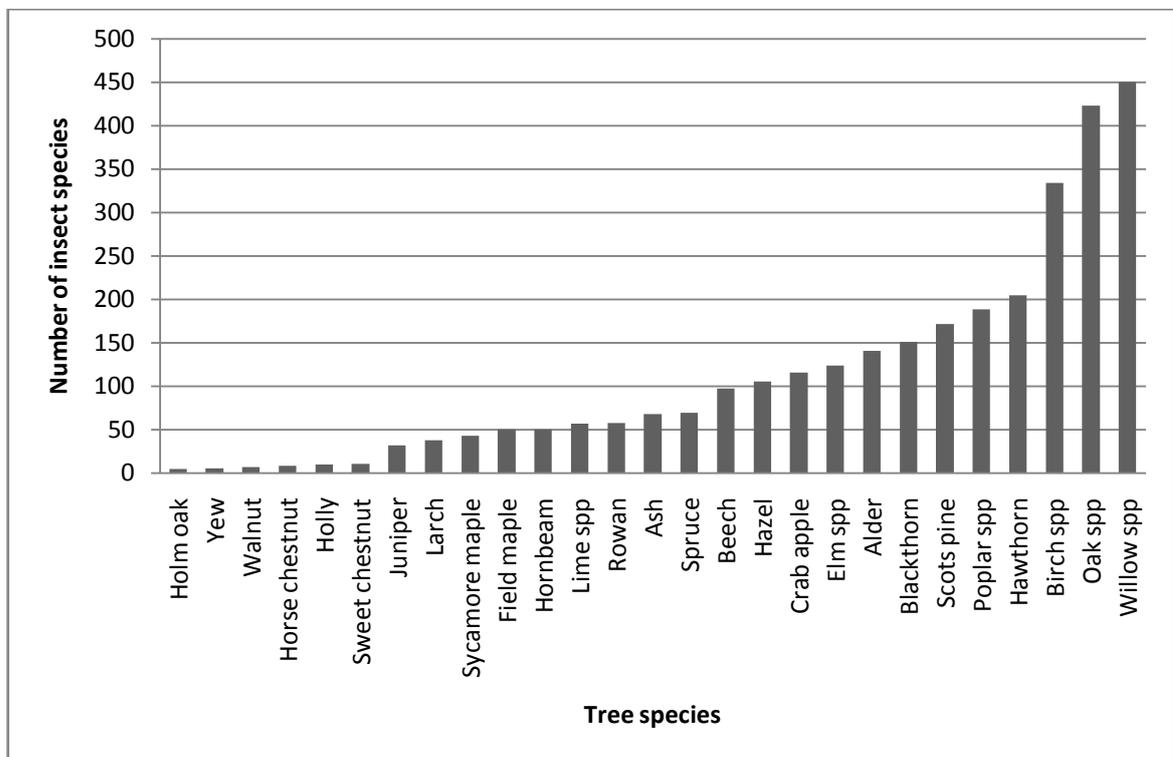
Figure 3.2 Histogram of insect species supported by different tree species in Britain (after Southwood, 1961, Southwood et al., 1982, Kennedy and Southwood, 1984, DBIF, 2012)

As these categories increased with large steps, the scores allocated doubled for each category to reflect the non-linear increase in numbers of insects supported (Table 3.1).

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Table 3.1 Tree insect categories and associated scores. Due to the large increments in the increase in the number of insects supported, the score doubled for each category to reflect this pattern. These categories and scores were then used to calculate the insect diversity of a site and analysed to assess the influence on the birds found there.

Category	Number of insect species associated	Score
1	<25	1
2	26-75	2
3	76-200	4
4	>250	8

All trees recorded at each site were then assigned to the appropriate category dependent on the number of phytophagous invertebrate species that they have been found to support (Table 3.2) according to estimates in Southwood (1961), Southwood et al. (1982), Kennedy and Southwood (1984). Where there were missing estimates in the above sources, the Database of Insects and their Food Plants (DBIF, 2012) was consulted.

Table 3.2 Tree species recorded at sites in surveys categorised according to associated insect species (figures from Southwood, 1961, Southwood et al., 1982, Kennedy and Southwood, 1984, DBIF, 2012)

Category 1 (<25)	Category 2 (26-75)	Category 3 (76-250)	Category 4 (>250)
Horse Chestnut	Beech	Apple species	Birch
Holly	Beech (hedge)	Alder	Crack willow
Sweet Chestnut	Bastard Service	Aspen-poplar sp	Goat willow
Yew	Copper beech	Blackthorn	Oak
Cedar species	Field maple	Crab Apple species	Willow species
Plum species (*Prunus*)	Field maple (hedge)	Elm	Weeping willow
London Plane (hybrid)	Ash	Hazel	Hawthorn
Elder	Horn beam	Hazel (hedge)	Hawthorn (hedge)
Cyprus species	Lime	Poplar	
Leylandii	Maple species	Scots Pine	
Eucalyptus	Rowan	Buddleja	
Laurel	Sycamore	Damson (*Prunus*)	
Magnolia species	Wild Service	Pine sp	
Tulip tree	White beam		
Acacia	Cherry (*Prunus*)		
Ginko	Lilac		
Monkey puzzle	Rhododendron		
Gorse	American oak		
Acer			

Native species of trees and plants support the most number of insect species due to the amount of time they have been in an area and thereby time for invertebrates to adapt and use it as a food plant. In addition, detailed features of the leaf such as surface type and palatability will affect its likelihood of becoming a food plant. It is also important to note that introduced species of trees will not exhibit a peak in insect numbers which is a very important source of food for birds provisioning chicks (Southwood et al., 2004).

For each site the total tree counts from both transects were then multiplied by the category score. For example, 12 trees for category 4 would have scored 96 (12 × 8) the score of potential insect diversity for the survey site.

3.2.3.3 Environmental variables for analysis

LULC summary data from both extraction methods along with the tree count scores for each site were then used to create response variables for statistical analysis where habitat factors were inspected for associations with bird distributions (Table 3.3).

Table 3.3 Details of the variables generated for statistical analysis from the survey work, GIS and literature review as described above. The name of the variable used in the statistical models is listed on the left and the details of the generation method and how it relates to the environment is described on the right.

Variable	Details
Ctrees	Fixed effect; Ctrees is a measure of heterogeneity of the trees. The actual tree cover was divided by the connectivity mask which creates a measure of how clumped the trees are.
ave	Fixed effect; mean tree height per site as calculated by the Zonal Statistics ++ tool in Hawth's Analysis Tools for ArcGIS. (ArcGIS 9.2, ESRI Redlands, USA)
stdv	Fixed effect; standard deviation of tree height per site as calculated by the Zonal Statistics ++ tool in Hawth's Analysis Tools for ArcGIS. (ArcGIS 9.2, ESRI Redlands, USA)
score	Fixed effect; an insect diversity score per site, calculated by assigning tree species to categories of insects supported. Then, tree count per site (presence/absence per 100 m) is multiplied by the category score; providing a score per site (see section 3.2.3.2. for further details)
built	Fixed effect; built land cover. The total land cover that can be categorised as built including buildings, roads, pavements, etc. These are collated from data extracted with the thematic raster summary tool in Hawth's Analysis Tools for ArcGIS (ArcGIS 9.2, ESRI Redlands, USA)
landclass	Categorical variable 1-6 across the urban gradient (after Owen et al., 2006)

The three-dimensional detail of the landscape was incorporated into analysis through the heterogeneity of the vegetation; a measure of how clumped the vegetation was (Ctrees), the mean height (ave) of the vegetation and the standard deviation of the height of the vegetation (stdv). A measure of the urbanisation of the site was included through a measure of the area of land with built land cover (built). This is to put into context the influence of the vegetation factors on birds with regard to the level of development of the surrounding area.

3.2.4 Data analysis

Prior to analysis the data were explored using a range of techniques (Zuur et al., 2010). Cleveland dot plots were used to confirm that there were no outliers. Co-linearity was examined using pairplots, and variance inflation factors were calculated to assess co-linearity amongst explanatory variables. All values were ≤ 3 and therefore it can be concluded that no co-linearity exists between the explanatory variables (Zuur et al., 2009).

Associations between avian abundance at each site and habitat characteristics were modelled using general linear mixed models (GLMMs) with a poisson distribution (Pinheiro and Bates, 2000)in R (R Core Development Team, 2011). GLMMs were run using the package lme4 (Bates et al., 2011). GLMMs were run for all 18 species and the standardised residuals were plotted against the fitted values and inspected for heteroscedasity. Where a cone distribution was seen the model was rejected (Crawley, 2007, Zuur et al., 2009). Ideally season would have been included as a random factor in the model but as it only had two levels this was not an option. In total 270 models were run, with 15 models for each of the 18 species including up to five fixed effects for both early summer and late summer.

Akaikes Information Criteria (AIC) were used to select the best-fit models (Burnham and Anderson, 2002) for each species in each season. The Akaike weights demonstrated that the best-fit model contained the most influential factors on the response variable (Whittingham et al., 2006). Quantile-quantile plots were created and suggested a lack of departure from the model assumptions. The histograms of the model residuals showed normality.

Spline (cross-)correlograms (package ncf; Bjornstad, 2009) using the residuals from the competing models showed that only limited spatial auto-correlation was present (Zuur et al., 2009). An example is presented in Figure 3.3.
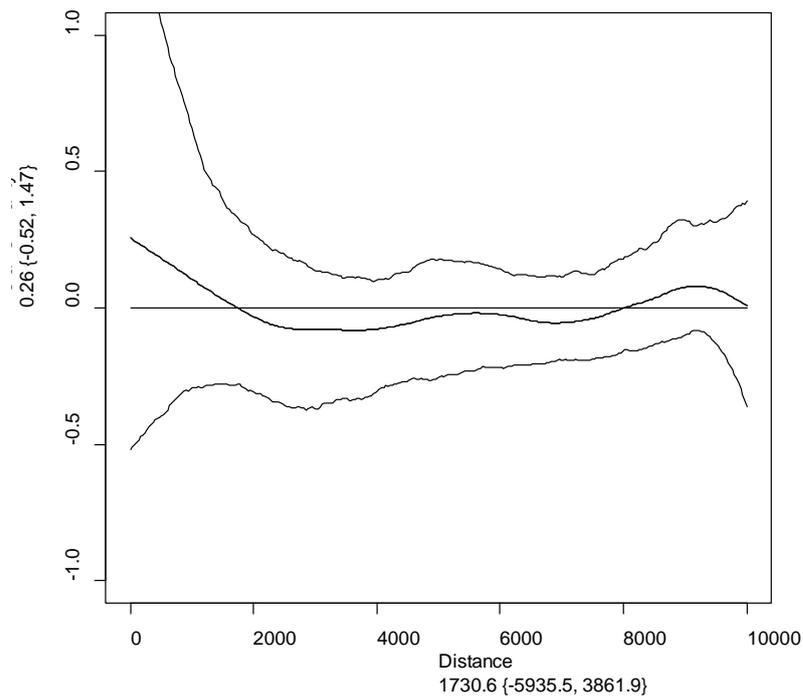
Figure 3.3 Example spline correlogram, with 95% pointwise bootstrap confidence intervals, of residuals of the best fit GLMM model for Great Tit for the early summer surveys demonstrating only a little spatial autocorrelation (see text for details)

3.3 Results

A summary of the results of the best-fit GLMM models for each species analysed is presented in Table 3.4 for the early surveys and in Table 3.5 for late surveys. The significant factors are presented along with the *p*-value.

Table 3.4 Summaries of the best-fit GLMMs for each species for the early summer (between 28/04/2009 and 29/06/2009) surveys species counts. The best-fit model is displayed for each of the 18 species, with interactions and the associated significant factors and *p*-value.

Species	Model	Significant factors	*p*-value
Common Blackbird	Score*built	none	-
Eurasian Blue Tit	Score*ave*built	built:ave	0.01
		score:built:ave	0.004
Eurasian Bullfinch	Score*ave*stdv	ave	<0.001
		stdv	<0.01
		score:ave	<0.001
		score:stdv	0.02
		ave:stdv	<0.001
		score:ave:stdv	<0.001
Common Chaffinch	Score*ave	ave	0.01
		score	0.05
		score:ave	0.02
Coal Tit	score*ave*stdv*built	None	-
Dunnock	Score*built	None	-
European Goldfinch	Ctrees*score*built*ave	Ctrees	0.008
		score	0.003
		built	0.02
		Ctrees:score	0.005
		Ctrees:built	0.02
		score:built	0.009
		Ctrees:score:built	0.01
European Greenfinch	score*ave*built*stdv	Built	<0.001
		score:ave	0.05
		score:built	0.004
		ave:built	0.02
		built:stdv	<0.001
		score:ave:built	<0.01
		score:built:stdv	<0.001
Great Tit	score*stdv	Stdv	0.01
House Sparrow	Ctrees*score*ave*built	ave	0.05
		Ctrees:built	0.05
		score:ave	0.05
		score:built	0.02
		ctrees:score:built	0.005
Long-tailed Tit	score*stdv*ave	None	-
Mistle Thrush	Ctrees*score	score	0.04
Eurasian Nuthatch	Ctrees*score	None	-
European Robin	Score*stdv*built	None	-
Skylark	Ctrees*score	Score	0.01
Song Thrush	score*ave*stdv	Score:ave	0.03
		Score:stdv	0.04

Common Starling	Ctrees*score*ave	Ctrees	0.02
		Score	<0.001
		Ctrees:score	0.02
		Ctrees:ave	<0.001
		Ctrees:score:ave	<0.001
Eurasian Wren	Ctrees*score	None	-

Table 3.5 Summaries of the best-fit GLMMs for each species for the late summer (between 08/06/2009 and 17/09/2009) surveys species counts. The best-fit model is displayed for each of the 18 species, with interactions and the associated significant factors and *p*-value.

Species	Model	Significant factors	*p*-value
Common Blackbird	Ctrees*score*ave*stdv*built	Score	0.003
		Built	0.01
		score:built	0.01
Eurasian Blue Tit	Score*built	Score	0.01
		built	0.02
Eurasian Bullfinch	Ctrees*score*ave*built	Score	0.03
		Built	0.01
		Ctrees:ave	0.05
		score:built	0.05
		ave:built	0.006
		score:ave:built	0.006
Common Chaffinch	Score*stdv*built	None	-
Coal Tit	Score*ave*stdv	None	-
Dunnock	Ctrees*score*stdv	stdv	0.05
European Goldfinch	score*stdv*built	score	<0.01
		built	<0.001
		score:stdv	0.02
		score:built	<0.001
		stdv:built	0.002
		score:stdv:built	<0.001
European Greenfinch	Ctrees*score*ave*stdv	ave	0.03
		stdv	0.02
		Ctrees:score	0.03
		Ctrees:ave	0.02
		score:ave	0.01
		ave:stdv	0.004
		Ctrees:score:ave	0.02
		Ctrees:ave:stdv	<0.001
		score:ave:stdv	<0.001
		Ctrees:score:ave:stdv	<0.001
Great Tit	Ctrees*score*ave*stdv	None	-
House Sparrow	Ctrees*score*ave*built	score	0.05
		Ctrees:score	0.02
		Ctrees:ave	0.02
		Ctrees:score:ave	0.003
		Ctrees:score:built	<0.001
Long-tailed Tit	Ctrees*score*stdv	score	0.02

		Ctrees:stdv	0.02
		Ctrees:score	0.03
Mistle Thrush	score*built	score	0.02
		Built	0.005
		Score:built	0.003
Eurasian Nuthatch	score*ave	none	-
European Robin	score*stdv*built	stdv	0.001
		Score:stdv	0.03
		Stdv:built	0.01
		Score:stdv:built	0.01
Skylark	score*built	built	0.05
Song Thrush	Ctrees*score*ave*built	score	0.02
		Ctrees:ave	0.03
		Ctrees:score:ave	0.04
Common Starling	score*ave*stdv*built	built	<0.001
		score:built	0.005
		stdv:built	0.02
		ave:stdv:built	0.03
Eurasian Wren	Ctrees*score*ave*stdv*built	Ctrees:ave:stdv	0.03
		Ctrees:score:ave:stdv	0.05

3.3.1 3D structure

The three-dimensional structure of the vegetation had a variable influence on the distribution of birds between bird species.

3.3.1.1 Tree height

A higher abundance of birds with lower height vegetation was found for House Sparrows, Eurasian Blue Tits, Eurasian Bullfinches, European Greenfinches (*Carduelis chloris*) and Common Starlings. Where there was a higher mean vegetation height, the abundance of Song Thrushes, Eurasian Wrens and Common Chaffinches increased.

The Great Tit, European Robin, Song Thrush, and Eurasian Wren were found to be more abundant at sites with higher levels variation of vegetation height. European Goldfinches, Dunnocks (*Prunella modularis*) and European Greenfinches were found in higher numbers where there was less variation in vegetation height.

3.3.1.2 Heterogeneity of tree distribution

At sites with a more heterogeneous arrangement of vegetation (or more edge for the volume of trees) European Goldfinches, Common Starlings and House Sparrows were more abundant. A less heterogeneous arrangement of vegetation was correlated with an increase in numbers of Eurasian Bullfinches, European Greenfinches, Song Thrushes and Eurasian Wrens.

3.3.2 Invertebrate diversity

On average non-native tree species have lower insect productivity, for example the Holm Oak has 5 insect species associated, and the Sweet Chestnut 11 species. Consequently areas with higher numbers of non-native and ornamental tree species resulted in areas with less insect diversity and lower numbers of bird species. An increase in invertebrate diversity in an area was associated with an increase in abundance of Common Blackbirds, Eurasian Blue Tits, Eurasian Bullfinches, European Greenfinches, Long-tailed Tits, European Robins, Common Starlings, Song Thrushes, Eurasian Wrens and Common Chaffinches. There was also a significant interaction ($p < 0.05$) with invertebrate diversity and an increase in tree height for Common Chaffinches. An increase in invertebrate diversity and a decrease in vegetative spatial heterogeneity showed a significant correlation ($p < 0.05$) to explain the distribution of Long-tailed Tits. The best-fit model for Eurasian Blue Tits in the early survey (Table 3.4) showed a significant interaction with an increase in invertebrate diversity and lower mean tree height ($p = 0.01$).

European Goldfinches, House Sparrows and Mistle Thrushes (*Turdus viscivorus*) were less abundant in areas with higher levels of invertebrate diversity but showed an increase in numbers with more built space.

3.3.3 Season-specific associations

The Common Chaffinch had significant explanatory variables in the early survey (Table 3.4) but none were significant in explaining the distribution of this species in the best-fit model in the late survey. This species showed a significant positive association with mean tree height ($p < 0.05$).

There were significant explanatory factors in the best-fit models for the Dunnock, Long-tailed Tit, European Robin and Eurasian Wren in the late survey analysis (Table 3.5) but not in the early survey.

The model with the best fit for Eurasian Wrens in the late survey showed a complex interaction of factors to explain distributions. It indicated an association with habitats that have trees with high insect diversity, horizontally homogeneous habitat and taller vegetation with variable height.

The best-fit model for the European Robin in the late survey (Table 3.5) showed a significant interaction between high insect diversity, vertical heterogeneity and higher levels of built space to explain their distribution. The best-fit model in the early survey (Table 3.4) also showed a significant interaction with an increase in variability of tree height and in invertebrate diversity ($p < 0.05$).

For a summary of the main responses of all the bird species to the environmental factors see Table 3.6.

Table 3.6 Summary of the significant environmental factors which led to either an increase or decrease in numbers for the best-fit model each bird species across all three surveys. An upwards arrow (green cells) indicates increased numbers of birds, a downward arrow (red cells) indicates decreased numbers of birds. Species with no arrows in cells had no significant factors influencing abundance in the best-fit models. Birds were surveyed across 70 sites in Birmingham.

Species	Insect diversity (score)	Built space (built)	Connected habitat (Ctrees)	Average height of vegetation (ave)	Standard deviation of vegetation (stdv)
Coal Tit	↑			↑	↑
Common Blackbird	↑	↑			
Common Chaffinch	↑			↑	
Common Starling	↑	↑	↑	↓	
Dunnock					↓
Eurasian Blue Tit	↑	↑		↓	
Eurasian Bullfinch	↑	↑	↓	↓	
Eurasian Wren	↑		↓	↑	↑
European Goldfinch	↓	↑	↑		↓
European Greenfinch	↑	↑	↓	↓	↓
European Robin	↑	↑			↑
Great Tit	↑				↑
House Sparrow	↓	↑	↑	↓	
Long-tailed Tit					
Mistle Thrush	↓	↑		↓	
Nuthatch					
Song Thrush	↑		↓	↑	↑

3.4 Discussion

The impacts of the detail of the habitat on 18 species of passerine birds were investigated across an urban gradient. Birds are highly diverse in their ecology and the diverse response to characteristics of the urban habitat as found in this study reflects this (Cannon et al., 2005, Daniels and Kirkpatrick, 2006, Evans et al., 2009b).

The land cover, spacing and species of trees were important factors in maintaining bird diversity in this study as they were in the study by Mills et al. (1989). For some bird species the spacing of trees was important with some showing a preference for more patchily distributed trees (e.g. House Sparrows, Common Starlings and European Goldfinches), while some preferred a more aggregated

distribution of trees (e.g. Song Thrushes, Eurasian Wrens, Eurasian Bullfinches and European Greenfinches).

3.4.1 3D structure

Lower heights of vegetation and increased built space were associated with increased abundance of House Sparrows, Mistle Thrushes, Eurasian Blue Tits, Eurasian Bullfinches, European Greenfinches and Common Starlings. Tree taxa such as hawthorn (*Crataegus* spp.) and blackthorn (*Prunus spinosa*) which are usually lower in height than other vegetation (Johnson, 2006) provide fruit, bud, seed and insect prey and dense nesting sites and, therefore, many resources for Eurasian Bullfinches, European Greenfinches (Newton, 1967, Newton, 1972) and House Sparrows (Summers-Smith, 2003, Robinson, 2005). Lower vegetation is likely to be dense hedges providing protective cover and allowing movement for species in urban areas (Hinsley et al., 1995b, Summers-Smith, 2003).

Where there were areas with stands of taller trees Common Chaffinches, Song Thrushes and Eurasian Wrens were all found to be more abundant. Taller trees (e.g. European Beech [*Fagus sylvatica*]) have been considered a good indicator of site quality with an association with higher numbers of earthworms (family Lumbricidae) (Ponge et al., 1999) which may explain the association with Song Thrushes (Simms, 1978, Gruar et al., 2003). Taller trees may provide broader foraging niches for insectivorous birds due to the complex structure and often dead and decaying branches (Hansson, 2000, Stagoll et al., 2012) which would explain the association with species such as Eurasian Wrens (Cramp et al., 1988) which are insectivorous, and for Common Chaffinches which provision their young with invertebrate prey in the summer months (Newton, 1972). Mature woods are a preferred habitat for Common Chaffinches (Newton, 1972) and Song Thrushes (Simms, 1978), which tends to be the tallest vegetation on a British landscape and so relates well with the preferences found for higher vegetation in these species in this study.

Many birds species select relatively high song perches as it decreases interference with sound transmission (Ward and Slater, 2005), and this may explain the association of Song Thrushes (Simms, 1978) and Common Chaffinches (Newton, 1972) with taller trees. Eurasian Wrens generally sing and forage low in vegetation, but in the summer territorial males will forage and sing higher in the vegetation than female birds are located and occasionally reach the canopy (Cramp et al., 1988).

These results suggest that vegetation with a diversity of heights, perhaps of mixed age or species, are a preferred habitat for several species such as Great Tits, European Robins, Song Thrushes and Eurasian Wrens. An increased variation in vegetation height may indicate diverse vegetative

structure or physiognomy, and could indicate a variety of habitat and resource availability (MacArthur and MacArthur, 1961, Anderson and Shugart, 1974, Lancaster and Rees, 1979, Müller et al., 2010). The association of these species may also point to them being generalists and being able to take advantage of many habitats types by breeding or feeding in them (Simms, 1978, Perrins, 1979, Cramp et al., 1994, Robinson, 2005). Eurasian Wrens have been found to prefer woodland with connected hedges (Hinsley et al., 1995b) which could be reflected in variable vegetation height.

European Goldfinches and Greenfinches were found in higher numbers where there was less variation in vegetation height. These two species are widely distributed and forage in a variety of habitats in the winter, but in the summer, when the data were collected, their preferences are for dense vegetation where they can find their preferred seed-based diets (Newton, 1972). These are likely to be found in specific habitat types with less variable vegetation heights. These two species also showed an increased abundance with more built space, due to vegetation management in urban areas and in domestic gardens vegetation is likely to be less variable in height (Loram et al., 2008). With a decreased variability in vegetation height, Dunnocks were also found to be more abundant reflecting their consistent preference for low, thick vegetation (Davies, 1992).

At sites with a more heterogeneous arrangement of vegetation (or more edge for the area of trees) European Goldfinches, Common Starlings and House Sparrows were more abundant. European Goldfinches are known to nest in scattered trees in open country (Newton, 1972) and fragments of woodland (Hinsley et al., 1995b) and to forage at woodland edges (Newton, 1972, Hinsley et al., 1995b). Such preferences were reflected in this study with the preference for heterogeneity of vegetation. Common Starlings use the tops of tall, exposed trees for daytime roosts, where they perch, preen and rest (Feare, 1984). They are primarily grassland feeders which might have scattered trees throughout, but when the invertebrates from the ground are limited, they switch to foraging in trees for defoliating caterpillars (Feare, 1984). These characteristics of habitat use by Common Starlings were reflected in their preference for patchy vegetation and an interaction with areas of vegetation with high invertebrate diversity.

An increase in built land cover was also found to correlate with increased abundance of European Goldfinches, Common Starlings and House Sparrows. House Sparrows and Common Starlings both use building cavities for nesting sites (Feare, 1984, Summers-Smith, 2003). The existence of buildings and built land cover reduces the available land for vegetation and, therefore, will increase the distance between vegetated patches. An increase in patchiness of vegetation cover may reflect characteristics of the built landscape.

A less heterogeneous arrangement of vegetation was correlated with an increase in numbers of Eurasian Bullfinches, European Greenfinches, Song Thrushes, Long-tailed Tits and Eurasian Wrens. Eurasian Wrens (Cramp et al., 1988) Eurasian Bullfinches (Newton, 1972) and Long-tailed Tits (Perrins, 1979) breed in woodland undergrowth and hedgerows and are reluctant to break cover. Therefore it may be expected that they prefer a less fragmented arrangement of vegetative cover.

3.4.2 Invertebrate diversity

The association between areas that were calculated to have higher invertebrate diversity and an increased abundance of many species is a good indicator that birds associate with vegetation productive in invertebrate food, possibly choosing habitat areas based on sign stimuli that indicate potential high production of food (Anderson and Shugart, 1974, Wiens and Rotenberry, 1981, Mills et al., 1989).

For most of the year finches are granivorous, feeding on seeds, fruit and buds (Newton, 1972). However Eurasian Bullfinches, European Greenfinches and Common Chaffinches were found to have increased abundance in areas with vegetation that is productive in invertebrate prey. This is likely due to them foraging for invertebrate food when raising young during the summer months (Newton, 1972) which is a period that these survey data were collected in.

Leaf-gleaning insectivores such as Long-tailed Tits (Perrins, 1979) and Eurasian Wrens (Cramp et al., 1988) were found to have increased abundance in areas with increased invertebrate diversity as would be expected. These species of small body size spend a large majority of their time foraging and adjusting their feeding habits in relation to trees in leaf, maximising their access to invertebrate prey (Perrins, 1979, Cramp et al., 1988).

An increase in bird abundance with higher invertebrate diversity and an interaction with an increase in built space was found for six species, indicating that bird populations can be supported across the urban gradient with natural food resources such as native trees that produce a high diversity of invertebrate prey.

The abundance of ground-feeding species such as the thrushes (*Turdus* spp.) has a significant positive relationship with tree genera that have high insect diversity despite the preference for earthworms and soil macrofauna as prey (Robinson, 2005). This, however, may be explained by the interaction between tree taxa and the abundance of earthworms, for example. Tree taxa determine the quality and quantity of leaf litter produced, the litter decay processes, humus formation, nutrient cycling and, hence, the earthworm assemblages (Muys et al., 1992, Ponge et al., 1999). Muys et al. (1992)

found that stands of Wild Cherry (*Prunus avium*) and Broad Leaved Lime (*Tilia platyphyllos*) produced relatively unpalatable litter and an associated lower number of earthworms. Pin Oak (*Quercus palustris*) stands produce poor quality litter whereas stands of Alder (*Alnus glutinosa*) and Ash (*Fraxinus excelsior*) produce highly palatable litter. It would seem that where the leaves are palatable to phytophages (most commonly native tree species), they also produce palatable leaf litter for saprophagous fauna, apart from in the case of *Quercus* spp. which supports the highest number of arthropods (Southwood et al., 1982, Kennedy and Southwood, 1984) but produces unpalatable leaf litter for saprophages. This pattern may explain the significant correlation of soil-foraging bird species with areas with trees producing high numbers of invertebrate species.

European Goldfinches, House Sparrows and Mistle Thrushes were found in greatest numbers in areas of increased built space but there was a negative relationship between their abundance and insect diversity of tree taxa. This is likely to be due to the fact that Goldfinches and House Sparrows are primarily granivorous and are likely to show a strong association with bird feeders when available (Robinson, 2005, Ockendon et al., 2009, BTO, 2012). Furthermore, European Goldfinches and Mistle Thrushes often forage for seeds, fruit and soil macrofauna on the ground away from tree-lines (Newton, 1972, Simms, 1978) and this may explain the lack of association with invertebrate diversity.

3.4.3 Season-specific associations

Several species were found to have explanatory factors in the best-fit models in either the late or early survey but not in the other. The Common Chaffinch has significant explanatory variables in the early survey but none in the best-fit model in the late survey. Conversely there are significant explanatory factors in the best-fit models for the Dunnock, Long-tailed Tit, European Robin and Eurasian Wren in the late survey analysis but not the early survey. These patterns are not easily related to any distinct breeding stage of the focal bird species (e.g. hatch date) and, therefore, increased provisioning activity, the fledging of nestlings, or territory holding activities (Robinson, 2005). Overarching explanations in the effects of habitat on bird species' abundance in relation to season were not possible. Differences in relationships between bird abundance and habitat from summer and winter survey data are likely to be explained by changes in foraging behaviour of many avian species invertebrates to seeds and fruit (Mills et al., 1989). However, it was not possible to analyse winter distributions of birds due to the lack of information about the diversity of seeds by UK tree species.

Nine species showed a significant positive trend with increasing built space, often with interactions with vegetative characteristics, and none showed a decline. However, only 18 species were analysed

in this study – those that are resident and abundant passerines in this urbanised area. This subset of species is likely to influence these findings, in terms of the response to the built environment as their abundance in urban areas demonstrates an ability to exploit the urban landscape. Garden bird feeding is also likely to have a significant effect on the distribution of birds in the city (Fuller et al., 2008) but this was not part of this study, nor an easily measured variable.

3.4.4 Conclusions

This study demonstrates the wide variety of responses by the avian community to the habitat available to them, with complex relationships with the environment becoming apparent. The majority of the species examined here displayed a preference for a combination of structural and tree species composition (Wiens and Rotenberry, 1981). The invertebrate scoring gave an overview of tree species and feeding resources provided and the environmental factors gave an overview of structural features of the vegetation.

Urban areas tend to have an abundance of non-native, ornamental tree species (Beissinger and Osborne, 1982), which support fewer insect species than do native tree species (Southwood, 1961, Kennedy and Southwood, 1984). The evidence suggests that birds depend on a diversity of native tree species with high arthropod diversity (e.g. *Quercus, Salix* and *Betula* spp.) and those that produce palatable leaf litter, as these can be a source of food for both insectivorous birds and ground feeders that forage for soil macrofauna. Increasing vegetative cover in urban areas and recreating and preserving complete habitat profiles (Beissinger and Osborne, 1982) so that there is vegetative cover at many heights and distributions as well as invertebrate food resources, would ensure suitable habitats for many different species of birds. These could include those that might occur in the UK for the first time as their ranges expand North due to climate change (Huntley et al., 2007).

The results demonstrate the functionality of urban spaces for birds as long as appropriate tree species in certain configurations are available. Supported by other research (e.g. Lancaster and Rees, 1979, Beissinger and Osborne, 1982, Goldstein et al., 1986, Mills et al. 1989, Shanahan et al., 2011), this study suggests that natural assemblages of native tree species are the most appropriate for avian populations.

This supports town planners in designing new urban spaces and in the re-vegetation of existing urban areas for avian populations. These findings may be particularly important where there are pressures to increase built space to accommodate the burgeoning urban human population resulting in the expansion and densification of UK cities and large alterations in the ecology (Tratalos et al., 2007b).

Chapter 4.   Should I stay or should I go? Factors that influence bird movement in an urban landscape

4.1 Introduction

4.1.1 Movement in birds

Movement of individual animals is one of the most fundamental features of life on Earth and is a crucial component of many ecological and evolutionary processes (Nathan et al., 2008). It is widely recognised as an essential part of bird ecology, behaviour and life history (Verhulst et al., 1997, Rubenstein and Hobson, 2004, Newton, 2007) and is required for individuals to find resources such as food, nest sites, mates and protective cover (Taylor et al., 1993, Van Dyck and Baguette, 2005).

Dispersal can be defined as a movement of individuals away from each other (Van Dyck and Baguette, 2005) that leads to the establishment of a new home range or breeding site (Bowne and Bowers, 2004) and is key for gene flow and a driver of ecological and evolutionary patterns (Wiens, 1976, Verhulst et al., 1997, Paradis et al., 1998, Van Dyck and Baguette, 2005, Bonte et al., 2012). Daily movements to forage or seek shelter and directed long distance movements moving away from a natal site or from a previous breeding site may lead to dispersal (Van Dyck and Baguette, 2005).

Natal dispersal is the permanent movement made by juveniles from their birth site to their first breeding or potential breeding site (Greenwood and Harvey, 1982, Morton, 1992). This type of movement can be made after only two or three weeks of fledging in passerines and the distances moved are known to be of several kilometres (Morton, 1992, Newton, 2007) and in various directions (Newton, 2007). In sedentary or resident bird species in the temperate zone (e.g. Northern Europe) that stay in the same general area year-round, populations make no obvious large-scale movements (Newton, 2007), and there is selection for early natal dispersal, before the arrival of the winter months (Morton, 1992).

Breeding dispersal is the process of adult birds changing their nest site between successive years while, wintering dispersal is the process by which birds change their non-breeding locations from

year to year (Newton, 2007). In most species natal dispersal is far more extensive than breeding dispersal (Greenwood and Harvey, 1982, Newton, 2007). One major reason for this is due to philopatry of established breeding birds and, consequently, young birds are forced to disperse away from their natal sites by established territory holders. Young birds often excluded from high quality breeding habitats near their natal sites are likely to take advantage of vacancies when they occur (Greenwood and Harvey, 1982).

Migration is one of the most visible and widespread phenomena (Wilcove and Wikelski, 2008) where individuals make regular, often long-distance return journeys, with stopover periods when energy stores are replenished (Seewagen et al., 2010). It occurs at roughly the same stage of the annual cycle (in annual breeders) and is often to specific destinations (Newton, 2007). It is a critical period in the annual cycle of birds with a great risk of mortality (up to 85%) in some species (Matthews and Rodewald, 2010) and it requires high energy expenditure both during flight and stopovers due to thermoregulatory demands (Wikelski et al., 2003).

Breeding ties birds to one area for part of the year when adults are required to visit nests to incubate eggs or to provision a mate during incubation, and subsequently to provision fledglings in altricial and some precocial systems (Newton, 2007). In some habitats with unpredictable resources, or in the winter months, bird movement takes the form of nomadism, where birds range from one area to another residing temporarily where there is an abundant, yet ephemeral, source of food (Newton, 2007). As the needs of birds change through the seasons and across a lifetime, bird movements vary considerably both temporally and spatially (Barraquand and Benhamou, 2008).

4.1.2 Habitat influences on movement

A bird's movement across a landscape and ability to utilise a resource is dependent on the habitat through which it travels, which must be functionally connected and permeable to the species. Functional connectivity refers to the behavioural response of a species to the various elements of a landscape, including both habitat patches and the matrix (Tischendorf and Fahrig, 2000). A species' response to a landscape may facilitate or impede its movement, thereby influencing its population dynamics (Pe'er et al., 2006). For example, a fragmentation sensitive species may not move across a landscape if the configuration is too patchy (Bolger, 2001) and species that are reluctant to cross habitat boundaries are likely to alter their behaviour and therefore, their movement patterns as they encounter different habitats (Morales and Ellner, 2002). Urbanisation has been shown to affect species differently according to their dispersal ability suggested by wing span (Croci et al., 2008).

Edges in fragmented landscapes may create boundaries and influence species' behaviour and distributions. For example, edge sensitivity was shown in bird species in a study in a fragmented suburban landscape in New South Wales, Australia (Hodgson et al., 2007) where nectarivorous species were more likely to cross edges in vegetation areas of high-density housing. Insectivores were more likely to cross edges in areas of low-density. In urbanised areas road networks are prominent linear features, and they have been shown to act as barriers to movement (Tremblay and St. Clair, 2009, Kociolek et al., 2011). Flocks of Black-capped Chickadees (*Poecile atricapillus*) in fragmented forest in Alberta, Canada, respond strongly to forest boundaries and use them as movement conduits within home ranges (Desrochers and Fortin, 2000).

4.1.3 Do corridors connect?

Due to the recognition that connectivity plays an important role in preserving or enhancing biodiversity (Angold et al., 2006) wildlife corridors and urban greenways have become a popular conservation tool (Dawson, 1994, Beier and Noss, 1998, Hess and Fischer, 2001, Levey et al., 2005) and are often advocated in urban landscape planning to encourage animals and plants to move in urban areas (Small, 2002, Angold et al., 2006). Corridors, which can be defined as a linear habitat embedded in a dissimilar matrix that connects two or more larger and otherwise isolated habitat patches (Beier and Noss, 1998, Haddad et al., 2003), can evolve out of habitat fragments if the configuration is appropriate. They have the potential to play an important role in the landscape, acting as conduits for the movement of organisms, creating shelter, a protected route to travel across the landscape (Dawson, 1994, Hess and Fischer, 2001), 'rescuing' isolated populations, allowing gene flow and maintaining biodiversity (Haddad et al., 2003). To function as corridors linear habitat features in the landscape must act as a conduit for movement or as habitat for the species in question (Bolger et al., 2001, Hess and Fischer, 2001).

Just because a corridor exists from a human's perspective does not necessarily mean that it is used as a movement conduit (Young and Jarvis, 2001) or that it provides functional connectivity (Hess and Fischer, 2001). Corridors may not be relevant to all organisms and there is mixed evidence in support for their functionality (Beier and Noss, 1998, Haddad et al., 2003, Levey et al., 2005, Angold et al., 2006), especially for very mobile taxa living in a complex environments. Instead, functional connectivity may be provided through the matrix of green infrastructure and trees in gardens. The matrix between habitat patches has often been categorised as homogeneous and unsuitable as habitat (Kuefler et al., 2010) in paradigms for spatially structured populations such as metapopulations, but in urban landscapes which are complex, the matrix is likely to vary considerably

in permeability. Due to the impact that habitat structure can have on behaviour, bird movements are essential for interpreting apparent urban fragmentation (Bolger, 2001).

Birds can fly and, therefore, among higher vertebrates they are highly mobile (Newton, 2007). Flight is often fast but also has the highest energy demands (per unit time), compared with other locomotor modes such as running, walking or swimming. Nevertheless, it facilitates the coverage of relatively large distances and is, therefore, the most efficient locomotor mode (Newton, 2007). Despite flight being the most efficient locomotor mode, it still requires energetic requirements. In addition to these, the time it takes to make a movement and the risk of predation all make movement between patches expensive for individuals (Wiens et al., 1993, Bonte et al., 2012). Habitats that are easy to move through, due to vegetative structure or low predation risk, incur a lower energetic cost than ones that are more difficult or dangerous to move through (Graham, 2001).

The urban landscape is fragmented, patchy, and spatially heterogeneous (Young and Jarvis, 2001) often resulting in unevenly distributed resources across the landscape (Fernández-Juricic, 2000b) which may drive birds to move through a mosaic of habitats and matrix in order to fulfil their requirements (Johnson et al., 1992, Taylor et al., 1993, Forman, 1995, Barraquand and Benhamou, 2008). Patchy habitats found in urban areas will have variable degrees of predation risk due to domestic pets (Sims et al., 2008), habitat structure and composition, and changes in the natural predator community (Thorington and Bowman, 2003) such as an increase in corvids (Sims et al., 2008) or Eurasian Sparrowhawks (*Accipiter nisus*) (Bell et al., 2010). These factors will also explain variation in reproductive success across the landscape, in addition to variation in factors such as anthropogenic noise (Schroeder et al., 2012) and invertebrate availability (Richmond et al., 2012). Such landscape variability results in bird movements to locate the most profitable areas (Johnson et al., 1992, Morales and Ellner, 2002) and contributes to overall breeding performance at the population level (Bowne and Bowers, 2004). The quality of the habitat is also expected to have an influence on bird movements, where poorer quality habitat is likely to result in increased incidents of bird movements as birds search more extensively for food, nest sites etc. (Winker et al., 1995).

Few studies have investigated the influence of urban habitat quality on bird movements and those that have, have considered gap-crossing behaviour rather than overall movements (e.g. Hodgson et al., 2007). Tremblay and St. Clair (2009, 2011) found that both anthropogenic and natural linear features such as roads, railway lines, transportation bridges across riparian corridors and rivers can impede bird movements, creating barriers in the landscape.

Those that have studied limitations on animal movements through heterogeneous landscapes have taken a modelling approach (e.g. Johnson et al., 1992, Zollner and Lima, 1999, Morales and Ellner, 2002, Pe'er et al., 2006, Barraquand and Benhamou, 2008). None of these studies has resolved the fine-scale movements of birds through a heterogeneous landscape such as a city and its suburbs. In part this is because bird movements are difficult to measure (Haas, 1995). The movements of British birds' have rarely been described in the literature (e.g. gap-crossing studies such as Creegan and Osborne, 2005; species profiles such as Hawthorn and Mead, 1975, Perrins, 1979) and no papers describe movements in a British urban context. Ringing records are a useful tool to understand movements of individuals (Redfern and Clark, 2001), but studies of the movement of passerines that have employed intensive approaches (e.g. re-trapping effort) are rare (Clark et al., 2011), especially in an urban setting.

It is important to understand how habitat influences bird movements in order to explain how an urban landscape might influence population dynamics, ecology and life history of birds (Verhulst et al., 1997, Rubenstein and Hobson, 2004). There is a lack of literature investigating whether birds use corridors in the urban environment (Bowne and Bowers, 2004) and it is imperative that this is addressed due to the prominence of corridors in applied conservation efforts.

This is not a study of dispersal. Rather, it focuses on movement between sites, although it is important to note that the shorter movements and the impact that an urbanised environment has on them, could have wider scale impacts on gene flow and population persistence (Van Dyck and Baguette, 2005).

Chapters 2 and 3 showed the sensitivity of birds to habitat factors in the urban landscape. Native trees, vegetation heterogeneity, higher levels of connected habitat and low levels of built space were all shown to affect bird species' abundance positively. However, the methods employed in those chapters could not demonstrate whether individuals move away from these more urbanised sites to find resources that may not be available.

4.1.4 Aims

Sites across an urban area were regularly trapped to create an extensive dataset to understand individual bird movements in relation to habitat characteristics within an urban landscape.

The study aimed to:

i) quantify the distances that bird species move in an urban landscape

ii) assess whether mobility varies across bird species

iii) assess whether habitat characteristics and level of connectivity influence bird movement

iv) assess whether the presence of corridors, or linked green habitats, influence bird movements.

4.2 Methods

4.2.1 Study site

This study was carried out in Birmingham, UK, in 27 sites (Figure 4.1) which were identified to sample a green corridor in the south and a larger expanse of green space in the north of the city.
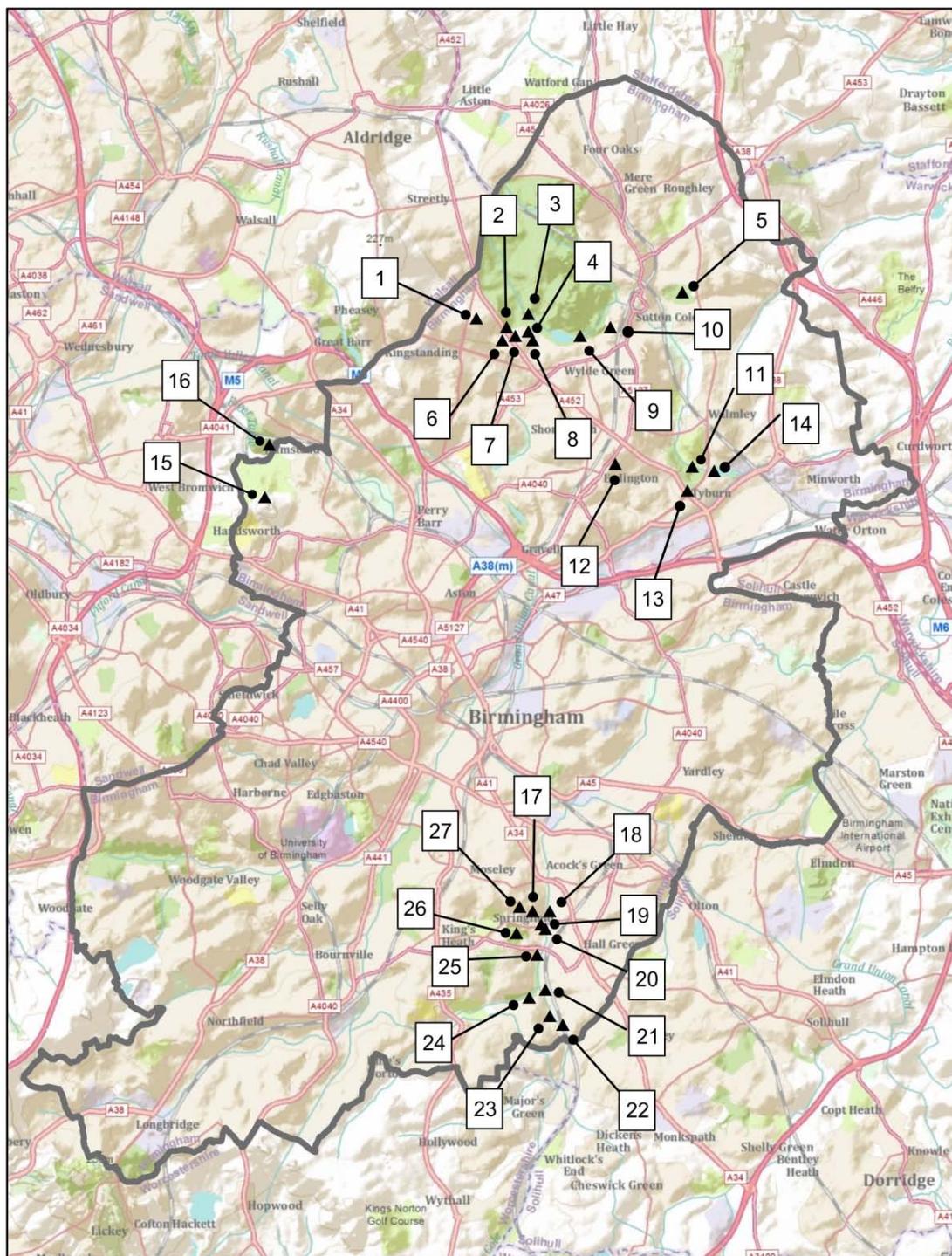
Figure 4.1 Map showing the city of Birmingham, UK with its local authority boundary and ringing sites (shown as black triangles, labelled with numbers) that were used to study the movements of birds within the urban matrix, from 2008 to 2011 inclusive.

The sites in the south were located along a green river corridor (the River Cole Valley) (Figure 4.2) and ringing sites were added over the years along the corridor, and between and beside sites and to capture movements and to elucidate whether birds show preferences for moving along corridors. Due to the urban nature of the study, site position was limited to available and secure sites.
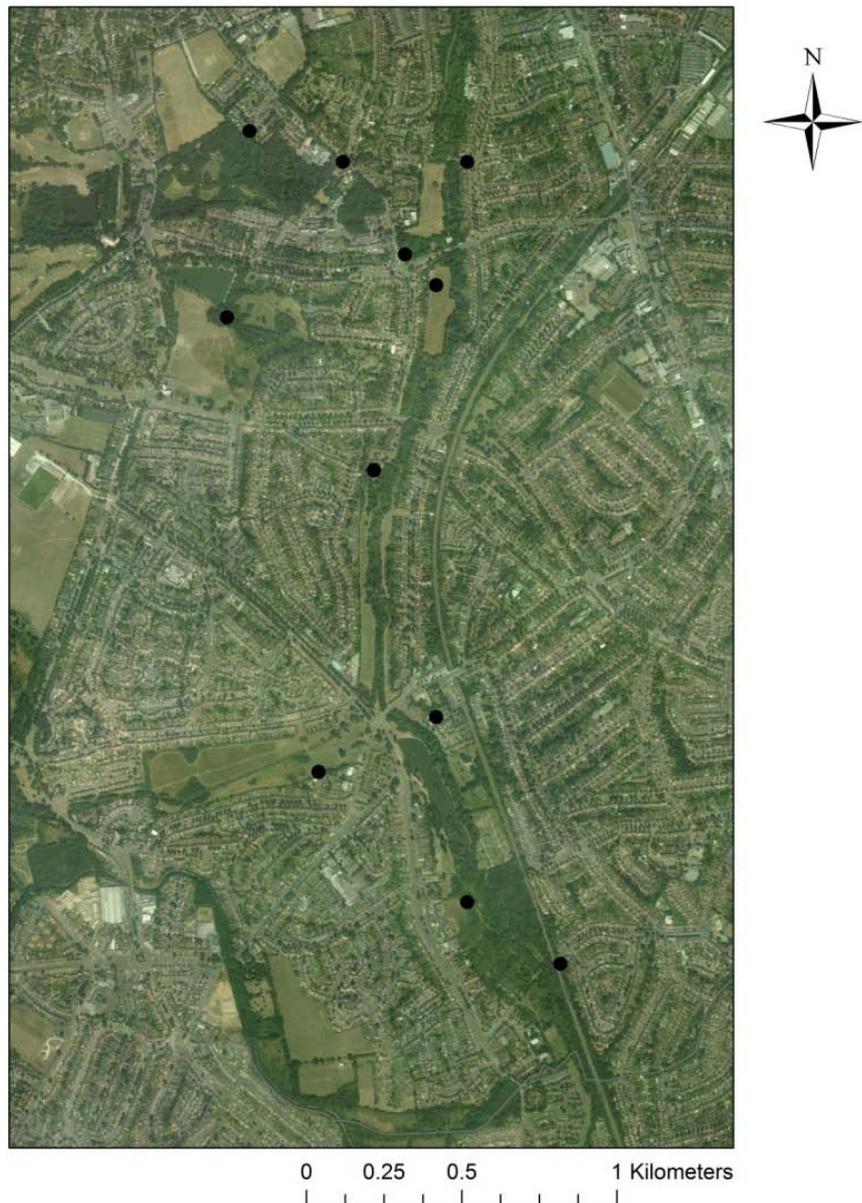
Figure 4.2. Ringing sites (shown as black circles) along and adjacent to the River Cole corridor, in South Birmingham, UK.

A total of 223 visits were carried out at the 27 sites during 2008, 2009, 2010 and 2011 (Table 4.1). Mist-nets were erected along net rides that were cut through vegetation and, due the urban context, positioned carefully to minimise disturbance by members of the public. Net length was kept consistent for each site across ringing sessions. Sites were kept baited with mixed seed and

sunflower hearts from at least two days before mist-netting and all through the winter ringing season (November-January in 2008, 2009, 2010 and 2011). During the rest of the year no bait was used. Volunteers assisted in the collection of data through the ringing of birds when a BTO licensed ringer was present and in various other tasks when not. Sites were sampled at least once per month during the winter ringing season.

Sites were mist-netted between 06:00 to 13:00 hrs GMT with occasional afternoon sessions when ringing took place in private gardens. Records from other ringing activity in Birmingham led by S. Bodnar were included in the analysis (SB unpubl. data).

Table 4.1 Sampling effort and distribution of re-trapped birds in a study of the movement of bird species movements at 27 sites in the city of Birmingham from 2008 to 2011. For each site, the corresponding number of ringing dates and the number of re-trapped birds are listed.

Site number	Site name	Number of ringing dates	Number of re-trapped birds
1	Coppice View	6	5
2	Banner's Gate	5	3
3	Longmore	15	83
4	Durley	2	5
5	Rectory Lane	7	1
6	Greenway	4	3
7	Dunchurch	3	1
8	Princess Alice	5	13
9	Boldmere	19	151
10	Wyndley	1	1
11	Pype Hayes	37	55
12	Holly Lane	12	1
13	Pype House	4	1
14	Plantsbrook	15	116
15	Hilltop	5	10
16	Sandwell Valley	24	78
17	Wake Green	8	34
18	Ford	13	64
19	Mill	8	21
20	Sarehole	24	78
21	Trittiford	7	10
22	Slade Lane	8	19
23	Scriber's Lane	15	37
24	Chinn Brook	2	3
25	Dingles	6	20
26	Swanshurst Park	5	17
27	Moseley	3	7

For each unringed bird caught a uniquely numbered BTO metal ring was fitted on to its left leg. When ringed (i.e. re-trapped) birds were caught, the ring number was recorded. Standard biometrics were collected for all trapped birds; species, sex, age, wing length and body mass (Redfern and Clark, 2001).

Records of bird ringing were sorted into new birds and re-trapped birds with the latter matched to original ringing records, where available, and to any subsequent trapping records of the same

individual within the dataset collected in Birmingham and made available by S. Bodnar (SB unpubl. data).

4.2.2 Environmental variables

The distance between sites was calculated with the Distance Between Points tool (within layer) in Hawth's Tools (Beyer, 2004) in a GIS (ESRI). Distances were assigned to each recorded bird movement.

A 500 m radius around the site was selected as an appropriate scale as it is a reasonable estimate of foraging (Wilkin et al., 2009), breeding home range and territory of most of the study species (Perrins, 1979, Snow, 1988, Davies, 1992, Cramp et al., 1993, 1994, Naef-Daenzer, 1994). A third of all bird movements were within 500 m indicating a grain size for landscape perception (Lima and Zollner, 1996, Baguette and Van Dyck, 2007) which was used as a further justification for scale selection.

Land use and land cover (LULC) and the amount of connected tree cover (as described in Chapter 2) were summarised with the Thematic Raster Summary tool in Hawth's Tools (Beyer, 2004). From the extracted LULC data a category of grey space (the variable 'grey') was created by combining buildings, roads, railway etc., representing the built land cover and a measure of urbanisation (see Table 4.2 for full details of variables generated for statistical analysis). LULC data extracted for each site was assigned to the re-trap record and the corresponding original trapping.

Table 4.2 Details of variables generated for statistical analyses in an investigation of habitat factors influencing bird movements in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive.

Variable	Details
Continuous variables	
grey	Fixed effect. Total area of grey space within 500 m. Grey space encompasses all built space, including buildings, roads, pavements etc.
ctrees	Fixed effect. Total area of connected habitat within 500 m. Connected habitat is classified as habitat within 15 m of trees above 3 m in height – see Chapter 2 for details.
Ctreesch	Fixed effect. Calculated as ctrees at site 1 - ctrees at site 2. Demonstrates difference in the amount of connected habitat between site 1 and 2 at successive trapping sites and represents the difference in connected available habitat experienced by a bird moving between sites.
Greych	Fixed effect. Calculated as grey at site 1 - grey at site 2. Demonstrates difference in the amount of grey space between site 1 and 2 at successive trapping sites.
Categorical factors	
move	Response variable. Binomial category: 0 – no movement between sites; 1 – movement between sites.
ID	Random effect. Individual bird based on its ring number.
SPEC	Species of bird.
Site1	Random effect. The first site at which a bird was caught in successive trapping sites. This may have been the original trapping record or a re-trap. This variable ensured that unbalanced sampling effort was accounted for in the subsequent statistical analyses.
Corr1	Fixed and random effect. Binomial category: 0 – site outside of a green corridor; 1 – site on a green corridor.
ryear	Random effect. Year in which the re-trap occurred.

4.2.3 Statistical analysis

Prior to analysis the data were explored using a range of techniques (Zuur et al., 2010). Cleveland dot plots were used to confirm that there were no outliers. Variance was found to be considerably larger than the mean and, therefore, a negative binomial error structure was applied to the regression models (Zuur et al., 2007). A histogram to investigate distribution of data when distance was the response variable, demonstrated zero-inflation in the data. Variance inflation factors were calculated to assess co-linearity amongst explanatory variables. All values were ≤ 3 indicating that no co-linearity existed between the explanatory variables (Zuur et al., 2009).

Zero-inflation was present in the data because many birds were re-trapped at the same site continually without any movement. These contributed a considerable number of 'true' zeros (i.e. zeros not due to design, survey or observer error; Zuur et al., 2009) to the model. To overcome this

issue a binomial model was used where a '0' represented a bird that had made no movement while a '1' represented a move between sites.

Binomial mixed models were run in glmmML and lme4 (Bates et al., 2011) in R (R Core Development Team, 2011). The package lme4 was required for residuals and the consistency of model outputs between packages were confirmed. Sampling effort was incorporated into GLMMs as a random factor to account for any lack of balance in sampling effort (see Table 4.1 for details of number of samples at each site). In total, 21 models were run.

Akaike's Information Criteria (AIC) were used to select the best-fit model (Burnham and Anderson, 2002). The Akaike weights demonstrated that the best-fit model contained the most influential factors on the response variable (Whittingham et al., 2006). A quantile-quantile plot was created and suggested a lack of departure from the model assumptions. The histogram of the model residuals showed normality.

No spatial autocorrelation was found in the spline (cross-)correlograms (package ncf; Bjornstad, 2009) of the residuals of the best-fit model (Zuur et al., 2009) (Figure 4.3).
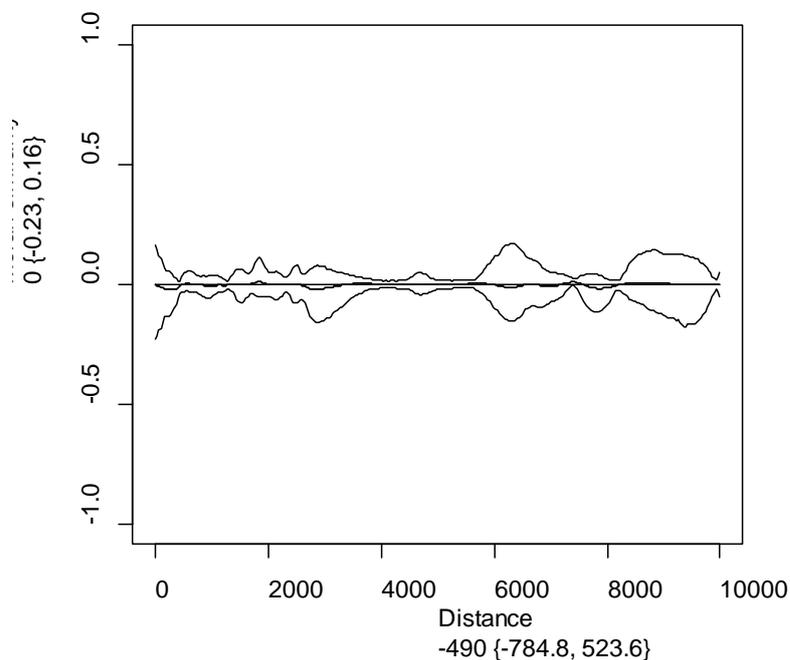
Figure 4.3 Spline correlogram, with 95% pointwise bootstrap confidence intervals, of residuals of the best-fit GLMM model demonstrating a lack of spatial autocorrelation

4.3 Results

The study sites represent a gradient of grey space within the urbanised landscape (Figure 4.4) and, therefore, represent a range of environmental conditions to which moving birds are exposed.
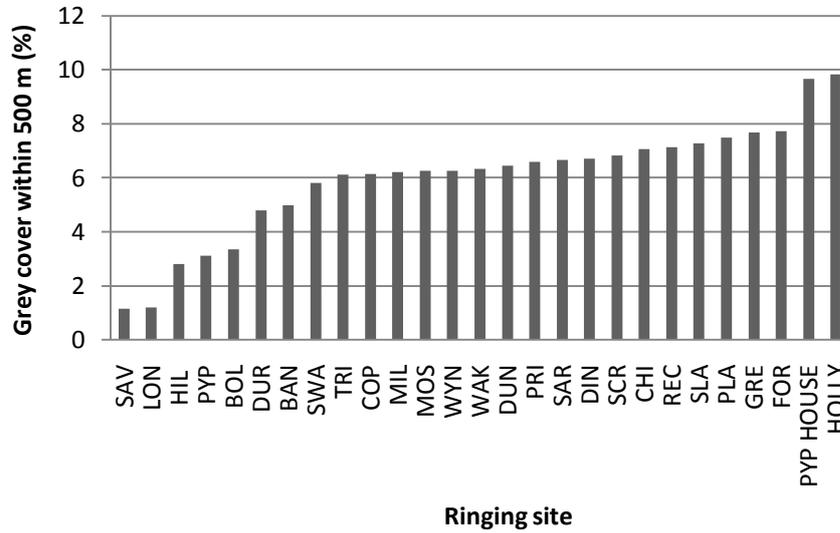
Figure 4.4 The percentage of built space ('grey' land cover; see Table 4.2 for details) within 500 m of the centre of each ringing site in Birmingham. This graph demonstrates the urban gradient that the study sites capture.

4.3.1 Re-trapped birds

There were 1,087 re-trap records of which 837 paired records were used in the analysis. A total of 249 movements were identified across the four year study period. The largest total number of movements were recorded for Great Tits and Eurasian Blue Tits, followed by Long-tailed Tits and European Robins (Table 4.3).

Table 4.3 The number of occasions a bird was re-trapped (No. Re-traps), the number of occasions a movement was recorded (moves) and the proportion of re-traps that a movement was recorded (% moves) categorised per species included in this study. Where a "-"is recorded this indicates no recorded movement and therefore no associated proportional value. European Goldfinch was removed from the study as n=1. These are descriptive data on bird movement activity recorded in Birmingham, UK.

Species	No. re-traps	moves	% moves
Common Blackbird	26	11	42
Eurasian Blackcap	8	1	12
Eurasian Blue Tit	206	65	31
Eurasian Bullfinch	46	8	17
Common Chaffinch	11	2	18
Coal Tit	25	10	40
Dunnock	40	12	30
European Goldfinch	1	1	100
Great Spotted Woodpecker	1	-	-
Great Tit	267	67	25
House Sparrow	2	-	-
Lesser Redpoll	1	-	-
Long-tailed Tit	65	33	51
Eurasian Nuthatch	20	9	45
Reed Bunting	26	2	7
European Robin	61	18	29
Song Thrush	7	1	14
Eurasian Treecreeper	6	2	33
Common Whitethroat	2	-	-
Willow Tit	5	-	-
Eurasian Wren	11	7	63

Eurasian Wrens were shown to make the largest percentage of movements followed by Long-tailed Tits (Figure 4.5).
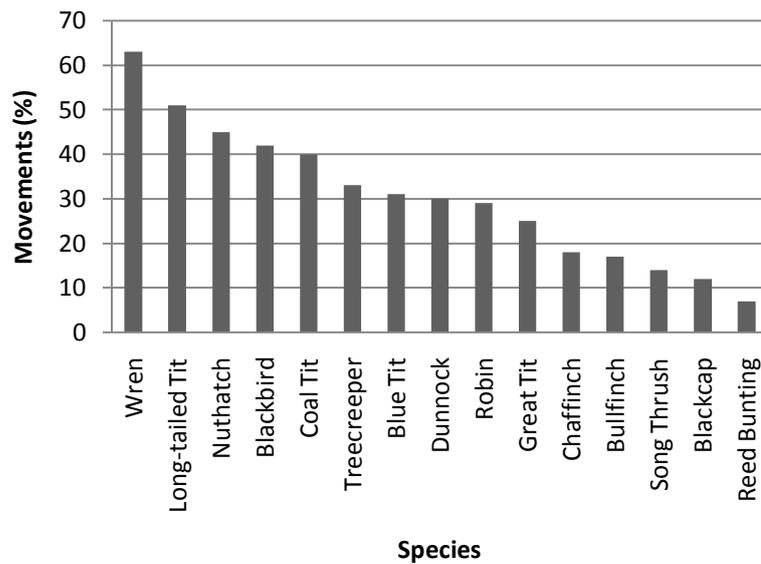
Figure 4.5 The percentage of movements within re-trap records of birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive.

Eurasian Wrens and Dunnocks made some of the longest movements with both species recorded to make movements of >14 km (Figure 4.6).
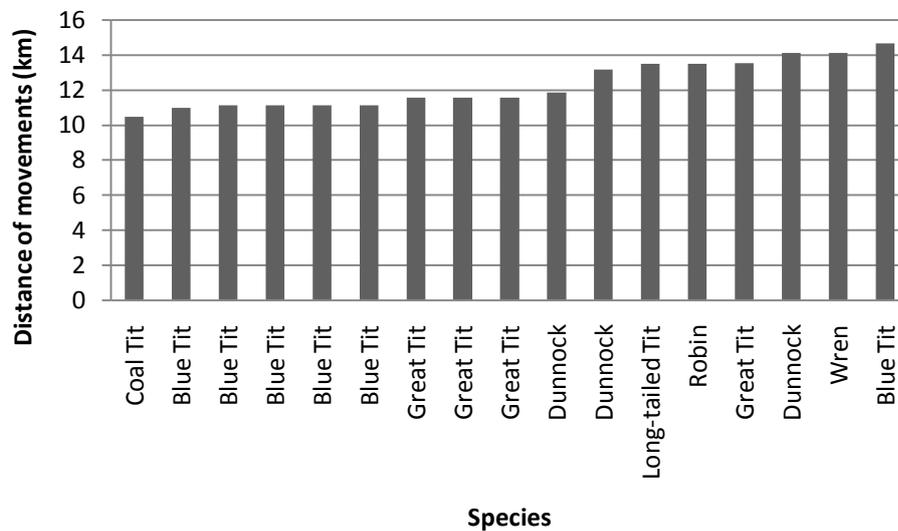
Figure 4.6 Distance of the longest movements (in km) of birds ringed and re-trapped in the city of Birmingham between 2008 and 2011 inclusive.

However, the Dunnock showed a greater range in the distance of movements (4161.34 ± 1555 m) (see Table 4.4 for movement distances for all species).

Table 4.4 Maximum and mean (± 1 SE) distances moved by 10 species of common birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive.

Species	Distance (m)	
	Maximum	**Mean (± 1 SE)**
Common Blackbird	3970	1552.05 ± 314.3
Eurasian Blue Tit	14667	1819.66 ± 405.0
Eurasian Bullfinch	5161	1842.93 ± 747.7
Coal Tit	10466	1634.49 ± 992.3
Dunnock	14091	4161.34 ± 1555.1
Great Tit	13530	1955.35 ± 372.0
Long-tailed Tit	13503	1297.95 ± 397.6
Eurasian Nuthatch	1300	1041.54 ± 111.0
European Robin	13503	1703.85 ± 710.6
Eurasian Wren	14091	3402.62 ± 710.6

The majority of the longest distances moved were carried out by Eurasian Blue Tits, Great Tits and Dunnocks (Figure 4.7).
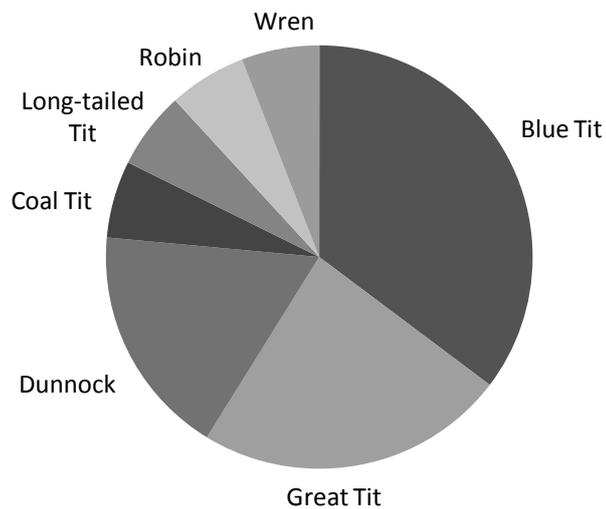
Figure 4.7 The proportions of the longest movements recorded of birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive, divided into species.

4.3.2 Environmental influences

The best-fit model contains amount of connected habitat, the change in connected habitat between the re-trap sites, amount of grey space and the change in grey space between re-trap sites (Table 4.5).

Table 4.5 Summary of the mixed models for bird movements of birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. All predictors from Table 4.2 were included in the modelling process. The table indicates the fixed variables included in the model (indicated in each model by ✓), the total number of fixed variables (K), the AIC, corrected AIC (AICc), delta weight (difference between the AIC for a given model and the best fitting model) and the model selection probability (w) (see text for further details).

model	response	ctrees	grey	ctreesch	greych	SPEC	corr1	K	AIC	AICc	Δ_i	exp'-½Δi	*w*	Sum(exp'-½Δj)	N
d8	move	✓	✓	✓	✓			4	759.4	759.45	0.000	1.000	0.987	1.013	835
f8	move	✓	✓	✓	✓			4	768.5	768.55	9.100	0.011	0.010		
nc8	move	✓	✓	✓	✓		✓	4	771.8	771.85	12.400	0.002	0.002		
nc9	move	✓	✓	✓	✓		✓	4	773.8	773.85	14.400	0.001	0.001		
f17	move	✓	✓	✓	✓	✓		5	786.3	786.37	26.900	0.000	0.000		
d1	move	✓	✓	✓	✓			4	832.2	832.25	72.800	0.000	0.000		
f15	move	✓	✓	✓	✓			4	898.6	898.65	139.200	0.000	0.000		
f16	move	✓	✓	✓	✓			4	899.6	899.65	140.200	0.000	0.000		
f3	move	✓	✓	✓	✓			4	905.8	905.85	146.400	0.000	0.000		
f11	move	✓	✓	✓	✓			4	907.2	907.25	147.800	0.000	0.000		
f2	move	✓	✓	✓				3	909.2	909.23	149.800	0.000	0.000		
f12	move	✓	✓	✓				3	910.4	910.43	151.000	0.000	0.000		
f5	move	✓	✓	✓	✓	✓		5	916.7	916.77	157.300	0.000	0.000		
f10	move	✓	✓					2	932.6	932.61	173.200	0.000	0.000		
f14	move	✓	✓					2	932.6	932.61	173.200	0.000	0.000		
f4	move	✓	✓			✓		3	941.6	941.63	182.200	0.000	0.000		
f18	move					✓		1	942.9	942.90	183.500	0.000	0.000		
f6	move	✓	✓	✓	✓	✓		5	960.5	960.57	201.100	0.000	0.000		
f7	move	✓	✓	✓	✓			4	960.5	960.55	201.100	0.000	0.000		
f9	move	✓	✓					2	971.2	971.21	211.800	0.000	0.000		
f1	move	✓	✓					2	974.6	974.61	215.200	0.000	0.000		

The model selection probability (w) demonstrated the strength of the best-fit model ($w_{best} \geq 0.09$) (Johnson and Omland, 2004) in comparison with the competing models. The output of this model demonstrated that grey space and change in grey space were particularly influential ($p<0.001$) in whether birds moved or not (see Table 4.6).

Table 4.6 Summary of the output from the best-fit model for bird movements of birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive

Best-fit model	Significant factors	*p*-value
move~ctrees*ctreesch+grey*greych+(1|site1)+(1|ryear), family=binomial)	greych	<0.001
	grey:greych	<0.001

A negative relationship exists between a change of grey space and the likelihood of birds making a movement (Figure 4.8). It indicated that where there is an increase in grey space in the second site compared with the original site the chance of bird movement is significantly less.
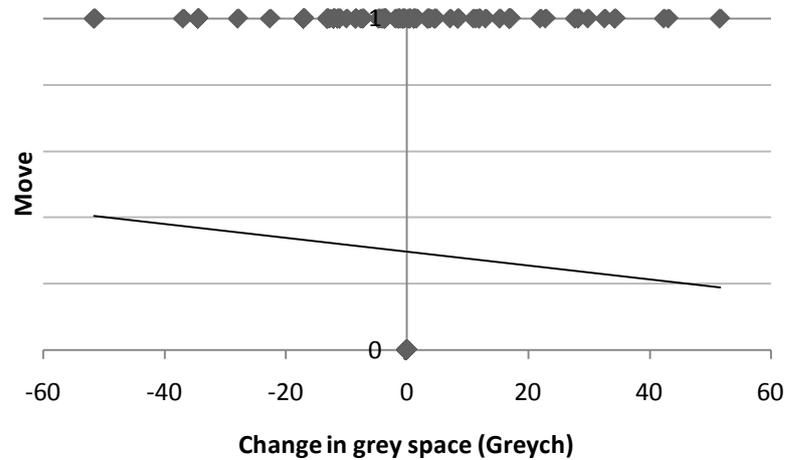
Figure 4.8 The relationship between change in grey space between sites and the likelihood of a bird moving sites in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. The change in the amount of grey space between the site the bird is first caught at and the second capture site on the x-axis (Greych) and the binomial category of whether a bird moved between sites or not on the y-axis (move). If Greych has a negative value there is less grey space within 500 m of the site at the second capture site. If Greych has a positive value there is more grey space at the second site. The trendline demonstrates that birds are less likely to move sites if the second site has more grey space than the first site. The single point on the x-axis is due to the fact that if a bird didn't move sites (move = 0) then there is inevitably no change in the amount of grey space between sites resulting in a value of 0 for change.

The amount of grey space shows a positive trend where a higher level of grey space around the site is more likely to result in the bird moving to another site where there is less total grey space (Figure 4.9).
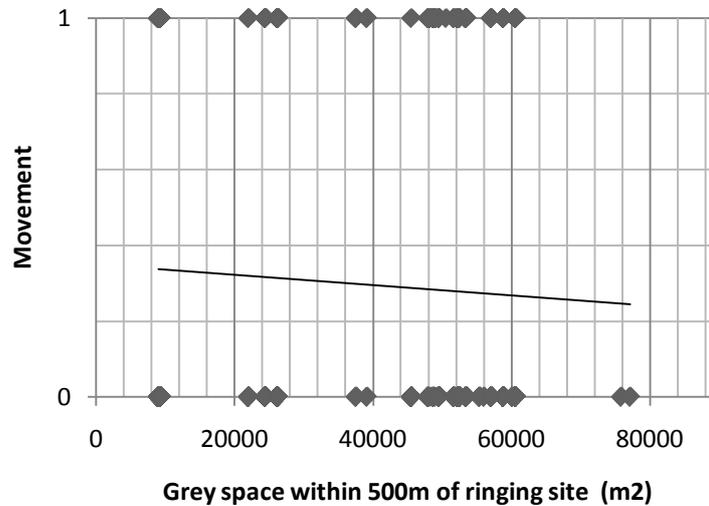
Figure 4.9 The relationship between the amount of grey space at sites and the likelihood of a bird moving between sites in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. An increase in the amount of grey space at the site that the bird is first caught at results in an increased possibility that the bird will move to another site.

4.4 Discussion

The results presented in this chapter show for the first time that features of the urban environment influence the movements of birds. There are two important patterns: (i) more grey space is related to a greater number of movements in several bird species; and (ii) birds move away from areas with more built space and are more likely to remain in habitats with green space and high connectivity.

4.4.1 Frequency of movements

Eurasian Wrens exhibited highest proportion of movements within the re-trap dataset. Hawthorn and Mead (1975) used BTO ringing records to demonstrate that this species was highly mobile even if their finding of 23% of birds making a movement does not compare favourably with the 63% that was found here. However, Hawthorn and Mead (1975) studied records collected nationally whereas the data collected for in this study were within an urban area where birds might be expected to move more due to scattered resource distribution (Fernández-Juricic, 2000b), intense predation risk and competition (Barraquand and Benhamou, 2008, Sims et al., 2008).

Long-tailed Tits also made a large number of movements, a finding that was not too surprising given that they are known to be mobile and display 'hedge-hopping' behaviour (Hinsley et al., 1995b), in order to find sufficient insect prey (Fuller et al., 2005). In the winter Long-tailed Tits join mixed feeding flocks (Székely et al., 1989) which aid in reducing predation risk due to increased vigilance from the flock and increase foraging efficiency due to a variety of opportunities to exchange

information (Harrison and Whitehouse, 2011). These flocks remain mobile which increases their chance of exploiting novel food sources with food more scarce in winter. Inevitably, however, they may suffer a trade-off due to increased energetic requirements of flight (Székely et al., 1989, Harrison and Whitehouse, 2011). High mobility of Long-tailed Tits may indicate a predator avoidance strategy, a low food availability in the urban environment (Marzluff, 2001), or permeability of the urban landscape.

Although the Eurasian Nuthatch is a sedentary species (Hinsley et al., 1995b, Fuller et al., 2005) 45% of re-traps of this species were found to demonstrate a movement. Movements were, however, short range (i.e. 1,042 ± 111 m) suggesting that birds may invest in minimal movements to find food, shelter or a nest site. Such movements concur with natal dispersal distances of a median of around 1 km (Matthysen and Schmidt, 1987), however, the data was not investigated for age trends in this study. Hinsley et al. (1995b) suggested that this species makes short dispersal movements in well-wooded habitats while in a more fragmented landscape their movements are longer suggesting that the urban landscape of Birmingham was sufficiently connected that Nuthatches do not have to increase their movement distances.

Within the number of re-trap records for Common Blackbirds, there were a large number of movements (Table 4.3). Greenwood and Harvey (1976) examined BTO ringing records of Common Blackbirds and found that birds could travel up to 3 km to a summer roost and classified birds that travelled less than this distance as not dispersing. All but one of the movements captured in this study were below 3 km, indicating that these movements may be seasonal or routine such as foraging sorties rather than dispersal to a new site.

A quarter of records for Great Tits demonstrated a movement. It is not possible to know from the literature whether this is typical for the species (e.g. Greenwood et al., 1979, O'Connor, 1980, Naef-Daenzer, 1994, Dingemanse et al., 2003). It has been suggested that long-distance movements can be due to poor conditions in winter such as a lack of food (Báldi and Csörgö, 1991) or due to increased population density (Van Balen and Hage, 1989, Báldi and Csörgö, 1991). In an urban environment, supplementary feeding is more prevalent than in suburban and rural habitats (Jones and Reynolds, 2008); this creates rich foraging patches that attract birds, especially in winter months (Báldi and Csörgö, 1991) and may lead to increased movements to maintain access to food supplements.

Similarly, a third of the records for Eurasian Blue Tits showed a movement between sites. This species has been found to be more sensitive to cold weather (Báldi and Csörgö, 1991) perhaps resulting in them moving more regularly throughout the colder months to find food, much of which is likely to be from supplementary feeding in suburban and urban areas (Jones and Reynolds, 2008). It is a species that readily joins mobile mixed species flocks as described for the Long-tailed Tits.

4.4.2 Long distance movements

Eurasian Blue Tits were found to have made some of the longest movements of any species in this study. Few studies before now have considered Blue Tit movements in this respect. Van Balen and Hage (1989) investigated environmental influences (i.e. food and weather) on the movement of Great Tits and Eurasian Blue Tits in The Netherlands and found no influence of environmental factors. However, they examined only Beech crop (categories of poor, a small and a medium to large crop) and winter severity (characterised by the Hellmann figure, i.e. the absolute sum of all daily mean temperatures below 0°C, over the months November-March) and population density (population index from recorded breeding pairs across the country) in relation to movement data and the study was not in an urban setting. Blackwell and Dowdeswell (1951) described local and short range movements of Eurasian Blue Tits but provided little information on landscape-scale movements. Consequently, this study is perhaps the best record of the movements of this species within an urban environment.

Some of the longest movements recorded in this chapter were those of Great Tits (maximum: 13,530 m, mean ± SE: 1,955 ± 372 m). Previous studies of Great Tit movements have most often reported movements of just 1 km (Greenwood et al., 1979, Verhulst et al., 1997, Van Overveld et al., 2011). In a study investigating natal dispersal of Great Tits in Wytham Woods, Oxford, UK, Greenwood et al. (1979) found that by September Great Tit offspring would be 700-1,100 m from their natal site. Greenwood and Harvey (1982) suggested that natal and breeding dispersal rates of Great Tits within populations were low, while O'Connor (1980) used BTO ringing records in combination with Common Bird Census (CBC) data (now replaced with the Breeding Bird Survey [BBS]) and the Nest Record Scheme (NRS) to reveal a density-dependence in several aspects of the population ecology of the Great Tit. He reported that in years of high population density birds will increase the distances moved, including distances greater than 10 km. Some of the longer distances recorded in the present study would suggest that the movements might be due to high population density; however, this was not quantified in this study. It has also been reported that Great Tits with faster exploring parents have larger dispersal distances (Dingemanse et al., 2003) suggesting learnt behaviour from parents,

or the heritability of dispersal behaviours. This may have great consequences for the genetic composition of populations. This is the first study in which distances such as these have been recorded for Great Tits in an urban context.

Eurasian Wrens and Dunnocks made the longest distance movements in the present study. Wrens have previously been described to move over 250 km (Hawthorn and Mead, 1975). The longer distance movements recorded in this study may be natal dispersal movements, or when other territorial birds drive them out of the area. A connected environment will have been important to allow these movements as this species shows a strong association with a connected green habitat (Chapter 3). Until now, we have known little about movement distances of Dunnocks. This may be because the influence of habitat on their distribution is difficult to quantify as discussed by Evans et al. (2009b). It was also found and shown in this study that there were no clear habitat patterns to explain Dunnock distribution (see Chapters 2 and 3). The inability to predict their occurrence in relation to habitat characteristics may be due to their generalist nature, and in turn their use of a wide variety of habitats and their omnivorous diet (Robinson, 2005). Dunnocks, however, have an Amber Conservation status due to a recent population decline (Robinson, 2005) and so it is important that researchers continue to investigate their movements and dispersal, and the importance of factors that underlie their distribution.

4.4.3 Environmental influences

The data presented here demonstrate that many birds of different species readily move through urban landscapes and that the frequency and distances of such movements are governed to a large extent by landscape composition. The analyses indicate that birds move away from habitats when they are located in areas with more built space, and make fewer movements where habitat is well connected. The latter finding may reflect higher habitat quality (Winker et al., 1995). Sites with more connected habitat may provide more resources (see Chapter 3) and birds may only need to make short routine movements to access them. In Chapter 2 an increase in available connected habitat was found to result in an increase in the abundance of several species. Sites with more built space are likely to be lower in quality, providing less cover and nesting sites and patchily distributed food resources (Báldi and Csörgö, 1991), resulting in birds moving away from these sites to areas with less built space. These trends were highlighted in Chapter 3 where an increase in habitat, characterised by a diversity of vegetative structure and native trees that supported more invertebrate prey explained increased bird abundance.

It was investigated whether the existence of 'corridors', as seen from a human perspective (i.e. a green linear feature on the landscape) would increase the probability of movement by a bird. No clear impact of green corridors was found; the probability of a movement down the corridor was not higher than one off the corridor. Overall landscape connectivity, however, had a large impact on bird distribution and probability of movement. Trees within 30 m of one another provide a good level of functional connectivity and improve the quality of the habitat for the bird populations. Therefore, green corridors are not necessarily an effective management tool to achieve functional connectivity, although they may provide valuable habitat for a variety of taxa (Hess and Fischer, 2001).

4.4.4 Conclusions

This study demonstrates the importance of a connected, green environment for bird populations in the urban landscape. It has shown that several bird species moved between the urban ringing sites regardless of the existence of a corridor, thereby demonstrating the permeability of the landscape.

Species such as the Eurasian Blue Tit in the urban environment increase in abundance with more built space (Chapter 3). It may be that habitats located in landscapes with more grey space provide profitable foraging habitat due to supplementary feeding, for example (Barraquand and Benhamou, 2008, Jones and Reynolds, 2008). Species that are generalist in ecology (Evans et al., 2011), sedentary in nature, gregarious, omnivorous (Kark et al., 2007, Croci et al., 2008) and birds that nest high off the ground (Croci et al., 2008, Evans et al., 2011) can all be expected to adapt to urban spaces and to be urban tolerators. Many species in the present study show a tendency to move away from such locations into areas with more connected, green habitat. This is likely to be due to the patchy distribution of resources, increased disturbance (Mockford and Marshall, 2009, Schroeder et al., 2012) and increased predation risk (Sims et al., 2008).

To maintain movement and, therefore, gene flow and population persistence, spatially regular tree planting across the landscape and through the urban matrix is likely to provide much more functional connectivity for avian populations than corridors.

Chapter 5. The occupancy and turnover of bird populations in urban areas

5.1 Introduction

A series of spatial population structure theories has been used to describe the distribution and dynamics of animals in fragmented landscapes dominated by two classical paradigms; island biogeography and metapopulation dynamics. These supply theoretical frameworks for ecological research and conservation methods (Ricketts, 2001).

The term metapopulation was coined by Levins (1969) and refers to a population of populations or a group of conspecific subpopulations linked by rare dispersal events in a dynamic equilibrium of extinctions and re-colonisations (Forman, 1995, Hanski, 1998, Fronhofer et al., 2012) relating local population dynamics to landscape patterns and processes at a wider scale (Baguette, 2004). In order to be a classic metapopulation four conditions have to be fulfilled: (1) each habitat patch should be able to support a breeding population; (2) any subpopulation must not be large enough to ensure long-term survival; (3) the isolation of the patch must not prevent the possibility of re-colonisation; and (4) there must be an asynchrony of subpopulation dynamics in order to avoid the extinction of the entire metapopulation (Harrison, 1991, Hanski et al., 1995, Fronhofer et al., 2012).

Extinction is a key feature of metapopulation dynamics and causes may be stochastic or deterministic. Stochastic drivers of extinction include demographic, genetic, environmental stochasticity and catastrophes (Shaffer, 1981). Demographic stochasticity such as randomness in the order of births and deaths can lead to extinction and can be particularly important if the population is below a threshold size. A loss of heterozygosity through drift and inbreeding depression is categorised as genetic stochasticity. Environmental stochasticity is a variation in factors such as weather or food supply driving the temporal variation in the net rate of population growth. Catastrophes such as extreme and infrequent environmental events such as drought or fire can also lead to extinction events. The changing of habitat so that it becomes unsuitable for habitation by a particular species is a deterministic driver of extinction (Harrison, 1991).

Classic metapopulations remain rare in nature and the literature (Harrison, 1991, Baguette, 2004, Fronhofer et al., 2012) due a lack of adherence to the conditions of metapopulations (Fronhofer et

al., 2012). The best models have been found for invertebrates, especially butterflies (Lepidoptera, *Rhopalocera* spp.) (Baguette, 2004, Hanski, 2004, Fronhofer et al., 2012). Due to the dispersal ability of birds (Andrén, 1994) and the fact that a British urban landscape is often a habitat with indistinct habitat patches (Young and Jarvis, 2003, Chapter 3), extinction events are unlikely (Fronhofer et al., 2012).

5.1.1 Alternative paradigms

Inter-patch movements are rare in metapopulations but when a collective response of many individuals moving in and out of patches creates sufficient flux for sub-populations to be dynamically tied together, this becomes a 'patchy' population (Bowne and Bowers, 2004). A patchy population can be thought of as a set of habitat patches distributed over a patchy and/or a spatio-temporally variable habitat linked by such high levels of dispersal that local extinctions are prevented by a rescue effect (Fronhofer et al., 2012) and are effectively united into a single population (Harrison, 1991). 'Turnover' in patchy populations is due to movements of individuals rather than mortality (Harrison, 1991).

Mainland-island metapopulations exist when some habitat patches are orders of magnitude larger than others but similar in quality. These larger patches act as a source population from which the smaller populations can be colonised (Fronhofer et al., 2012). Source-sink metapopulations work on a similar basis to mainland-island but where the mainland is bigger than islands, sources and sinks differ in quality (Harrison, 1991). There is a net flow of individuals from persistent populations in good habitats 'sources' which are always occupied, to populations in inferior habitat, 'sinks' which are rarely occupied (Harrison, 1991). Local extinctions occur mainly among the sub-set of populations (islands or sinks) and have little effect upon regional persistence since the extinction-resistant mainland or source populations are the major provider of colonists. Extinction may not happen at all if migration between patches is sufficiently high (Harrison, 1991).

Populations which are declining or expanding due to an imbalance in extinctions and re-colonisations are referred to as non-equilibrium metapopulations (Fronhofer et al., 2012). Re-colonisation is either absent or insufficient to balance extinction. Local extinction is deterministic and occurs as part of an overall regional decline, which is usually due to the reduction, fragmentation or deterioration of the habitat (Harrison, 1991).

5.1.2 Landscape composition

5.1.2.1 Patch

Due to a recognition that many animals live in a fragmented and discontinuous habitat with patches embedded in a matrix (Wiens, 1976), much of contemporary ecology has become focused with how the structure of spatio-temporal populations map onto habitat patch templates (Hanski and Gilpin, 1991, Bowne and Bowers, 2004). Patches were defined by Wiens (pg. 82; 1976) as 'a surface area differing from its surroundings in nature or appearance'. From an ecological perspective, patches or patchiness should be described according to the habitat requirements and mobility of the species of interest (Bowne and Bowers, 2004).

Differences between the quality of sites tend to increase the variability in species' performance across the sites and individuals will move to even out this variability (Bowers and Dooley, 1991, Bowne and Bowers, 2004). A high quality site that provides numerous resources such as protective cover or food could be expected to influence the likelihood of individuals moving to the area (Graham, 2001). Subsequently, if a site continues to provide the required resources, it is plausible that individuals would remain in a site for longer or establish and maintain a territory. In order to find a higher quality site animals may compare between sites (Lima and Zollner, 1996, Graham, 2001) and select the relatively better site dependent on, for example, more food resources or protective cover.

High quality sites may, therefore, hold many more resident individuals than lower quality ones (Cressman and Křivan, 2006) but this may lead to high population density and a rapid depletion of resources that attracted birds to the area originally but are the cause of intense intra-specific and inter-specific competition (Lima and Zollner, 1996). During seasons when territorial behaviour is intense (e.g. spring at temperate latitudes) subordinate and non-territory holding individuals may be driven out of the area (Winker et al., 1995, Eycott et al., 2012). This may result in further movement due to searching for a territory or a foraging resource.

Sporadic resource availability and environmental variability are likely to influence bird residency at a site (Forman, 1995). Food availability, for example, has been shown to affect bird movements in heterogeneous landscapes (Neuschulz et al., 2012). Graham (2001) found that Keel-billed Toucans (*Ramphastos sulfuratus*) tracked fruit resources in fragmented forests in Mexico. The patchiness of the urban environment is likely to mean that natural food resources are unevenly distributed (Threlfall et al., 2011) and supplementary food may be sporadic in availability (Hamilton, 1971).

Patches with more built space and less natural habitat could be expected to have more birds moving on to new areas, due to the unpredictability of food resources (Threlfall et al., 2012).

The kind or degree of connectedness between patches or populations is a critical feature in models of spatially structured populations (Harrison, 1991). Re-colonisation is enhanced by increased connectivity (Forman, 1995) and so an area with more connected habitat might, therefore, allow more bird movements, and perhaps promote residency by those arriving birds. Conversely, a lack of connected habitat is likely to restrict bird movements due to less protected cover, consequently increasing risk of predation and increasing energetic costs of travel (Dawson, 1994, Graham, 2001, Marzluff and Ewing, 2001).

A habitat patch is a part of a landscape mosaic and any species found there will not only be affected by the features of that patch (e.g. size, isolation) but also by the features of the surrounding matrix (Andrén, 1994, Castellon and Sieving, 2006). Functional connectivity incorporates the combined effects of matrix structure and its influence of movement on a species (FitzGibbon et al., 2007).

5.1.2.2 Matrix

There has been a dichotomous view of the landscape in ecological theory, resulting in a focus by the researchers on patch characteristics without an emphasis on the landscape context (e.g. Ricketts, 2001, Kupfer et al., 2006, Prevedello and Viera, 2010) . Not only are the habitat patches themselves important in influencing extinction of, and rate of colonisation by bird species but so too is the matrix surrounding them (Forman, 1995, Cook et al., 2002, Radford and Bennett, 2007, Prevedello and Vieira, 2010).

Unlike oceanic islands, terrestrial habitat patches are not truly isolated nor surrounded by a uniformly hostile matrix. Animals leaving a habitat patch may find suitable conditions to move, forage and possibly even reproduce (Prugh et al., 2008), making the idea of patch and matrix as a binary concept of habitat and non-habitat less relevant (Ricketts, 2001). A more realistic view is that the landscape is a grade of habitats that may be used to different degrees or for different functions such as foraging or nesting (With et al., 1997).

The "matrix matters" (Ricketts, 2001), and affects both within- and between-patch processes in heterogeneous landscapes (Prevedello and Vieira, 2010). For example the structure, permeability and features of the matrix have been shown to affect survival and reproduction (Gustafson and Gardner, 1996), composition (Chapters 2 and 3) and dynamics of communities (Hinsley et al., 1995b,

Stouffer et al., 2006). They can influence movements of individuals and be alternative habitat (Prugh et al., 2008, Prevedello and Vieira, 2010).

Eycott et al. (2012) carried out a cross-species meta-analysis to assess the impact of matrix structure on the rates of bird movements. They found that on mean movement was greater and more functional connectivity (i.e. the behavioural response of a species to the various elements of a landscape, including both habitat patches and matrix; Tischendorf and Fahrig, 2000) was provided when a matrix was similar in structure to the 'home' habitat. A structurally similar matrix to the home habitat has also been found to lead to higher patch occupancy (Watling et al., 2011) and to be of higher quality to species in terms of functional connectivity (Prevedello and Vieira, 2010). Findings reported in Chapters 2, 3 and 4 also support higher patch occupancy and functional connectivity with a matrix more similar to the home habitat.

The features of the matrix are a particularly important aspect of the urban landscape (Ricketts, 2001, Kupfer et al., 2006, Laurance, 2008, Prevedello and Vieira, 2010) due to its fragmented nature and the variable nature of the matrix. It is important to take into consideration both patch and matrix level variables (Forman, 1995, Cook et al., 2002, Radford and Bennett, 2007, Prevedello and Vieira, 2010).

5.1.3 Distribution of individuals in the landscape

Drivers of the spatial distribution of animals across a landscape are a function of environmental diversity in combination with animal interactions such as predator-prey, competition or social interactions that go towards explaining species distribution (Křivan et al., 2008). If all animals make the same habitat choice, the habitat will become crowded and evolutionary fitness will decrease, and so other habitats may be a better choice. Animals maximise their evolutionary fitness through habitat selection and they will disperse among habitat until no individual can improve its fitness by moving (Morris, 2006).

The Ideal Free Distribution (IFD) theory of Fretwell and Lucas (1969) assumed free movement of individuals between food or habitat patches (Palmqvist et al., 2000, Cressman and Křivan, 2006, Křivan et al., 2008) with the following assumptions: (1) resources are distributed in habitat patches; (2) animals are equal competitors for resources and their numbers do not change; (3) animals are free to settle in any patch and there is no cost to movement between patches; (4) animals have complete knowledge of the distribution of resources (i.e. they are ideal); (5) quality of patches does not change over time; and (6) an individual's resource intake decreases with increased population

density within the patch (Křivan et al., 2008). However, these assumptions were relaxed in subsequent refinements of the IFD (e.g. Sutherland, 1983, Weber, 1998, Morris, 2003).

The IFD theory predicts that individuals settle in patches that provide the most resources (Cressman and Křivan, 2006) and that patch selection is dependent on the current population occupying that patch. Food should be easier to find at high prey densities, thereby attracting predators, but then interference will be greater due to high predator densities, resulting in a redistribution of predators. The IFD theory took into consideration the distribution of predators by trying to balance the opposing effects of food availability and interference (Sutherland, 1983)

5.1.4 'Turnover' of individuals

The turnover of birds at a site – the number of new birds immigrating to a site compared with the number of resident birds – is likely to reflect habitat characteristics and site quality (Hinsley et al., 1995a, Winker et al., 1995, Bélangera and Rodríguez, 2002). However, the term 'turnover' in ecology refers to colonisation and extinction events as postulated originally by the Island Biogeography Theory of MacArthur and Wilson (1963) and is a critical attribute of classical Metapopulation Dynamics (Fronhofer et al., 2012). Although turnover refers to a distinct process unlikely to be found in an urban landscape, some aspects of the theory and findings of studies of metapopulation biology may be applicable to birds in urban landscapes. Therefore, the turnover described in this study is likely to be more akin to patchy population turnover (due to movements of individuals rather than to extinction and colonisation events; Harrison, 1991).

Extinction and turnover rate are higher in smaller and lower quality patches (Forman, 1995, Hinsley et al., 1995a). Hinsley et al. (1995a) found that turnover of bird species in fragmented woodland in eastern England was highest for common species with small numbers in the smallest woodlands. Turnover was calculated between successive breeding seasons by a change in breeding activity between years (i.e. a bird found in one breeding season and not in the next). Extinction and colonisation rates were calculated as the number of species lost and gained respectively, between one breeding season and the next. In the urban landscape where habitat remnants are found (Young and Jarvis, 2001), it would be expected that there would be higher turnover of bird populations in some of the smaller fragments of natural habitat.

5.1.5 When does a bird become resident or move on?

If a site provides all the resources such as food and protective cover that a bird requires, it may make sense, ecologically speaking to remain at that site, become resident and maintain a territory.

However, there can be costs to remaining resident such as the risk of inbreeding, kin competition and resource competition (Bonte et al., 2012).

IFD theory assumes no costs to dispersal (Křivan et al., 2008), but in reality it is expensive in terms of increased (i) flight energy costs, (ii) predation risk and (iii) time required to locate and move to a new patch (Bonte et al., 2012). Furthermore, information concerning the location of better quality patches may not always be readily available (Křivan et al., 2008). Therefore, birds must balance the cost of staying against that of dispersing to a new site (Bonte et al., 2012).

Habitat factors, resources available at the site, knowledge of the landscape and sex and age (Greenwood et al., 1979) may all influence the decision to remain at the current site or to move on to an alternative. Verhulst et al. (1997) found that females disperse from natal sites further than males, but no sexual asymmetry was found in movement between mature deciduous woodland and the surrounding area. Dingemanse et al. (2003) found that fast exploring females (i.e. those that are aggressive, bold in exploration, insensitive to external stimuli and rely on routines; Dingemanse et al. 2004) had greater dispersal distances.

Sexual asymmetry in natal dispersal is found in most passerines in sedentary and migratory species alike, with females dispersing further than males (Morton, 1992). It is suggested that this asymmetry avoids the detrimental effects of inbreeding. Males defend a resource or territory rather than a mate and their ability to do so is greater in familiar surroundings. Thus males should be philopatric and establish themselves in areas close to natal area. Then the risk of inbreeding is left for the females to avoid, and thus they should disperse. Alternatively the female searches for a high quality territory which includes the resident male and in the process she ends up further from the natal area.

Whether a bird displays natal philopatry has been shown to be more strongly influenced by ecological than genetic factors (Weatherhead and Forbes, 1994). The quality of the habitat in which a bird hatches can influence the likelihood of staying or moving on to a new habitat patch. Verhulst et al. (1997) found that birds of high phenotypic quality (of high nestling mass) disperse when they hatch in a low quality habitat. Mature deciduous woodland was classified as high quality habitat while the surrounding area of gardens, hedgerows and small woodlands were classified as low quality habitat as defined by previously found differentiation in reproductive success.

The hypothesis that sites with higher available connected habitat in the matrix should provide more resources such as food, nesting sites, access to potential mates and protective cover and so are expected to have higher levels of occupancy and lower levels of turnover is proposed in this study.

A sexual asymmetry in occupancy and emigration is expected due to previous findings (e.g. Morton, 1992, Verhulst et al., 1997, Dingemanse et al., 2003) and variation in the age of birds emigrating due to natal and breeding dispersal (Greenwood and Harvey, 1982).

5.1.6 Aims

Using ringing records over three years coupled with habitat information across Birmingham, the factors influencing the occupancy of bird populations at sites across the suburban gradient using Blue Tits and Great Tits as candidate common species is investigated in this chapter.

The aims were to:

i)   Assess whether the habitat in the matrix influences the occupancy of birds in an area

ii)   Define the life history, sex-specific and/or matrix habitat factors that influence whether birds become resident at a site or move on.

5.2 Methods

5.2.1 Data collection

This study was carried out across the 27 study sites in Birmingham, UK (Figure 4.1) using mist-netting and bird ringing as described in section 4.2.1.

5.2.2 Environmental variables

Sites were buffered at 500 m (due to literature and mean distance moved; see section 4.2.2) and land use and land cover (LULC) and the amount of connected tree cover (as described in Chapter 2) was summarised with the Thematic Raster Summary tool in Hawth's Tools (Beyer, 2004) (see section 4.2.2). LULC data extracted for each site were assigned to re-trap record and the corresponding original trapping event.

'Turnover' was calculated for each site as the number of birds caught and ringed for the first time and the number of birds that had not been encountered at that site before (i.e. that were new birds) divided by birds re-trapped at that site. All same-day re-trapped birds were excluded from the analysis to avoid inflation of residency measures. Table 5.1 outlines the details of all the variables generated for statistical analyses.

Table 5.1 Details of variables generated for statistical analyses in an investigation of turnover and occupancy of birds

Variable	Details
Continuous variables	
turnover	Response variable. Created for each site by calculating the number of new birds divided by re-trapped birds. This gives an indication of turnover of birds moving through the site.
grey	Fixed effect. Total area of grey space within 500 m. Grey space encompasses all built space, including buildings, roads, pavements etc.
ctrees	Fixed effect. Total area of connected habitat within 500 m. Connected habitat is classified as habitat within 15 m of trees above 3 m in height, see Chapter 2 for details.
Ctreesch	Fixed effect. ctrees site 1-ctrees site 2, variable to demonstrate difference in the amount of connected habitat between site 1 and site 2 at sequential trapping sites.
Greych	Fixed effect. grey site 1- grey site 2, variable to demonstrate difference in the amount of grey space between site 1 and site 2 at sequential trapping sites.
Categorical factors	
move	Response variable. Binomial category, 1 = movement between sites, 0 = no movement between sites
sex	Fixed effect: Male or female
age	Fixed effect: Upon capture birds are aged using EURING age codes:

3. Definitely hatched during current calendar year (e.g. first-years in autumn)
4. Hatched before current calendar year - exact year unknown (e.g. many adults in autumn)
5. Definitely hatched during previous calendar year (e.g. first-years in early spring)
6. Hatched before last calendar year - exact year unknown (e.g. many adults in spring) (BTO)

Age 3 birds were classified as juvenile (juv), age 5 birds were classified as first year birds (1y) and ages 4 and 6 birds were classified as Adult (ad).

5.2.3 Statistical analyses

Prior to analysis data were explored using a range of techniques. Cleveland dot plots were used to confirm that there were no outliers. Variance inflation factors (VIFs) were calculated to assess co-linearity amongst explanatory variables using a threshold for inclusion of VIFs ≤ 3 (Zuur et al., 2010). For site turnover variance was found to be larger than the mean so a negative binomial structure was

appropriate (Zuur et al., 2007). A negative binomial GLM using MASS (Venables and Ripley, 2002) in R (R Core Development Team, 2011) was applied to these data. AIC were used to select the best-fit model (Burnham and Anderson, 2002).

Great Tits and Eurasian Blue Tits were studied as candidate common species to investigate the factors influencing occupancy and movement from an area. Binomial GLMs were run in R (R Core Development Team, 2011) for Great Tit and Eurasian Blue Tit movement data using the binomial category of movement (i.e. movement/no movement) as the response factor. Data exploration and *a priori* assumptions from studies such as Greenwood et al. (1979), Perrins (1979), O'Connor (1980), Verhulst et al. (1997) and Dingemanse et al. (2003) led to the suite of models run for Great Tits and Eurasian Blue Tits. AIC and Akaike weights were used to find the relative likelihood of the model and to select the best-fit models (Burnham and Anderson, 2002) for both datasets.

Quantile-quantile plots were created and they suggested a lack of departure from the model assumptions. Spline (cross-)correlograms (package ncf; Bjornstad, 2009) of the residuals of the best-fit models for Blue and Great Tits (Zuur et al., 2009) indicated no spatial autocorrelation in the data (Figure 5.1).
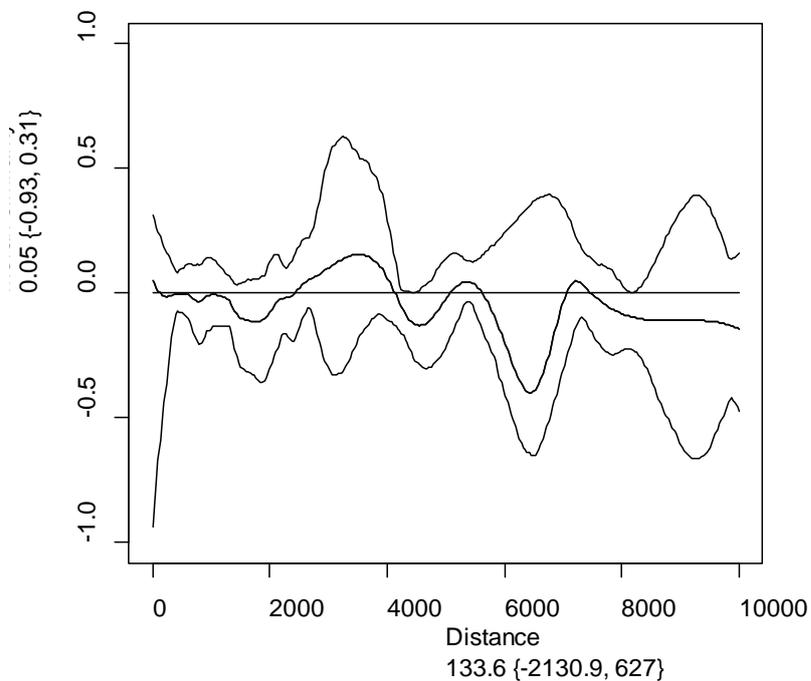
Figure 5.1 Spline correlogram, with 95% pointwise bootstrap confidence intervals, of residuals of the best-fit GLM model for Great Tit demonstrating a lack of spatial autocorrelation, due to the lack of a pattern.

5.3 Results

5.3.1 Site turnover

The best-fit model to explain turnover was:

$$glm.nb(turnover\sim ctrees+grey)$$

Both the level of connected habitat and the amount of built space were highly significant ($p < 0.001$) in influencing the turnover of populations of birds in a given area. There were more new birds in relation to resident birds at sites with an increase in built space within 500 m of a ringing site. An increase in the amount of connected habitat within 500 m also demonstrated an increase in new birds being encountered at a site in comparison to resident birds, but the gradient of the trend was much less steep.

5.3.2 Species-specific drivers of movement

5.3.2.1 Eurasian Blue Tit

The top weighted model (bt16) was overwhelmingly supported by the data, and is the only model lying within the 95% confidence interval (Table 5.2). No model averaging was required (Johnson and Omland, 2004). The top weighted models all contained age, ctrees and grey indicating that the categorical age of Blue Tits explained a lot of the variation in the data along with grey space and connected available habitat LULC in the matrix surrounding the ringing site. The variable ctreesch: the change in connected habitat between the first site at which a Eurasian Blue Tit was caught and the second, was less consistent in the suite of models but featured in the top weighted model.

Table 5.2 Summary of the mixed models for movement of Eurasian Blue Tit ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. All predictors from Table 5.1 were included in the modelling process. The table indicates the fixed variables included in the model (indicated in each model by ✓), the total number of fixed variables (K), the AIC, corrected AIC (AICc), delta weight (difference between the AIC for a given model and the best fitting model) and the model selection probability (*w*).

model	response	age	sex	ctrees	grey	ctreesch	greych	K	AIC	AICc	Δ_i	exp'-½Δi	*w*	Sum(exp'-½Δj)	N
bt16	move	✓		✓	✓	✓		4	226.35	226.55	0.000	1.000	0.900	1.111	208
bt12	move	✓		✓	✓			3	231.20	231.32	4.850	0.088	0.080		
bt15	move	✓		✓	✓	✓		4	235.48	235.68	9.130	0.010	0.009		
bt1	move	✓		✓	✓	✓	✓	5	237.02	237.32	10.670	0.005	0.004		
bt14	move	✓		✓	✓	✓	✓	5	237.48	237.78	11.130	0.004	0.003		
bt2	move		✓	✓	✓	✓	✓	5	238.38	238.68	12.030	0.002	0.002		
bt4	move	✓	✓	✓	✓	✓	✓	6	240.69	241.11	14.340	0.001	0.001		
bt13	move		✓	✓	✓			3	243.03	243.15	16.680	0.000	0.000		
bt11	move	✓		✓	✓			3	243.16	243.28	16.810	0.000	0.000		
bt6	move	✓	✓	✓	✓	✓	✓	6	244.74	245.16	18.390	0.000	0.000		
bt8	move		✓	✓	✓			3	248.36	248.48	22.010	0.000	0.000		
bt9	move	✓	✓	✓	✓			4	249.85	250.05	23.500	0.000	0.000		
bt3	move	✓	✓					2	268.45	268.51	42.100	0.000	0.000		
bt10	move	✓	✓	✓	✓			4	271.85	272.05	45.500	0.000	0.000		

The best-fit model for Eurasian Blue Tits is summarised in Table 5.3.

Table 5.3 Summary of the output from the best-fit model of residency of Eurasian Blue Tit ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive

Best-fit model	Significant factors	*p*-value
glm(move~age*grey*ctrees+ctreesch, family=binomial)	ctrees	0.001
	ctreesch	< 0.05
	age[T.Ad]:ctrees	< 0.05
	grey:ctrees	< 0.005
	age[T.1y]:grey:ctrees	0.01
	age[T.Ad]:grey:ctrees	< 0.05

The best-fit model demonstrates that the amount of connected habitat is highly significant (p = 0.001), especially for adult birds ($p < 0.05$). If the recipient site is also better connected there was also an enhanced likelihood of bird movement (Figure 5.2).
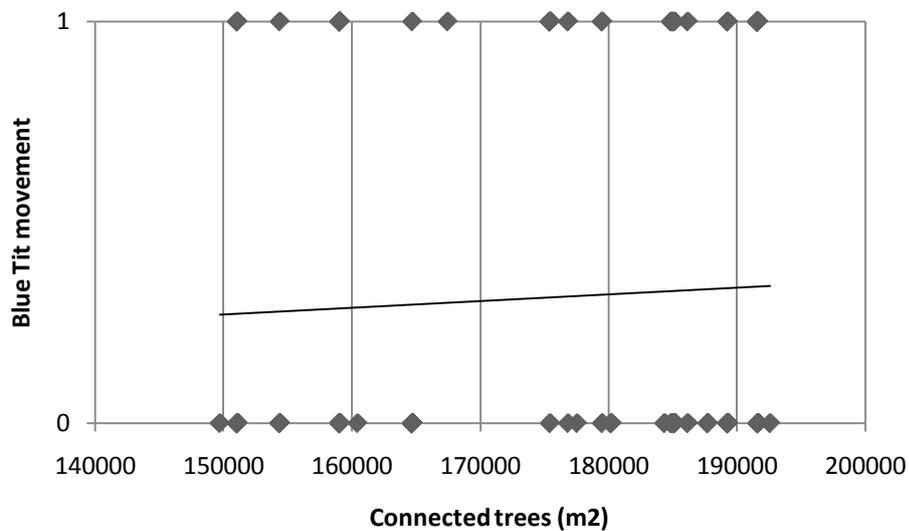
Figure 5.2 The influence of available connected habitat within 500 m of the ringing site on Eurasian Blue Tit residency (0) or movement (1) in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive.

There was a highly significant ($p < 0.005$) influence of the interaction between the amount of built space (grey) and connected habitat on the likelihood of movement in Eurasian Blue Tits, where a decrease in grey space (Figure 5.3) and an increase in available connected space increased the chance of movement. This interaction was particularly influential on bird movements during their

first year (i.e. BTO age 5: definitely hatched during previous calendar year) and those that are adults (i.e. BTO ages 4 and 6: hatched before current or previous calendar year).
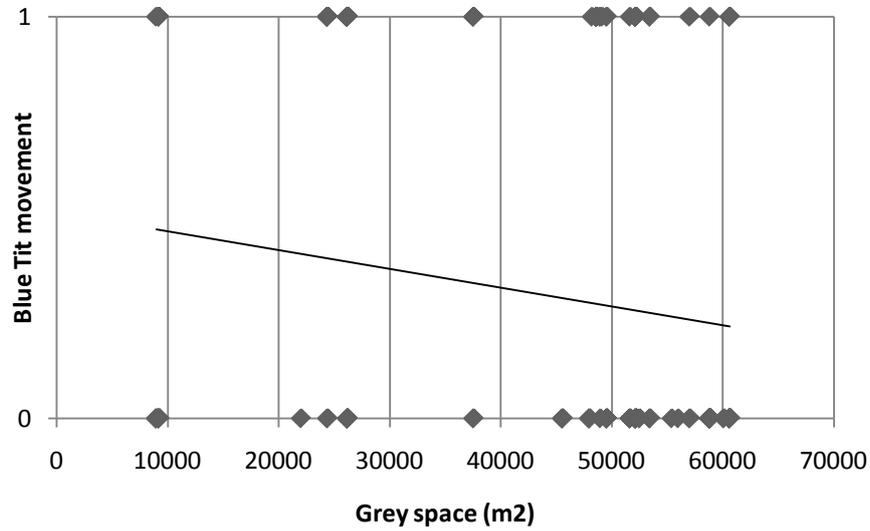
Figure 5.3 The influence of available connected habitat within 500 m of the ringing site on Eurasian Blue Tit residency (0) or movement (1) in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive.

An increase in available connected habitat between the first site at which a Eurasian Blue Tit was caught and the second was significant ($p < 0.05$) in influencing the likelihood that a bird moves on to another site rather than remains resident (Figure 5.4).
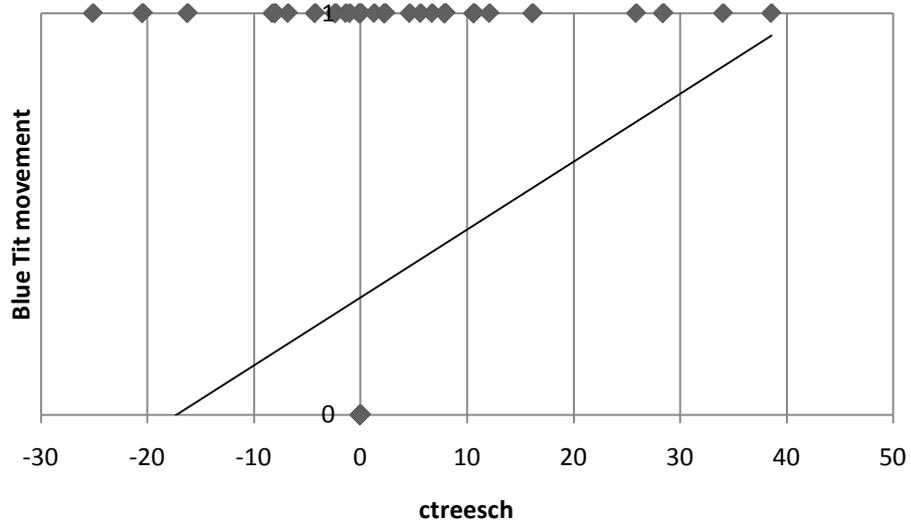
Figure 5.4 The influence of a change available connected habitat (within 500 m) between the site at which the bird was first caught and the second capture site on the x-axis (ctreesch) on Eurasian Blue Tit residence (0) or movement (1) in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. If ctreesch has a negative value there is less connected habitat within 500m of the site at the second capture site, if there is a positive value there is more connected habitat within 500m of the second site. The trend line demonstrates that Eurasian Blue Tits are more likely to move sites if the second site has more connected habitat than the first site. The single point on the x-axis is due to the fact that if a bird didn't move sites (move = 0) then there is inevitably no change in the amount of grey space between sites resulting in a value of 0 for change.

5.3.2.2 Great Tit

For Great Tits five models (gt15, gt17, gt16, gt14 and gt13) were considered plausible as they sat within the 95% confidence interval (Whittingham et al., 2005). All of these models included the variable ctreesch which represents a change in connected habitat between the site at which a bird was first caught and the second where it was re-trapped. Two models also included grey, three included ctrees, three sex and one age. The selection probability (0.99) for ctreesch was very high indicating strong support for model g15 as a candidate model (Whittingham et al., 2005). Table 5.4 provides a full a summary of all candidate models.

Table 5.4 Summary of the mixed models for Great Tit movements ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. All predictors from Table 5.1 were included in the modelling process. The table indicates the fixed variables included in the model (indicated in each model by ✓), the total number of fixed variables (K), the AIC, corrected AIC (AICc), delta weight (difference between the AIC for a given model and the best fitting model) and the model selection probability (w).

model	response	age	sex	ctrees	grey	ctreesch	greych	K	AIC	AICc	Δ_i	exp'-½Δi	w	Sum(exp'-½Δj)	N
gt15	move					✓		1	295.09	295.11	0.000	1.000	0.390	2.567	267
gt17	move		✓			✓		2	295.78	295.83	0.690	0.708	0.276		
gt16	move		✓	✓		✓		3	296.64	296.73	1.550	0.461	0.179		
gt14	move		✓	✓	✓	✓		4	298.16	298.31	3.070	0.215	0.084		
gt13	move	✓		✓	✓	✓		4	300.29	300.44	5.200	0.074	0.029		
gt3	move	✓	✓	✓	✓	✓		5	301.48	301.71	6.390	0.041	0.016		
gt10	move	✓	✓	✓	✓	✓		5	302.44	302.67	7.350	0.025	0.010		
gt9	move	✓	✓	✓	✓	✓		5	303.14	303.37	8.050	0.018	0.007		
gt4	move	✓	✓	✓	✓		✓	5	303.37	303.60	8.280	0.016	0.006		
gt5	move	✓	✓					2	305.77	305.82	10.680	0.005	0.002		
gt8	move	✓	✓	✓				3	306.22	306.31	11.130	0.004	0.001		
gt1	move	✓	✓	✓	✓			4	307.16	307.31	12.070	0.002	0.001		
gt7	move	✓	✓					2	307.17	307.22	12.080	0.002	0.001		
gt12	move	✓	✓	✓	✓			4	307.59	307.74	12.500	0.002	0.001		
gt11	Move	✓	✓	✓	✓			4	308.58	308.73	13.490	0.001	0.000		
gt6	Move	✓	✓		✓			3	308.76	308.85	13.670	0.001	0.000		

The best-fit model for Great Tits was:

$$glm(move \sim ctreesch, family=binomial)$$

An increase in available connected habitat between the first site at which a Great Tit is caught and the second was significant (p = 0.01) in influencing the likelihood that a Great Tit moves onto another site rather than remains resident (Figure 5.5).
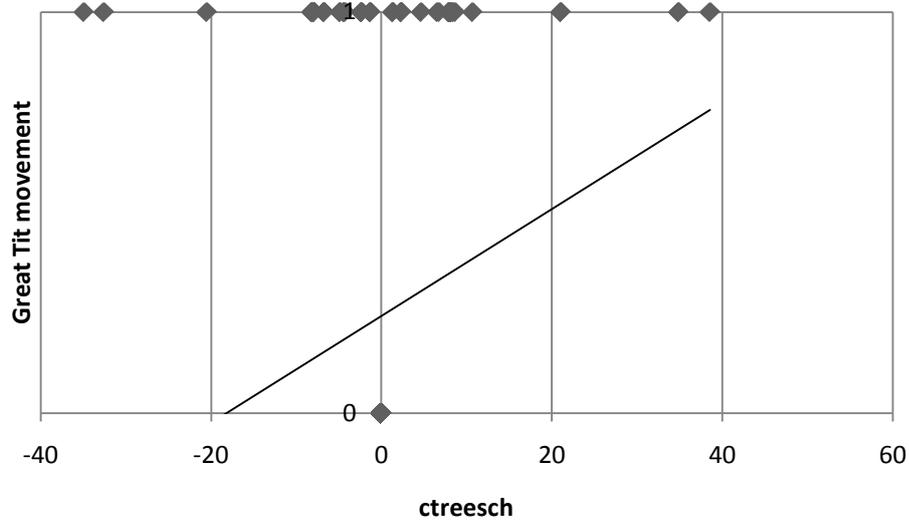
Figure 5.5 The influence of a change available connected habitat (within 500 m) between the site the bird is first caught at and the second capture site on the x-axis (ctreesch) on Great Tit residency (0) or movement (1) in birds ringed and re-trapped in the city of Birmingham from 2008 to 2011 inclusive. If ctreesch has a negative value there is less connected habitat within 500m of the site at the second capture site, if there is a positive value there is more connected habitat within 500m of the second site. The trend line demonstrates that Great Tits are more likely to move sites if the second site has more connected habitat than the first site. The single point on the x-axis is due to the fact that if a bird didn't move sites (move = 0) then there is inevitably no change in the amount of grey space between sites resulting in a value of 0 for change.

5.4 Discussion

The unique results presented in this chapter demonstrate a relationship between habitat features in the matrix and turnover of sites by birds within urban populations. Both the level of connected habitat and the amount of built space were highly influential in the turnover of populations of birds in a given area with more new birds in relation to resident birds at sites with both an increase in built space and connected available habitat. The habitat of the matrix surrounding where a bird was ringed was more influential than age or sex factors in whether Blue and Great Tits stayed or moved onto a new site.

5.4.1 Turnover of birds at sites

Both the level of connected habitat and the amount of built space in the matrix surrounding the site were highly significant ($p < 0.001$) in influencing the turnover of populations of birds in a given area. There was a higher level of turnover of bird populations at sites with a higher level of built space in the matrix. This is likely to reflect the decrease in natural resources such as protective cover, nesting sites and food found in more urbanised areas (Hamilton, 1971, Graham, 2001).

An increase in the amount of connected habitat in the matrix within 500 m was also found to result in an increase in numbers of birds moving through a site, but less so than built space. This may reflect the permeability that trees within 30 m of one another provide in the landscape, facilitating the movement of birds (Hinsley et al., 1995a) when it is required to move to a new site when the likelihood of inbreeding or of resource competition increases (Bonte et al., 2012). These findings enhance the importance of the matrix for patch processes (Prevedello and Vieira, 2010, Eycott et al., 2012).

No extinctions or new colonisations of species were found at any ringing site in the duration of this study. This suggests a patchy population rather than a metapopulation due to the nature of the turnover and high levels of movement between sites (Harrison, 1991).

5.4.2 Species-specific movement drivers

Great Tits and Eurasian Blue Tits are common birds in cities and knowing about how they respond to habitat parameters in the matrix, and how sex and age of birds influences their movement 'decisions' are important when addressing other species' responses. In order to consider the broader applicability of these findings, it would be necessary to compare and contrast these model species with other species of interest. A species-centric investigation of factors that influence residence at a site or movement into new areas for Great Tits and Eurasian Blue Tits found that habitat and LULC were the most influential factors but there was with no particular propensity for movement in any age or sex class. This may be due to the habitat being much more influential in dispersal processes in an urban landscape due to the patchy nature and resource distribution. Sex and age are good predictors to bird movement in a natural habitat, but where the habitat is fragmented available habitat might be a more prominent driving factor.

Several factors were found to influence the likelihood of whether Eurasian Blue Tits moved away from a site or remained resident. Sites with more built space in the surrounding area led to birds remaining resident more often and when they left the area, they dispersed to areas with more

connected habitat. This is likely to reflect the urban exploiter role of the Eurasian Blue Tit which succeeds in areas of high built space due to, amongst other things, their generalist ecology and omnivorous diet (Kark et al., 2007, Croci et al., 2008, Evans et al., 2011). Their success in areas of increased built space may reflect their use of suburban and urban anthropogenic resources such as gardens (BTO, 2012), bird feeders (Perrins, 1979), and nestboxes (Perrins, 1979, Johnson et al., 1992, du Feu, 2005). Findings here are supported by those in Chapter 2 where it was found that Eurasian Blue Tits increased in number with more built space but also required natural vegetation with high insect diversity. Furthermore, the data presented showed in Chapter 3 an increase in a connected habitat in the winter resulted in an increased abundance of the species.

Eurasian Blue Tits were also found to be more likely to move sites rather than remain resident if the second site had more connected habitat than the first. This may indicate that although the species can be successful in urban areas, when they move they favour areas with more natural resources such as invertebrate prey and protected cover.

There was a highly significant influence of the interaction between the amount of built space and connected habitat on the likelihood of movement in Eurasian Blue Tits, where a decrease in grey space and an increase in available connected space increased the chance of movement for adult birds and those in their first year. These findings might indicate breeding dispersal with birds moving to find novel breeding sites, or birds being driven out by territory holders (Winker et al., 1995, Lima and Zollner, 1996, Eycott et al., 2012).

Great Tits were more likely to move if the destination site has more connected habitat which may have more cover and natural resources such as food and protective cover. Verhulst et al. (1997) found that birds of high phenotypic quality dispersed when they hatch in a low quality habitat. Verhulst et al. classified mature deciduous woodland as high quality habitat with the surrounding gardens, hedgerows and small woodlands classified as low quality habitat due to unpredictable food availability (Riddington and Gosler, 1995, Verhulst et al., 1997). These findings tie in well with the findings in this study where Great Tits moved to areas of higher habitat connectedness. Matthysen (2002) investigated the relationship between proximity to a habitat edge and natal dispersal in Great Tits and found no relationship between proximity of hatching site to a boundary, although where a bird hatched related to the direction of dispersal suggesting that the matrix between forest patches were barriers to dispersal. Matthysen's findings suggest that the structure of the matrix habitat and connected habitat are important in Great Tit dispersal and settlement, as reflected in the findings of this study.

The findings presented in this chapter provide further insights into this species' urban movements. Chapter 3 demonstrated the importance of connected habitat in promoting abundance of Great Tits across the urban gradient, and this study shows that they moved into areas with more connected habitat. This may indicate that this species compares between sites (Lima and Zollner, 1996, Křivan et al., 2008), before settling at a site to breed, for example, as when they left a site to move to a new one, they had a choice in the landscape whether to move to a location with more available connected habitat or less, and a clear trend was shown in the data that Great Tits selected sites with more connected habitat than over sites with less.

Exploratory behaviour of parental Great Tits has been linked to the natal dispersal distance of their offspring. The fastest exploring parents have offspring that disperse furthest and this may be influenced by parental behaviour such as aggression towards offspring or a parent leading their offspring to good foraging sites (Dingemanse et al., 2003, Matthysen et al., 2010, Van Overveld et al., 2011). Of course, components of exploratory behaviour may be heritable in this species (Dingemanse et al., 2003). Dingemanse et al. found that immigrant Great Tits to an area were faster explorers than locally hatched birds. Due to the heritability of components of exploratory behaviour and, therefore, a possible dispersal tendency, movement of Great Tits may have consequences for the genetic composition of populations (Dingemanse et al., 2003).

Dingemanse et al. (2004) investigated the fitness consequences of Great Tit personalities in a fluctuating environment and showed that annual survival of adults and of offspring to first breeding was related to behaviour in novel environments. When resources are unevenly distributed (e.g. in non-beech mast years; Dingemanse et al. 2004) fast-exploring females may benefit from being aggressive when competing for food while slow-exploring territorial males may benefit due to reduced competition for high-quality breeding territories. A patchy urban environment with variable levels of resources such as breeding sites or food may then allow a diverse population of Great Tits to survive from year to year.

Age or sex does not predict the likelihood of movement of Great Tits. This opposes findings of other studies such as that of Greenwood et al. (1979) who examined natal dispersal in Wytham Wood, Oxfordshire, Dingemanse et al. (2003) who found that fast exploring females (i.e. aggressive, bold in exploration, insensitive to external stimuli and rely on routines; Dingemanse et al. 2004) had greater dispersal distances, and Verhulst et al. (1997) who found that females dispersed further than males in a study investigating natal dispersal in a patchy environment. This may indicate that the landscape

fragmentation found in an urban landscape overrides these natural sex-specific trends and that the likelihood of movement comes down to landscape factors.

5.4.3 Conclusions

The occupancy and turnover of bird populations in urban areas shown here demonstrate the permeability of the urban landscape, and the likelihood that bird populations have sufficiently high dispersal rates to function as a single, extinction-resistant population (Hinsley et al., 1995a, Bonte et al., 2012). This is instead of them functioning as a metapopulation, and instead possibly functioning as a patchy population due to turnover being due to movements of individuals rather than of mortality (Harrison, 1991).

This study further demonstrates the importance of a connected habitat in the matrix for the permeability of the urban landscape and habitat value for bird populations. Sites with more connected habitat in the matrix show higher occupancy and birds preferentially emigrated to them. This may be related to an increased availability of resources such as nest sites and food or the conduit value of a connected habitat (Ricketts, 2001, Kuefler et al., 2010, Eycott et al., 2012) and the ability of birds to move under cover. It is, therefore, advisable for urban planners to carry out habitat improvement through regular planting of trees to promote matrix similarity to habitat patches to complement habitat improvement and patch expansion. This should lead to the enhancement of population persistence and dispersal through the increase in functional connectivity (Hodgson et al., 2009, Prevedello and Vieira, 2010, Eycott et al., 2012).

Monitoring the extent of bird movements through an urban landscape could be a tool to demonstrate the degree of success of habitat improvement or a restoration project (Lindell, 2008) where a very high frequency of movements may indicate low habitat quality while less frequent movements may indicate acute patch isolation which would suggest further habitat and matrix improvements were required. It was demonstrated here that the movement of common birds such as Great Tits and Eurasian Blue Tits is affected by the composition of the matrix. This might suggest that the level of connectivity would be even more crucial for fragmentation-sensitive species and birds shifting their ranges due to climate change (Hodgson et al., 2009).

Chapter 6.   Synthesis

The aims of this research were to understand the impact of landscape connectivity and structure on bird populations in urban environments and to assess the nature and permeability of the landscape matrix for bird movements using Birmingham, UK, as a case study. It enabled a landscape-scale assessment of the importance of connectivity to bird populations across an urban gradient looking beyond the constraints of the habitat patch and corridor, and demonstrated the permeability and functional connectivity of a large city to birds.

All of the key objectives stated in the General Introduction (Chapter 1) were met through the studies carried out and the findings reported in Chapters 2 to 5. The results presented are novel, enhance our previous understanding of avian population biology and provide insights on bird movements in an urban landscape.

A gradient approach was adopted as it enabled the complexity of the urban landscape to be taken into consideration. Birds were surveyed at sites that were highly urbanised to those with scarce built space, as well as on a gradient of available connected habitat as displayed in Figures 2.9 and 2.10. This is an important and leading feature of this work as until now no studies had used a true urban gradient to study birds in an urban landscape. Many ecological studies in urban environments (e.g. Blair, 1996, Reale and Blair, 2005, Blair and Johnson, 2008) have used a categorical approach where sites are classified as urban or non-urban, but a true gradient was employed in this research which considered the land use in the vicinity of the sites surveyed at a scale relevant to the organisms in question. By utilising a gradient approach with a fine scale assessment of LULC the findings are widely applicable to urban areas worldwide. Urban-rural gradients approached in a meaningful way are a key element of this research, and should be used more consistently in future urban ecology studies.

Below is an evaluation of the significance of the findings presented on a thematic basis considering:

   i)   Connectivity
   ii)   Vegetative structure and diversity

Which is followed by a discussion of the study limitations and future work, concluding with the implications of the findings for urban bird conservation in the UK and the rest of the world.

6.1 Connectivity

A key objective of this thesis was to assess the importance of connectivity to birds in the urban landscape. This work demonstrated the importance of the degree of connectedness of Birmingham's urban environment for avian species.

For the first time connectivity of an urban landscape was modelled for birds in a GIS and used to analyse abundance and movement in the landscape. The field methods employed to capture bird abundance (i.e. transect surveys; Chapters 2 and 3) and movement (ringing; Chapters 4 and 5) were the most extensive examples reported until now. The study of bird movements demonstrated that the connectivity of the landscape was functional which built upon the structural connectivity demonstrated by the GIS mapping (Mills et al., 1991, Shanahan et al., 2011).

Structural linear features of the landscape such as green corridors were not found to increase the likelihood of bird movement. Instead functional connectivity of the matrix mediated through trees was a much more important feature of the landscape to predict bird movements. These findings contribute to previous literature (e.g. Beier and Noss, 1998, Haddad et al., 2003, Levey et al., 2005, Angold et al., 2006) and suggest that the role of corridors in the landscape as conduits are debatable. The green corridors that were studied in the ringing study (Chapter 4) appeared as linear features to the human eye, but there was no evidence that they provided enhanced functional connectivity in comparison to other habitat features, such as tree-lines in the matrix (Hess and Fischer, 2001). This is a significant finding with consequences for the prediction of bird movements in fragmented urban landscapes, and for urban planners as it suggests that green corridors may not necessarily enhance connectivity. Instead, for functional connectivity in the environment, the focus should also be placed on the often unaccounted for matrix habitats (Ricketts, 2001).

Connectivity across the urban landscape was positively related to the abundance of birds (Figure 2.5). Private land , including domestic gardens and street trees are not always considered as habitat in studies due to the difficulty of surveying them. The importance of the matrix has become increasingly recognised as important, especially when discussing the connectivity of fragmented landscapes. Previously landscapes have been classified as binary (i.e. habitat or non-habitat), but several studies have shown that "the matrix matters" (Ricketts, 2001). Data employed in this research demonstrated a relationship between habitat features in the matrix and bird turnover in sites within urban populations and bird movement between sites. It showed that a detailed and nuanced view of the matrix can be achieved, which is of considerable value in aiding the understanding animal

distributions and movements across a cityscape. This thesis underscores this knowledge and demonstrates, for the first time, the importance of the matrix for bird abundance and movements in the urban landscape.

Both the level of connected habitat and the amount of built space were highly influential in the turnover and occupancy of birds in a given area demonstrating the permeability of the urban landscape. This highlighted that birds have sufficiently high dispersal rates to potentially function as a single, extinction-resistant population (Hinsley et al., 1995a, Bonte et al., 2012) rather than as a metapopulation. This suggests that the structure of the city may not lead to isolation and then potentially to phenotypic and behavioural interspecific divergence (e.g. Slabbekoorn and Peet, 2003, Isaksson et al., 2005, Partecke et al., 2006b, Partecke and Gwinner, 2007) for all species. The few population genetics studies that exist support this assertion. For example, Partecke et al. (2006a) showed a lack of genetic differentiation in Common Blackbirds along an urban gradient suggesting limited population isolation.

When birds moved between sites they tended to move away from areas with more built space into areas with more connected, green habitat. This is likely to be due to characteristics of the former such as the patchy distribution of resources (Fernández-Juricic, 2000b), increased disturbance (Mockford and Marshall, 2009, Schroeder et al., 2012) and increased numbers of predators (Sims et al., 2008, Bell et al., 2010). Previously, Tremblay and St. Clair (2011) studied gap-crossing behaviour in an urban landscape when the studied anthropogenic linear features. They addressed the permeability of an urban landscape but not the destinations and timings of bird movements as undertaken here. These findings are the first of their kind and highlight the importance of enhancing the urban landscape in terms of habitat quality as many bird species will move away from areas with more built space into more 'natural' habitat types.

The findings also reinforce the message that in order to support passerine species it is important that urban planners take the urban green infrastructure and matrix into consideration in decision-making to ensure functional connectivity across the city and greater conservation returns (Prugh et al., 2008). Conservation of functional connectivity is central to long-term conservation of wildlife in urban landscapes (FitzGibbon et al., 2007). Functional connectivity can support birds on a local basis, providing cover and foraging opportunities, as well as enhancing population persistence and species' occupancy in complex landscapes (Marzluff and Ewing, 2001, FitzGibbon et al., 2007). Such knowledge is particularly important where there are pressures to increase built space to

accommodate the burgeoning urban human population resulting in the expansion and densification of UK cities and large alterations in the ecology (Tratalos et al., 2007b, Dallimer et al., 2011).

Ideally, built space would be limited and large expanses of natural habitat would be preserved, but where there is planned urbanisation it is advisable for planning decisions to incorporate vegetated areas and to ensure spatially regular native planting through the matrix. Within existing urbanised areas re-vegetation should be promoted to increase the conservation value of the landscape. Habitat improvement should be carried out through spatially regular planting of a variety of native species to promote matrix similarity to habitat patches. These processes are likely to enhance population persistence and dispersal through the increase in functional connectivity complementing habitat improvement and patch expansion (Hodgson et al., 2009, Prevedello and Vieira, 2010, Eycott et al., 2012).

Monitoring the extent of bird movements through an urban landscape could be a tool to demonstrate the degree of success of habitat improvement or a restoration project (Lindell, 2008). Frequent bird movements may indicate low habitat quality with infrequent movements perhaps revealing acute patch isolation; both might suggest further habitat and matrix improvements were required.

6.2 Vegetative structure and diversity

The diversity of responses shown by the avian community to the habitat available to them was demonstrated, showing that relationships are far from simple. The majority of the species examined preferred a combination of structural and compositional features (Wiens and Rotenberry, 1981) highlighting the importance of a species-specific approach to avian research as adopted here; however, it does complicate conservation measures.

Some avian species (e.g. Eurasian Blue Tits) exploited urban areas where they maintained large population sizes, occupying habitats with significant built land cover. While its demographics are usually explained in terms of availability of vegetative cover within the urban matrix and the generalist nature of the species, in a large city such as Birmingham habitats located in landscapes with more grey space may provide good foraging opportunities due to supplementary feeding, for example (Barraquand and Benhamou, 2008, Jones and Reynolds, 2008).

The results demonstrated the functionality of urban spaces for birds as long as appropriate tree species (i.e. native species) in an appropriate configuration (i.e. the spacing of trees) to the species in

question are available (see Chapter 3). Results suggested that natural assemblages of native tree species are the most appropriate for avian populations as they provide the most invertebrate prey and appropriate nest sites supported by other studies (e.g. Lancaster and Rees, 1979, Beissinger and Osborne, 1982, Goldstein et al., 1986, Mills et al. 1989, Shanahan et al., 2011).

The planting of any species (i.e. non-native or native) at a completely impoverished site can enhance biodiversity by stabilising soil and creating conditions that can allow other plants and animals to colonise (Hartley, 2002). However, it is know that the most important factor for biodiversity in a stand of vegetation is the presence of native species (Hartley, 2002) as non-native plants are known to reduce native diversity of vegetation (Manchester and Bullock, 2000) and consequently invertebrate and vertebrate communities.

Increasing native vegetative cover in urban areas, and recreating and preserving complete habitat profiles (Beissinger and Osborne, 1982) so that there is vegetative cover at many heights and spatial distributions as well as invertebrate food resources (Lancaster and Rees, 1979, Beissinger and Osborne, 1982), would ensure suitable habitats for many different bird species, including those that might occur in the UK for the first time as their ranges expand north due to climate change (Huntley et al., 2007). In this age of climate change and urbanisation, the need for functional connectivity is becoming more acute as these changes drive shifts in species' ranges (Dawson, 1994, Huntley et al., 2007, Hodgson et al., 2009).

6.2.1 Measuring vegetation

Remote sensing has facilitated remarkable advances in the modelling, mapping, and understanding of ecosystems (Lefsky et al., 2002). It has evolved from its military origins to be used for a great variety of applications from utilising images from passive optical systems such as aerial photography, to classifying land-cover, measuring surface temperatures, vegetation cover, and phenology, with active systems such as RADARSAT and light detection and ranging (LiDAR) (Roughgarden et al., 1991, Wickland, 1991, Waring et al., 1995, Kasischke et al., 1997, Lefsky et al., 2002). Remote sensing can be used to interpret landscape patterns and to study ecological processes over wide geographic areas and over long time periods (Kasischke et al., 1997).

The global coverage, systematic and regular collection, often free access to images, many analysis methods, precise nature of the data make satellite imagery an accessible and cost effective tool to monitor landscapes (Morgan et al., 2010). This has led to its rapid increase in use and popularity. Radar is used extensively in ecological research as it provides complementary data and additional,

independent measures, to optical and thermal remote sensing methods of important ecological variables such as vegetation and water (Waring et al., 1995, Kasischke et al., 1997). In recent years laser altimetry, commonly referred to as LiDAR, has been recognised as a methodological solution to measuring the physiognomy of vegetation in an ecological context (Lefsky et al., 2002, Bradbury et al., 2005, Hinsley et al., 2006, Goetz et al., 2007, Vierling et al., 2008, Müller et al., 2010). LiDAR is a remote sensing technique that can provide fine-grained information about the three-dimensional structure of habitats, measuring the topography of both plant canopies and sub-canopies, thereby providing high-resolution topographic maps and highly accurate estimates of vegetation height, cover and canopy structure (Lefsky et al., 2002, Vierling et al., 2008). It introduces a third (z) dimension to other remote sensing techniques such as aerial photography, Landsat Thematic Mapper (Goward and Williams, 1997) or active radar sensors such as RADSAT (Waring et al., 1995, Kasischke et al., 1997, Lefsky et al., 2002).

The possibilities that remote sensed habitat data provide are significant (Vierling et al., 2008), especially in urban landscapes due to its fragmented nature and complications with access. Remote sensed data in this study to great effect allowed the modelling of the connected vegetation in the landscape which was a keystone for this thesis.

6.3 Study limitations and opportunities for future work

This study offers a unique insight into the connectivity of the urban landscape and its effects on bird abundance, distributions, movements and turnover. However, future work could provide greater clarity by addressing connectivity at a range of scales, both through varying gap sizes between vegetative cover in the GIS to reflect a range of gap-crossing abilities of different species (Creegan and Osborne, 2005, Shanahan et al., 2011) and by examining the impacts of extent of available connected habitat at different landscape scales (Hale et al., 2012). Natural gap-crossing behaviour (i.e. with no translocation or playback to induce movements) of birds has not been measured in British urban environments. Investigating urban gradient and matrix effects on their gap-crossing behaviours would further our knowledge of how birds use the urban environment.

Although movements were measured in this work, it was not possible to know the precise routes taken and, therefore, the habitat encountered by an individual. From the start and endpoints of movements, we can only interpolate movements through existing autecological knowledge (Tremblay and St. Clair, 2011). In order to elucidate the finer details of animal movements individuals would need to be tracked (Wikelski et al., 2007). Conventional radio telemetry tracking is possible for

small passerine species but triangulation is required to locate individuals (Wikelski et al., 2010). In a fragmented urban landscape this method is difficult and impractical (Vincent, 2005) as birds frequently cross roads, canals or boundaries of private properties making it difficult to follow and relocate individuals. Tracking devices are, however, miniaturising and in the future powered GPS units may be small enough due to batteries becoming lighter for deployment on passerines (Wikelski et al., 2007).

The ringing study was the first of its kind and scale (in terms of distribution of ringing sites across the urban landscape and effort employed at each one) and produced very valuable data on bird movement and occupancy as explored in Chapters 4 and 5. However, it is never possible to catch every bird in a population due to the nature of the habitat and avian mobility and so the movement ecology at the population scale remains irresolvable. Just because a bird was not re-trapped does not mean that it is dead or has emigrated; it may just be avoiding the mist-nets, or simply be elsewhere. In order to improve this approach even greater ringing effort could be employed, but in reality this is impractical and there is no guarantee that increased ringing effort would lead to greater data quality. Bird ringing requires large amounts of time, effort and volunteers; as it stands it is estimated that this study employed nearly 11,000 person-hours.

A more complete understanding of the urban landscape and its relationship with bird populations that occupy it can be investigated through a variety of means. For example, a study of reproductive success across the urban gradient in relation to the matrix content could reveal much about resource partitioning, predation pressure and levels of disturbance sustained by birds. Anthropogenic development brings with it several changes to a landscape including artificial lighting. This ecological alteration has already been shown to affect the breeding behaviour of birds (e.g. Kempenaers et al., 2010, Longcore, 2010). Artificial lighting may also have impacts on bird distribution and abundance due to their disturbance, or and may increase foraging opportunities due to artificially increased day length. Lighting across a city can be measured through aerial night photography and, through GIS processing, layers can be produced that can be examined with bird distribution data to find if lighting has landscape-scale effects on bird distribution.

Pre-existing literature was used to determine the potential invertebrate prey base supported by tree species for birds in the examination of the relationship of birds with vegetation structure and diversity in Chapter 3. To complement this work it would be interesting to survey a selection of native and ornamental tree species and grasslands across an urban gradient for invertebrate, fruit and seed diversity. This would be an extensive amount of work but it would reveal whether food

resources for birds vary according to the spatial context with which they occupy. Urbanisation has the potential to impact soil quality with soil compaction (Edmondson et al., 2011) and geochemical changes (Pavao-Zuckerman, 2008) which detrimentally impact on macroinvertebrate prey, by making the soils a less suitable habitat. Investigating the relationship between soil characteristics and invertebrate diversity could highlight additional processes that influence avian distribution, especially those species that forage in soil such as Common Starlings and thrush species. Such knowledge could have wider applications such as understanding the distribution of non-avian taxa such as urban populations of European Badgers (*Meles meles*), European Hedgehogs (*Erinaceus europaeus*) and Common Toads (*Bufo bufo*).

To make this research more widely applicable, comparative survey methods could be carried out in other cities across the urban gradient and the results modelled with the vegetative cover of those cities to describe the relationship between the connected matrix and bird abundance and distribution (McDonnell and Hahs, 2008). Currently, others are finding similar results in other taxa such as bats that confirm the importance of connectivity (e.g. Hale et al., 2012). An important next step would be to address a cross-taxa model of urban connectivity and the distribution of species dependent on scale, mobility and requirements.

6.4 Implications of the findings for urban bird conservation

With the increase of urbanisation, migrating birds are increasingly likely to encounter urbanised landscapes on their migration stopovers (Rolshausen et al., 2009, Matthews and Rodewald, 2010) and this is likely to continue to be the case as ranges and migratory routes shift with climate change. More time and energy are spent during stopovers than during flight due to thermoregulation and the energy spent foraging and finding appropriate locations to roost, for example (Wikelski et al., 2003, Matthews and Rodewald, 2010, Seewagen et al., 2010). The behaviour of birds during these sojourns has a great influence on the overall success of the migration (Seewagen et al., 2010). Stopover sites are critical for re-fuelling and they are selected to maximise refuelling efficiency and to avoid competition and predation (Seewagen et al., 2010). The habitat that birds encounter if these stopovers are in urban areas may be degraded or fragmented due to anthropogenic changes, and this may lead to birds failing to settle in any one area. The result might be birds leaving sites having failed to re-fuel adequately to sustain migration (Matthews and Rodewald, 2010, Seewagen et al., 2010). However, if urban landscapes are maintained as ecologically valuable areas with a wide range of native vegetation, migrating birds may find all of the resources they need to re-fuel and continue on their successful migrations (Matthews and Rodewald, 2010, Seewagen et al., 2010). Identifying

and improving important areas along migratory routes would increase their likelihood of supporting migrant birds (Seewagen et al., 2010).

Due to the gradient methodology used in this study, the methods and findings are widely applicable to other cities (McDonnell and Pickett, 1990, McIntyre et al., 2000, McDonnell and Hahs, 2008, Pennington and Blair, 2012). Data presented in Table 2.1 demonstrate that Birmingham is not unusual in the amount of green space within the city in comparison to other European cities. Therefore these findings have the potential to be applied to other UK and European cities. In order to make this more globally applicable an understanding of the local or regional ecology and individual species' requirements would be required. Mapping of the land use and cover would be required before proposing improvements within a focal city to increase its avian biodiversity (McDonnell and Pickett, 1990, McDonnell and Hahs, 2008).

Urbanisation is occurring across the planet threatening to impact ecosystem structure and function (Deng et al., 2009). However, the spatio-temporal pattern of development can vary. It is particularly rapid in developing countries (Deng et al., 2009) and changes in urban pattern and form are faster at earlier stages of economic development (Seto and Fragkias, 2005). For example, the urbanisation of India and China is particularly dynamic due to rapid population growth especially in cities (Seto and Fragkias, 2005, Taubenböck et al., 2009). The number of mega-cities (a city with a population of more than 10 million) is set to increase in India from the three currently to six (Taubenböck et al., 2009). In China rapid land-use changes with concomitant declines in water, forest and cropland are characteristic of urbanisation (Deng et al., 2009). Due to a lack of planning and policy urbanisation continues to sprawl in a compact manner but with no set form (Seto and Fragkias, 2005, Deng et al., 2009). The growth of existing Chinese urban areas is enveloping smaller suburban developments into larger cities leading to poly-nucleated urban spaces (Seto and Fragkias, 2005). Cities in India and Mexico can be characterised both by extensive sprawl addition to densification of the urban core (2008a, 2008b, Taubenböck et al., 2009). Towns in the periphery of Mexico City are also expanding, and are likely to be enveloped by the main city leading to a multi-centre mega-city (Taubenböck et al., 2008a). In the USA cities tend to sprawl and fragment the landscape (Luck and Wu, 2002, Weng, 2007). Phoenix, Arizona, is a young and rapidly growing city with a clear urban core with significant fragmentation, spatial complexity and a growing metropolitan area (Luck and Wu, 2002).

It is critical for all types of urbanisation such as the rapid sprawl and continual densification in developing countries or the fragmentation in developed countries, to put in place mitigation strategies to sustain biodiversity. A connected vegetative network is likely to provide some resilience

and habitat diversity for a variety of wildlife across the world in addition to aiding ecosystem services. This is critical if sustainable cities are to thrive (Botequilha Leitão and Ahern, 2002, Weng, 2007). There is a need to balance development with natural resources therefore ecological knowledge is essential if planning is to be sustainable (Botequilha Leitão and Ahern, 2002).

6.5 Concluding remarks

Connectivity of a landscape enables movement, be it for natal or breeding dispersal, predator avoidance, daily foraging sorties or seasonal migrations. This work showed, for the first time that native, diverse vegetation that is evenly distributed across the landscape provides functional connectivity and can increase abundance, support resident birds and enable their movements. Therefore, to enhance urban landscapes for bird populations and human well-being through biodiversity exposure, vegetation must be included in planning.

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