UNDERSTANDING THE DUAL IMPACTS OF URBANISATION AND CLIMATE CHANGE ON BREEDING IN ONE OF THE UK'S MOST COMMON CITY BIRDS, THE BLUE TIT (CYANISTES CAERULEUS)

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Abstract

Human activities cause widespread and irreversible modifications to once natural and semi-natural environments, creating novel conditions and challenges for wildlife. In particular, the ongoing combined effects of increasing urbanisation and global climate change are likely to result in some of the most extreme and significant changes to once natural landscapes, with profound impacts across multiple ecological levels, including individual organisms and populations. Yet despite increasing evidence to suggest that climate change is already exacerbating the effects of urbanisation, few studies have considered how species may respond to the combined impacts of these two factors. In particular, considering that reproductive success is crucial to the long-term stability of populations and the survival of species, there is a clear need to better understand how breeding phenology and success are affected by increasing urbanisation, and variation in weather conditions in these already heavily impacted systems.

This thesis focuses on a population of Blue Tits, a small hole-nesting passerine, that is widely considered to be an urban-adapted species and is commonly used in urban-rural comparative research. Using a quantitative and hierarchical mixed modelling approach I investigated how breeding success during two reproductive phases (pre-hatching and brood-rearing) varied across a short, high resolution intra-city urban gradient in the city of Birmingham, UK using demographic data from consecutive years (2013-2018). The aims of the work were to: 1) identify the key habitat and landscape-scale factors that impact

breeding outcomes, 2) determine if the strength and direction of these effects vary across the different phases of breeding, 3) use critical climate time window analyses to explore the influence of variation in both temperature and rainfall across the urban gradient on a selection of breeding responses identified as key drivers in determining breeding success in this population.

I found evidence for a subtle yet quantifiable negative effect of increasing urbanisation across both breeding stages. However, the brood-rearing phase appeared particularly sensitive to variation in urbanisation, with the mean body mass of nestlings, individual fledging probability and rates of fledging success all declining with increasing built landcover. Crucially brood reduction during the early phase of nestling development, and an increased risk of complete breeding failure during brood-rearing appeared to be the main drivers of observed reduced breeding success across a city scale urban gradient. At the site level, variation in the composition and structure of vegetation within greenspaces, in particular the number of native broadleaved trees and the diversity of tree species was also found to significantly influence breeding outcomes. Aligned with these findings, the early brood rearing stage was also determined to potentially be the most sensitive to changes in the prevailing weather conditions. The urban environment appeared to buffer the effects of cold temperatures, whilst increased maximum temperatures were associated with heavier nestlings and higher rates of fledging success. However, model predictions suggested a critical threshold at which point higher maximum temperatures were linked to lower fledging success. Higher rainfall during this period was also associated with lighter nestling body mass and reduced fledging success. Furthermore, there was tentative evidence to suggest that the detrimental effects of adverse weather may be compounded by the urban gradient. My study demonstrates that the impacts of both urbanisation and weather

variation are complex and unlikely to be consistent across the breeding season. However, findings did suggest that environmental conditions during the critical brood-rearing phase are likely crucial to nestling growth, development and survival to fledging. As condition of chicks when they leave the nest determines their long-term survival and future reproductive success these findings have wider implications for the future of this and other populations of urban breeding birds, already undergoing increasing environmental stress from the multiple threats of further rapid urbanisation and the increasing intensity and duration of extreme weather associated with climate change.

Keywords: Breeding success, birds, urbanisation, urban gradient, urban metrics, climate change, extreme weather events, hierarchical modelling, spatial scale, *Cyanistes caeruleus*

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To all the people, so many people, they all go hand in hand. Park Life. (Damon Albarn 1994).

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Glossary

ALD: April Laying Date. Estimated date that the first egg in a clutch was laid.

AHD: April Hatching Date. Estimated date that the first chick hatched.

ASYM: Brood weight asymmetry. The range in weight between the lightest and heaviest nestling within a brood.

%BLC: Percentage of built landcover within a 500m concentric buffer from the centre of each site.

BOS Trees: The average (combined) number of Birch, Oak, and Sycamore trees within a 10m radius of nestboxes. Average calculated from 4 nestbox surveys conducted at each site.

BROOD ID: Identifying code given to each breeding attempt using a combination of the site, nest box and year of the breeding season. (e.g. HOL310_18 = Holders Lane, nestbox 310/310 (of the total nestboxes distributed across 31 sites) and year = 2018.

BS: Proportional breeding success. The proportion of eggs that were initially incubated that successfully fledged a chick for each breeding attempt.

$_{prob}$BS: Binary Breeding Success. The probability (0,1) that a nest will fledge at least one chick from the initial clutch that was laid.

BTO: British Trust for Ornithology

CS: Clutch Size. The maximum number of eggs laid during a nesting attempt that reached the incubation stage.

EBS: Early stage brood success. The proportion of nestlings surviving to ringing age (at least 8 days post-hatching) relative to the number of chicks initially hatched.

Edge Distance: The mean distance of nestboxes within a site to the edge of connected tree cover.

FN: Fledgling numbers. The estimated number of nestlings that fledged the nest after ~20 days.

FS: Fledging success. The proportion of chicks hatched that successfully fledged after ~20 days.

$_{prob}$FS: Binary fledging success. The probability (0,1) of a nest fledging at least one chick that hatched.

GBH: Girth at breast height.

%GLC: Percentage of residential garden landcover within the urban matrix, (measured within a 500m concentric buffer from the centre of each site).

GLMMs: Generalised Linear Mixed Models

HN: Hatching numbers. The maximum brood size estimated at hatching.

HS: Hatching success. The proportion of eggs that hatched in each breeding attempt.

$_{prob}$HS: Binary hatching success. The probability that nests hatch at least one egg from the total clutch laid.

InvSI: Mean reciprocal Simpson's diversity index score calculated for each site from 4 habitat surveys. Diversity scores are for all native and non-native broadleaved trees counted within a 10m radius of nestboxes.

LBS: Late stage brood success. The proportion of nestlings surviving to fledge, relative to the number alive during the ringing visit.

LMMs: Linear Mixed Models.

LULC: Land-use and landcover

Mean BOS Trees: The mean number of Birch, Oak and Sycamore trees within a 10 m radius of nestboxes for each site. (Mean calculated from the total tree counts for the three species across 4 habitat surveys conducted at each site).

MeanRBC: Average body condition index: Residuals for all nestlings were extracted from the regression of raw body mass on tarsus length and an average residual value was derived for each brood.

Mean NDB: Mean number of native deciduous broadleaved trees within a 10m radius of nestboxes (calculated from 4 habitat surveys conducted at each site).

MNM: Mean nestling mass (g). Average weight of nestlings within each brood.

MTL: Mean tarsus length. Average length of the tarsi measured for all nestlings in a brood.

NDB Trees: The number of native deciduous broadleaved trees (averaged) within 10m of nestboxes within each site.

NESTBOX ID: Identifying code for each nestbox in each site (e.g. HOL310 = Holders Lane, Nestbox 310/310 (of the total nestboxes distributed across sites).

PBR: The proportion of nestling deaths that occurred during the early stage of brood rearing relative to all post-natal deaths.

PNS: Probability of individual nestling survival to fledging.

SITE ID: Identifying code for each of the 31 sites (e.g. WGVP = Woodgate Valley Country Park).

ULC: Urban land cover: Classification of sites into one of 5 urban land classes using arbitrary cut-off values of %BLC. Classes range from ULC1 = Suburban to ULC5 = Dense Urban.

UHI: Urban heat island effect.

VIF: Variance inflation factor.

ZI: Zero Inflation model used in glmers for ecological data that is zero inflated.

Chapter One

General Introduction

1.1. URBANISATION AS A DRIVER OF ENVIRONMENTAL CHANGE

The world's human population is growing rapidly (Mackay *et al.* 2017) and with it urbanisation is accelerating at an unprecedented rate (Grimm 2008; Seto *et al.* 2011, 2012). By 2050, 66% of the global human population will be living in urbanised areas (United Nations 2018), whilst the total area of urban landcover is projected to triple in extent from current levels (3-4%) by 2030 (Grimm 2008; Seto *et al*. 2011,2012). It is therefore not surprising that urbanisation is considered one of the most pervasive and extreme forms of environmental change globally (Sol *et al*. 2014), representing one of the biggest current threats to species extinction (Mcdonald *et al.* 2008*;* Goddard *et al*. 2010) and one of the major drivers of biodiversity loss (Marzluff 2016; Isaksson 2018). Consequently, the conservation of biodiversity in urban areas has become a leading priority (Marzluff 2001; Hostetler *et al*. 2011).

The UK has a long history of urban development, with growth having especially intensified since the end of World War II (Tratalos *et al*. 2007a). Approximately 6-10% of the land area is categorised as built landcover (Evans *et al*. 2011; Rae 2017) and 83% of the population is classified as living in urban/suburban areas (Hall 2022) making it one of the most urbanised countries in Europe (Nuissl *et al.* 2009). In the UK urban transformation and development is associated with both the densification of towns and cities (an increase in the density of urban land-use and landcover) and urban sprawl (the encroachment of the urban fringe into rural habitats), primarily to meet current and future housing needs (Marzluff 2001; Sadler *et al*. 2006; Dallimer *et al*. 2011). Such rapid, extensive and irreversible physical restructuring of the landscape leads to wide-ranging impacts on already human-altered ecosystems (LaPoint *et al.* 2015). This includes the further loss of natural vegetation and increasing fragmentation of remaining habitat (McKinney 2006; Tratalos *et al*. 2007b; Grimm *et al.* 2008); altered habitat connectivity (Trepl 1995; Niemelä 1999a,b) and the creation of novel habitat types (Goddard *et al*. 2010). Ultimately, and particularly in the industrial and commercial heartlands of cities where > 80% of landcover is typically artificial (McKinney 2008), only a few remnant smaller, more isolated patches of habitat that are less suitable for wildlife remain (Dallimer *et al*. 2011; Delaney 2014; LaPoint *et al*. 2015).

1.1.1. Biotic and abiotic impacts of urbanisation on wildlife

The environment of urban areas is markedly different compared with the natural and semi-natural landscapes that surround them (Marzluff 2001; Chace and Walsh 2006; Chamberlain *et al.* 2009). Urban areas are highly heterogenous (McDonnell and Pickett 1990; Sadler *et al.* 2006) and geometrically complex (McKinney 2008; Hale *et al.* 2012), encompassing a diverse range of habitats ranging from undisturbed remnant patches of native vegetation to brownfield sites and newly transformed, intensively managed greenspaces (Aronson *et al*. 2014; Lepczyk *et al*. 2017). Furthermore, they are characterised by human-mediated modifications to climate systems, hydrological and biogeochemical cycles and ecological processes resulting in novel conditions and pressures (Grimm 2008; Seto *et al*. 2011). Novel abiotic changes include, for example: higher ambient temperatures (the urban heat island effect Grimm 2008; Imhoff *et al*. 2010; Diamond and Martin 2020) and increased levels of pollutants including chemicals, particulates and heavy metals (Isaksson 2010; Brahmia *et al*. 2013; Salmón *et al.* 2018a), noise (Slabbekoorn and Ripmeester 2008; Halfwerk *et al.* 2011; Injaian *et al.* 2018a) and light (Gaston *et al.* 2013; Dominoni 2015; de Jong *et al*. 2015) as well as localised changes to weather conditions (Haggard 1990). Urbanisation also triggers changes in the biotic characteristics of the landscape (Marzluff 2001), through the introduction of invasive species (Gaertner *et al*. 2017; Borden and Flory 2021); disturbance due to human activity (Fernández-Juricic and Tellería 2000; Glądalski *et al.* 2016a); differences in the quality and availability of food resources (Fuller *et al*. 2008; Jones and Reynolds 2008; Robb *et al.* 2008a); variation in competition pressures (Anderies *et al*. 2007; Shochat *et al*. 2010a); altered risks of predation (Haskell *et al*. 2001; Sorace 2002; Baker *et al*. 2005) and exposure to novel parasites and disease agents (Brittingham and Temple 1986; Bradley and Altizer 2007; Evans *et al*. 2009a).

In turn, these changes have wide-ranging impacts on wildlife, leading to the decline and local extirpation of species, and driving both biodiversity loss (Evans *et al*. 2011) and biotic homogenization (Aronson *et al*. 2014; Sullivan *et al*. 2015). Urban development and its associated impacts, for example have been implicated in the recent widespread decline in the distribution and abundance of herpetofauna (Hamer and McDonnell 2008, 2010), the global collapse of insects (Fengolio *et al*. 2020, 2021) and the local loss of many terrestrial mammal species, in particular large carnivores, which being highly sensitive to habitat fragmentation avoid urban areas or are extirpated due to wildlife-human conflict (Crooks and Soulé 1999; Mueller *et al*. 2018; Łopucki *et al*. 2019). The diversity of bird assemblages in urban areas has also shown extensive declines globally, with losses particularly associated with habitat specialists including insectivores and open habitat species resulting in changes to community and guild structure (Clergeau *et al*. 2006a; Silva *et al*. 2016). In a global assessment of the status of bird diversity, Aronson *et al.* (2014) determined that on average only 8% of native species are present in urban areas.

1.1.2. Species' adaptations to the urban environment

The conditions, for wildlife in urban areas would, therefore, seemingly be unfavourable (Croci et *al*. 2008). However, the tolerance of species to disturbance caused by urbanisation (*sensu* Sol *et al*. 2014) is dependent upon a suite of physiological, behavioural and life-history traits that shape resource use, and ecological interactions of organisms (Bonier *et al*. 2007; Croci *et al*. 2008). Birds in particular, exhibit huge variation in their sensitivity to urban-driven environmental change, with the majority of species classified as urban avoiders (i.e. those with limited tolerance to disturbance) compared with those that persist ('urban adapters') or even thrive and expand their range ('urban exploiters') (Blair 1996; McKinney 2002; Sol *et al*. 2014; Fischer *et al*. 2015).
This creates a non-random filtering process (Shanahan *et al*. 2014; Hagen *et al*. 2017), resulting in the decline and localised loss of native species (Marzluff 2001; McKinney 2002), reduced species' richness (McKinney 2008; Evans *et al*. 2011; Newbold *et al*. 2015) and overall biotic-homogenisation (Clergeau *et al*. 2006a; McKinney 2006; Evans *et al*. 2011). In the long term this potentially can have widespread knock-on effects to overall ecosystem functioning and services (Shochat *et al*. 2010b; Solonen and Hildén 2014; Sol *et al*. 2020).

Urban adapted species are likely initially attracted to cities by a number of positive environmental cues that are normally used in the rapid assessment and selection of habitat, including the widespread availability of concentrated food resources (bird feeders, refuse and highly productive (fertilised) lawns and ornamental fruiting plants: Robb *et al.* 2008a,b; Chamberlain *et al.* 2009; Stracey and Robinson 2012) and the ready availability of nesting sites (nestboxes and buildings: Sumasgutner *et al.* 2014; Reynolds *et al.* 2019). However, these normally reliable cues are uncoupled from the true quality of the habitat in cities, leading to birds to settle in areas where their fitness, and in particular breeding productivity and survival are lower compared with more natural habitats (Robertson and Hutto 2006; Stracey and Robinson 2012; Hollander *et al*. 2013). Increased population density and associated competition for resources caused by the attraction of birds into cities by food and the warmer microclimate during the winter may also impose further constraints on urban-dwelling organisms (Chace and Walsh 2006; Hedblom and Söderström 2012; Demeyrier *et al.* 2017). Finally, mismatches between population density and habitat quality in urban environments may also arise as a consequence of dominant individuals forcing out less fit individuals from surrounding high quality natural landscapes into suboptimal habitats (i.e. despotic distributions; Fischer *et* al. 2015).

There is growing concern, therefore, that although adapted species are able to take advantage of and benefit from human-provided resources, cities may be acting as 'ecological traps' (reviewed in Battin 2004; Schlaepfer *et al*. 2002; Robertson and Hutto 2006; Robinson and Hoover 2011) resulting in mismatches between the quality of habitat and the size of populations that that they can support (Fischer *et al.* 2015; de Satgé *et al*. 2019; Corsini *et al.* 2021). Moreover, in the long-term, urban areas could become habitat sinks if population stability remains reliant on the immigration of individuals from surrounding areas (Pulliam 1988; Balogh *et al*. 2011; Robinson and Hoover 2011; Stracey and Robinson 2012).

1.1.3. Avian responses to urbanisation

Birds are one of the most intensively studied taxa in the field of urban ecology (McDonnell and Hahs 2015; Seress and Liker 2015). The impacts of urbanisation due to changes in spatiotemporal patterns of activity (Chace *et al*. 2003; Fuller *et al*. 2007; Dominoni *et al*. 2013, 2015) and behaviour (Lowry *et al*. 2013; Sol *et al*. 2013; Samia *et al*. 2017; Jarrett *et al*. 2020); morphology (Liker *et al*. 2008; Evans *et al*. 2009b; Thompson *et* al. 2022), metabolism (Nord and Nilsson 2011; DuRant *et al*. 2013; Brischoux *et al*. 2017) and physiology (Partecke *et al*. 2006; Isaksson 2010; Salmón *et al*. 2016, 2018b; Watson *et al*. 2017) and life history traits including reproduction (Chamberlain *et al*. 2009; Deviche and Davies 2014) have been well documented. Of particular significance to my research, marked disparities in the breeding density, phenology and success of urban compared with suburban and rural populations have been widely reported across a large number of studies and for several different species, which have been the focus of reviews and meta-analyses (e.g. Chamberlain *et al.* 2009; Seress and Liker 2015; Marzluff 2016; Sepp *et al.* 2018). More specifically, compared with their forest and suburban conspecifics, urban birds typically initiate breeding earlier (Dominoni *et al*. 2013, 2020; Solonen and Hildén 2014) and lay smaller clutches (Hedblom and Söderström 2012; Vaugoyeau *et al.* 2016; Glądalski *et al.* 2015; Wawrzyniak *et al.* 2015), fledge fewer young (Cowie and Hinsley 1987; Hõrak 1993; Solonen 2001), raise nestlings in lower body condition (Eeva *et al.* 2008; Mackenzie *et al.* 2014; Bailly *et al.* 2016; Biard *et al.* 2017) and suffer an increased frequency of partial or complete brood failure (Peach *et al.* 2008; Glądalski *et al.* 2017; de Satgé *et al.* 2019; Muller *et al.* 2020; c *et al.* 2020).

Using dichotomous urban-rural comparisons, studies have begun to disentangle the various biotic and abiotic components of urbanised environments that are likely driving lower reproductive performance and breeding success. In particular, comparative studies have highlighted that compared with natural breeding habitat, urban greenspaces are typically smaller and highly fragmented (Shanahan *et al*. 2014; Wawrzyniak *et al*. 2020), and have a widely contrasting vegetation structure and composition (Mörtberg 2001; Hinsley *et al*. 2008; Pennington and Blair 2011; Pollock *et al*. 2016). This reduces the quality of habitat with knock-on adverse effects on the availability and quality of preferred natural food resources including caterpillars (Demeyrier *et al*. 2017; Seress *et al*. 2020; Derryberry and Coomes 2020). Novel environmental conditions including higher ambient temperatures and increased light and noise pollution can also alter the seasonal cues many species use to initiate breeding, resulting in earlier and potentially mis-timed breeding (Partecke *et al*. 2004; Dominoni *et al*. 2013, 2020; Vaugoyeau *et al*. 2016; but see de Jong *et al*. 2018). Variation in breeding success between urban and rural areas has also been linked to physiological and phenotypic differences of breeding individuals, including parental quality (Doutrelant *et al.* 2008; Pagani-Núñez and Senar 2014), and fitness (Gustafsson *et al*. 1994; Norte *et al*. 2009; Knowles *et al*. 2010) and age (i.e. breeding experience: Pärt 1995; Sanz *et al*. 2001; Grieco *et al*. 2002).

1.1.4. Introducing the urban-rural gradient framework

Although breeding success in urban areas has been well described, the majority of studies up until recently have investigated urbanisation impacts on birds within a dichotomous urban-rural qualitative framework (e.g. Hinsley *et al.* 2008; Wawrzyniak *et al.* 2015, 2020; Glądalski *et al.* 2016b, 2017; Biard *et al.* 2017; Charmantier *et al.* 2017; Seress *et al.* 2018).

However, this coarse-grained comparative approach in which the urban-rural gradient is reduced to a simple dichotomy precludes the detection of fine-scale and potentially non-linear responses of birds to (sub)urban-rural transitions (Alberti 2015; Batáry *et al.* 2018), including parameters of breeding behaviour and success (Hedblom and Söderström 2012; Biard *et al.* 2017). Researchers such as Filloy *et al.* (2019), Xie *et al.* (2019), Moll *et al.* (2019) and Di Pietro *et al.* (2020) have also highlighted how differences in urban classification can bias conclusions of such research and inhibit the comparison of results between studies, regions, populations and species. This is particularly crucial as it is becoming increasingly apparent that the impacts of urbanisation on breeding behaviour and success are likely species-, population- and/or region-dependent (e.g. see Bailly *et al.* 2016; Vaugoyeau *et al*. 2016; Sepp *et al.* 2018; de Satgé *et al.* 2019). Therefore, there is a growing call to shift the focus of research to the adoption of high-resolution and quantitative approaches, and to incorporate multiple-spatial scale frameworks in study designs to investigate the potential scale-dependency effects of urbanisation (Hostetler 2001; Mayor *et al.* 2009; Goddard *et al.* 2010; Moll *et al.* 2019). Yet up until recently, very few studies have explicitly incorporated these recommendations (but see Demeyrier *et al.* 2016; Vaugoyeau *et al.* 2016; Corsini *et al.* 2017, 2021; de Satgé *et al.* 2019; Strubbe *et al.* 2020).

Less discussed is the paucity of information derived from the most densely built-up regions within cities, which is primarily due to a lack of suitable sample sites or available data at this extreme of the urban gradient e.g. as also discussed by de Jong *et al.* (2018). Gaps in data collection across such gradients are also common where, despite high sampling effort (e.g. Peach *et al*. 2008), few breeding attempts by target species are recorded. Ultimately few studies have specifically explored how breeding varies across fine-scale highly urbanised intra-city gradients. Additionally, relatively few studies have sought to investigate habitat-level factors (e.g. the vegetation structure and composition immediately surrounding nesting sites, habitat quality, patch size and fragmentation of urban greenspaces), coincidentally with the external influence of the urban matrix (e.g. extent of built landcover surrounding greenspace) and how they may interact to impact on avian breeding performance (Hedblom and Söderström, 2010, 2012; de Satgé *et al.* 2019).

Consequently, understanding how fine-scale variability within the urban landscape impacts on intra-city and individual-level breeding behaviour and reproductive success has been highlighted as a key research priority (Pollock *et al.* 2017; Moll *et al.* 2019; Plummer *et al*. 2020).

1.2. CLIMATE CHANGE AND EXTREME WEATHER EVENTS

In addition to urbanisation, human-induced global climate change is creating novel environmental conditions for wildlife (Coumou and Rahmstorf 2012; Marrot *et al*. 2018) and exerting an equally pervasive force on ecosystems (Shryock *et al.* 2017; Socolar *et al.* 2017). Over the last century global mean temperatures have warmed by approximately 1^{o}C in response to an increase in greenhouse gas emissions associated with human activities (IPCC 2021). Moreover, as the process of warming continues to accelerate (Heim 2015; Socolar *et al.,* 2017), global temperature increases could reach or exceed 1.5^{o}C within the next twenty years (IPCC 2018).

Whilst climate change is primarily characterised by a rise in the mean and variation in ambient temperature (Marrot *et al*. 2017, 2018) its effects are observable in changes to many other climate variables (Heim 2015; Pipoly *et al*. 2013). Minimum temperatures are rising faster than other temperature signals in many regions across the globe, resulting in reduced daily temperature ranges (Ummenhofer and Meehl 2017). In Europe there has been a shift in the ratio of daily high to low temperature records (Beniston 2015). Future projections suggest that the number of warm days will continue to increase, whilst the number of cold nights will decrease (Ummenhofer and Meehl 2017) resulting in a greater probability of more record highs (Beniston 2015). Concomitantly, mean rainfall levels (Marvel and Bonfils 2013) and windspeeds (Young *et al*. 2011) are also both projected to increase in temperate regions of Europe.

The frequency, duration and intensity of extreme climate events have also increased in recent decades (IPCC 2012; Alexander 2016), and are projected to continue increasing in the future, with predictions suggesting daily extremes in temperature and precipitation will be most affected leading to an increase in the number of hot days, extreme rainfall and longer drought periods (Pipoly *et al*. 2013; Marrot *et al.* 2017; Ummenhofer and Meehl 2017). More specifically, in Europe, which has witnessed a steady increase in the frequency of heavy rainfall events since the 1950s, extreme precipitation is expected to intensify in the future under the current climate change scenario increasing the risk of flooding (Buonomo *et al*. 2007; Pall *et al*. 2011; Hartmann and Stocker 2013).

1.2.1. The impacts of Climate Change on wildlife

Several ecological studies have been published over the last couple of decades documenting the biological impacts of climate change across many different taxa and regions including birds (Møller *et al*. 2010; Şekercioğlu *et al*. 2012; Simmons *et al*. 2014), insects (Robinet and Roques 2010; Kiritani 2013; Yang *et al*. 2021), plants (Short and Neckles 1999; Bellard *et al*. 2012; Parmesan and Hanley 2015) and mammals (Learmonth *et al*. 2006; Boutin and Lane 2014; Hetem *et al*. 2014) and across different ecological scales ranging from populations to communities and ecosystems (Parmesan and Yohe 2003; Marrot *et al*

2017; Bramer *et al*. 2018). From this research, a general pattern of important global effects of climate change, in particular the impacts of warming, on wildlife has emerged. This includes advances in early seasonal phenological responses (particularly in northern latitudes) including tree budburst and first flowering, insect emergence, migration and reproduction (Parmesan and Yohe 2003; Yang and Rudolf 2010); shifts in species distribution and ranges (Root *et* al. 2003; Lenoir *et al*. 2008; Chen *et al*. 2011); changes in physiological and morphological traits including body size (Sheridan and Bickford 2011), mass (CaraDonna *et al*. 2018; Prokosch *et al*. 2019) and fitness (Walker *et al*. 2019); behavioural traits (Sih 2013; Buchholz *et al*. 2019); demographic rates including survival and reproduction (McMahon and Burton 2005; Selwood *et al*. 2015) and multi-trophic interactions (Walther *et al*. 2002; Van der Putten *et al*. 2010; Walther 2010).

Some of the most significant impacts of climate change on weather variation, and in particular temperature and precipitation anomalies associated with weather extremes, have been observed during the spring and summer, therefore coinciding with breeding periods and the peak in biological productivity for many species including temperate passerines including the Blue Tit (Pipoly *et al*. 2013).

However, the majority of studies have focused on only a few biological responses, in particular including breeding phenology. Consequently, the influence of weather conditions on many other aspects of life-history, including the various components of the avian reproductive cycle, for example nestling development and survival are less well described and understood (Mainwaring and Hartley 2016; Radchuk *et al*. 2019; Marques-Santos and Dingemanse 2020).

Therefore, examining the effects of variation and extremes in weather characteristics on breeding phenology and reproductive success at the individual and population level has been highlighted as a research priority. In particular, such research will be fundamental to increasing our understanding of the underlying processes influencing demographic rates and species adaptations to climate change (through phenotypic plasticity and/or evolutionary change), and ultimately the resilience of animal populations facing future rapid climate change and an increase in the intensity and frequency of extreme weather (Pipoly *et al*. 2013; Marrot *et al*. 2017; Radchuk *et al*. 2019; D'Amelio et al. 2022).

1.2.2. The combined effects of urbanisation and climate change

One of the most well known and consistent changes to local and regional climate associated with urbanisation is the urban heat island effect (Manley 1958; Oke 1973; Chapman *et al.* 2017; Shryock *et al.* 2017). A unique form of meso- or micro-climate (Haggard 1990), the urban heat island is primarily attributable to the combined effects of higher absorption of heat by impervious buildings and other infrastructure and the scattering effects of air pollution which traps radiated heat within the atmosphere (Oke 1982; Quattrochi and Ridd 1994; Arnfield 2003; Imhoff *et al*. 2010). This results in a very distinctive climate, with the most noticeable changes including higher ambient temperatures and increased humidity (Haggard 1990; Imhoff *et al*. 2010): both of which are key climate variables that influence crucial life-history processes and events including reproduction and survival (Sumasgutner *et al*. 2020). More specifically cities are on average 2.9°C warmer compared with the surrounding countryside (Imhoff *et al*. 2010), have notably higher minimum night-time temperatures (Haggard 1990) and experience smaller fluctuations in daily temperatures (Arnfield 2003).

The associated changes to precipitation in urban areas are not as consistent (Shryock *et al*. 2017). However, several studies have documented localised increases of 5-15% in precipitation during autumn, winter and spring months in the northern hemisphere, with the down-wind side of urban centres experiencing the greatest modifications (Haggard 1990; Shryock *et al*. 2017). Additional urban-driven climate variations include increased wind and turbulence, changes to atmospheric moisture resulting in humidity anomalies, variations in surface heat flux as well as alterations to air chemistry and pollution (Haggard 1990).

Consequently, the impacts of climate change are likely to be particularly severe in urban habitats (Sumasgutner *et al*. 2020). Indeed, according to the United Nations Secretariat the combined effects of urbanisation and climate change are currently the most significant drivers of global change (United Nations 2019). Moreover, there is increasing evidence to suggest that climate change may exacerbate the effects of urbanisation (Shryock *et al.* 2017; Pipoly *et al.* 2022). Diamond *et al*. (2014), for example demonstrated a negative interactive effect of increasing urbanisation and geographic temperature (using a latitudinal gradient in mean temperature as a proxy for projected climate change) on the phenological response of 20 butterfly species in Ohio, USA. In one of the only other studies to explicitly investigate the combined influence of climate change and urbanisation, Sumasgutner *et al*. (2020) found that the strength and direction of interactive effects of weather and urbanisation on breeding phenology and success in an urban population of Peregrine Falcons (*Falco peregrinus*) in South Africa varied across the breeding season. Furthermore, the impacts of weather on breeding performance were found to be indirect, and there was evidence to also suggest nestboxes buffered extreme weather including high rainfall. This study, therefore was particularly important, in demonstrating the synergistic effects of urbanisation and climate change, with potentially both negative and positive impacts on breeding.

Yet, with the exception of a handful of studies, as highlighted above, despite the potential severity and complexity of the effects of urbanisation and climate change, and the unprecedented rate at which such changes to the environment are occurring, their combined impacts on biological systems have rarely been investigated (Zuckerberg *et al.* 2011; Møller 2013; Shryock *et al*. 2017).

There is, therefore a need for more comprehensive approaches that investigate the joint impacts of urbanisation and climate change on natural systems, not only to tease out and understand current impacts, but to better predict changes in the future (Pipoly *et al.* 2022). In particular, examining how weather variability and extreme events influence avian reproductive phenology and success in cities will be crucial in the development of effective mitigation measures (Sumasgutner *et al*. 2020).

1.3. BIRDS IN URBAN ECOLOGICAL AND CLIMATE CHANGE RESEARCH

Although urban adapted species benefit from the wide availability of human-provisioned resources, unlike urban exploiters they also depend on natural resources (McKinney 2006). Consequently urban adapters provide an ideal opportunity to explore and better understand urbanisation-driven shifts in the ecology and evolution of free-living animal populations (Corsini *et al*. 2020). Over the past couple of decades birds have become an increasingly important target for urban ecology and evolutionary research (Marzluff 2001, 2016; Chamberlain *et al.* 2009; Bailly *et al.* 2016; Isaksson 2018).

The majority of urban ecology studies have targeted synanthropic species that dominate the wider urban avifauna (Chamberlain *et al.* 2009; Biard *et al.* 2017). In particular hole nesting woodland passerines such as the Blue Tit (*Cyanistes caeruleus*) and Great Tit (*Parus major*), have been the focus of several long-term intensive research efforts both here in the UK and across Europe (e.g. Evans *et al.* 2011; Wawrzyniak *et al.* 2015; Bailly *et al.* 2016; Glądalski *et al.* 2017; Corsini *et al.* 2017; de Satgé *et al.* 2019).

Blue and Great Tits (hereafter referred to colloquially as 'tits') are widely considered model species for nest monitoring research. Their demography, life history, and ecology in natural landscapes are well known (Lambrechts *et al*. 2004; Blondel *et al*. 1991, 2006; Arriero *et al.* 2006; Wilkin *et al* 2009a; Maziarz *et al*. 2015; Shutt *et al.* 2019), providing a useful context and valuable tempo-spatial comparison from which the impacts of human-mediated environmental change can be inferred and evaluated (Newbold *et al.* 2015; Corsini *et al.* 2017). Aligned with this, tits are highly sensitive to fine-scale anthropogenic disturbance including the environmental and biotic impacts associated with both urbanisation (Ortega-Álvarez and MacGregor-Fors 2009; Atiénzar *et al.* 2010; Hinks *et al.* 2015; Bueno-Enciso *et al*. 2016) and climate change (Sæther *et al*. 2003; Visser *et al*. 1998, 2003; Leech and Crick 2007; Bordjan and Tome 2014). Moreover, because of their higher trophic position in the tri-trophic tree-caterpillar-Blue Tit system (see section 1.3.1.4), they play an important role in forest-based food webs (Dekeukeleire *et al.* 2019a,b). Finally, as common, conspicuous and mobile species that readily breed in nestboxes, breeding parameters can be closely monitored with little difficulty and with minimal risk to the health and wellbeing of the birds (Camacho-Cervantes *et al*. 2018; Dekeukeleire *et al*., 2019a; Jarrett *et al*. 2020). Altogether, therefore, they are considered reliable bio-indicators (Crick 2004; Markowski *et al*. 2014; Camacho-Cervantes *et al*. 2018), whose comprehensive study can be used to help guide urban landscape planning and management (Amininasab *et al*. 2016a) and contribute to furthering our knowledge of the future impacts of climate change on wildlife and the resilience of populations to aid conservation management (Radchuk *et al*. 2019).

1.3.1 The Blue Tit

The Eurasian Blue Tit (hereafter referred to as 'Blue Tit'), the focal species of this study, are small (approximately 10 g), hole-nesting arboreal insectivores and are easily recognisable by their blue and yellow plumage (Fig 1.1) (Perrins, 1979, 1991).

Figure 1.1. A female Blue Tit sitting tight on her nest incubating eggs in a nestbox located at one of the sites in Birmingham, UK. (Photo: the author).

1.3.1.1. Distribution and habitat preferences

Typically a non-migratory species, the Blue Tit (and its related hybrids) is widely distributed and considered a native species across much of temperate, Mediterranean and subarctic regions of Europe and parts of the Middle and Near East and North-west Africa (Fig. 1.2) (Perrins 1979, 1991; Gosler *et al*. 2020; British Trust for Ornithology 2023). It is a common breeder in Great Britain with approximately 3.4 million summer territories (Woodward *et al*. 2020) and is currently listed as being of least conservation concern (Stanbury *et al*. 2021).

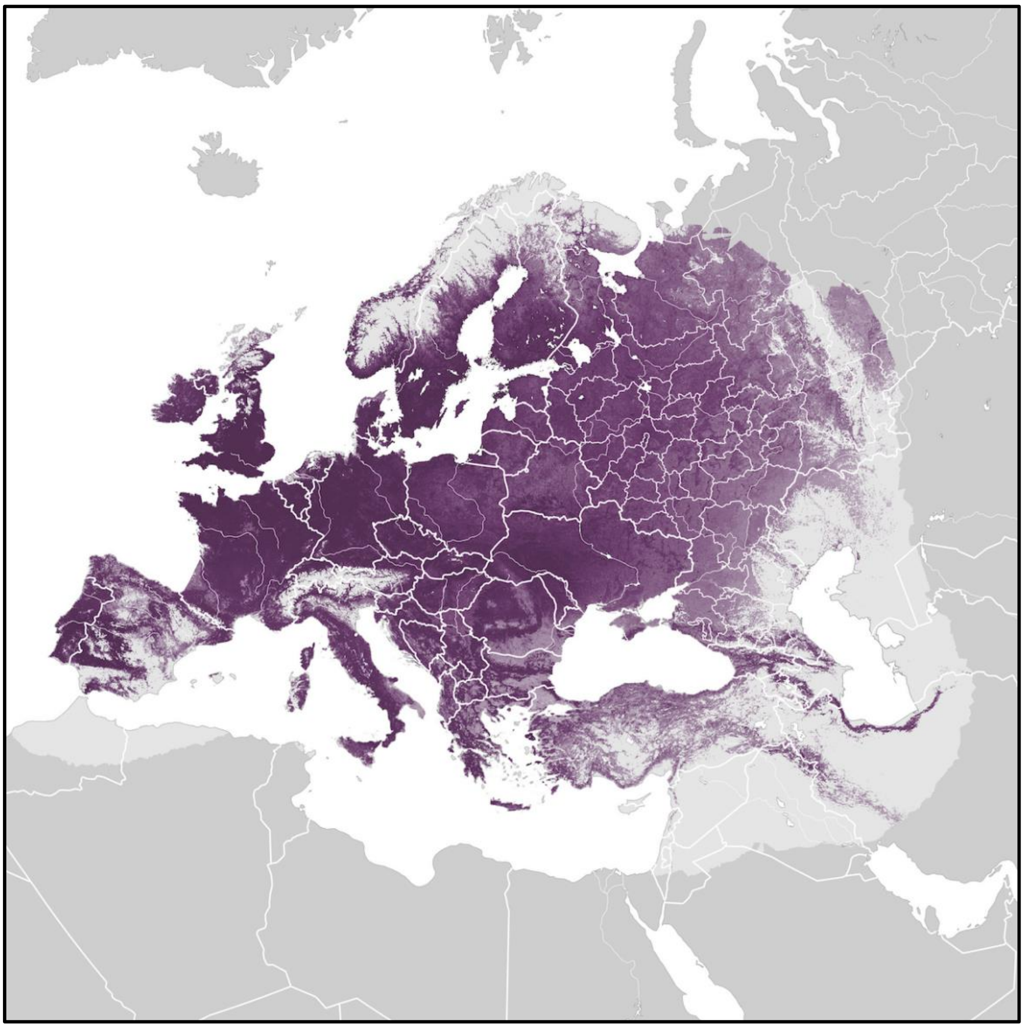


Figure 1.2. The estimated relative abundance of Blue Tit (*Cyanistes caeruleus*) populations across the UK and the rest of their range for 2021. Abundance was estimated as an average for the whole year (i.e. 52 weeks) from individual count data (2007 – 2021) collected as part of seasonal surveys and submitted to eBird. Darker colours indicate higher relative abundance. (Fink *et al*. 2022). Available from: https://doi.org/10.2173/ebirdst.2021 (accessed 28/02/2023).

Although their optimal breeding habitat is mature oak woodland (Perrins 1979; Stenning 2018), across their range Blue Tits commonly occupy a wide variety of lower quality, secondary habitats, including mixed forest (e.g. Blondel *et al*. 1993; Hinsley 2000; Tremblay *et al*. 2003; Lambrechts *et al*. 2004), farmland (Redhead *et al*. 2013) and urban green spaces (Mackenzie *et al*. 2014; Glądalski *et al*. 2016b; 2017). Significantly, they are one of very few

European passerine species that appear to have readily adapted to city-living and regularly breed in urbanised landscapes (Bańbura and Bańbura 2012; Reynolds *et al*. 2019).

1.3.1.2. Stages and phenology of the breeding season

The Blue Tit breeding season (Fig. 1.3) varies considerably depending on location (namely elevation and latitude) and by year (variation in weather conditions for example) but typically runs from the beginning of April to mid-June in the UK (Perrins 1979; Stenning 2018). In the period leading up to egg laying pairs prospect for potential nesting sites, typically in tree cavities, nestboxes and small cavities in manmade structures and buildings (Perrins 1979). In England first clutches are typically laid in mid to late April (mean = 26th April, range = 12th April – 11th May) (Joys and Crick 2004). The female lays one egg per day usually in the early morning, around 0600 hours (Perrins 1979). Blue Tits have one of the largest clutch sizes of any avian species: females nesting in optimal habitat (mature oak-dominated woodland) on average lay a clutch of 11 eggs (range 7-16 eggs), Dhondt 1989; Dhondt *et al.* 1992; Kempenaers *et al.* 1998). However, females may be constrained from laying such large clutches due to intrinsic factors such as their age, physiological condition or foraging ability, or due to extrinsic factors (i.e. pre-laying conditions including weather, habitat quality and the availability of food resources) (Chamberlain *et al.* 2009; Seress and Liker 2015; Seress *et al.* 2018).

The lead up to full incubation is a gradual process and once begun, females have limited options to delay or accelerate the breeding process (Naef-Daenzer and Keller 1999; Stenning, 2018). Females generally initiate full incubation around the time the ultimate or penultimate egg is laid thus maximising the chances that most of the young will hatch within a short period (Perrins 1979, Cooper *et al*. 2005). Although the total period of incubation varies depending on the females incubation rhythm, it normally lasts 13 – 15 days (BTO 2023).

Like most altricial species Blue Tit broods hatch to some extent asynchronously (Clark and Wilson 1981). However the degree of asynchrony varies, with some broods hatching within one day, whilst others hatch over a period of two to three days (Cramp and Perrins 1993; Stenning 2008; Mainwaring and Hartley 2016). During the first few days after hatching nestlings are poikilothermic (unable to maintain their own body temperature) and therefore require considerable amounts of parental care including intermittent brooding by the female for heat (Hohtola and Visser 1998; Visser 1998; Andreasson *et al*. 2016). At approximately one week post-hatch they begin to grow a covering of feathers and are gradually able to regulate their own body temperature (Perrins 1979; Stenning 2018). Nestlings are therefore very vulnerable and sensitive to environmental conditions, particularly during their first week of life. During prolonged periods of cold or rainy weather the female will remain on the nest, leaving the male responsible for collecting food for both adults and the brood. This can result in young suffering a shortage of food and ultimately the partial or total loss of the brood (Perrins 1979). As such periods of cold or bad weather, can have a significant and detrimental impact on the growth and survival of young, especially in environments with already low availability or poor quality food. Once nestlings are approximately half-way grown they require less brooding and the female can focus more of her time and energy on feeding them (Mainwaring and Hartley 2016; Stenning 2018). Nestlings fledge at approximately 18 – 20 days post hatch and usually all leave the nest within the same day (Perrins 1979; Stenning 2018). Many newly fledged Blue Tits are weak fliers, particularly if hatching within the brood was asynchronous (meaning later hatched nestlings are less well-developed on leaving the nest) (Stenning, 2018).

a) 1st egg laid mid to late April (as early as 1st April and as late as mid-June in Birmingham). 1 egg laid per day. Female covers eggs when she leaves the nest to keep concealed from predators & maintain temperature.

b) Average complete clutch size = 8 – 10 eggs (range 1 – 18 eggs in Birmingham). Each egg weighs 1g.

c) Female initiates full, consistent incubation after laying the penultimate or final egg. Incubation = 13 – 15 days.

d) Day 0: Majority of brood hatch within 1 day (any remaining eggs hatch within 2-3 days). Nestlings hatch naked & blind except for tufts of light 'hair' on their heads & are altricial & poikilothermic. During the first few days, females spend most of their time brooding young whilst males forage for food.

e) Day 3-4: Nestlings have a wide gape & stretch upwards to reach higher during begging contests. Larger nestlings, therefore, have a developmental advantage & receive more food. Each chick eats ~100 caterpillars a day. Feather development begins with appearance of dark lines on wings, head & back where feathers will grow.

f) Day 6-7: Feathers continue to develop. Earlier hatched nestlings remain larger than later hatched nestlings throughout the growth phase (e.g. here we see 1 runt that likely hatched a day later than its siblings). Daily weight gain increases to 1g by day 5 (inflection point).

g) Days 8–10: Eyes opening. Feathers continue to develop. Peak nestling demand for food (approx. 23-25 days after clutch completion). Nests are ideally timed if broods are 10-18 days old when caterpillars reach maximum size but have not left trees to pupate.

h) Day 15: Nestlings reach asymptotic (maximum) body weight by day 15. (chicks with heavier hatching weights reach their maximum weight faster). Mean body mass ~10-11g. Eyes fully open & feathers almost fully developed.

i) Days 18 - 21: Nestlings fledge as early as 18 days post-hatch. Parents continue to feed juveniles for the first couple of weeks. Later hatched chicks are less well-developed & unable to fly well and so are more susceptible to predators. Nestlings unable to fledge are left behind in the nest to perish.

Figure 1.3. Description of the key stages (including phenological timing and duration) in a typical Blue Tit (*Cyanistes caeruleus*) breeding season. Note that in this research the reproductive cycle refers to the period between laying and fledging during which comprehensive breeding data were collected from nestboxes. As such pre-laying (prospecting and nest building phases) and post-fledging (juvenile survival and recruitment) are not included here. Further detail on the reproductive cycle and its phenology can be found in the following sources from which the information in the figure was obtained: Gibb (1950,

1954); Perrins (1965, 1979,1991); Van Balen (1973); Blondel *et al*. (1991, 1993); Naef-Daenzer and Keller (1999); Tremblay *et al*. (2003, 2005); Mainwaring *et al*. (2010, 2011); Mainwaring and Hartley (2016); Morganti *et al*. (2017). (Photos: the author).

1.3.1.3. Breeding success

Under optimal conditions and in the absence of predation events, breeding success in Blue Tits tends to be very high, with 90-95% of eggs successfully hatching and the majority of nestlings that do hatch going on to fledge (Perrins 1979). Conversely, juvenile survival rates of Blue Tits within the first year are very low (estimated to range from 10 to 40%), with particularly high rates of mortality during the first winter (Perrins 1979; Nur 1984; Stenning 2018). Therefore few nestlings recruit into the breeding population the following year. For those Blue Tits that do make it through the first year, life expectancy is on average two to three years (Lack 1954). Average mortality rates for adult British Blue Tits (after their first breeding season) is approximately 50 to 72% (e.g. Snow 1956; Hildén 1982; Pampus *et al*. 2005).

1.3.1.4. Diet, food provisioning and the tri-trophic food web

Blue Tits are generalist insectivores, with a diet that consists of a broad range of invertebrate taxa and seeds (Betts 1955; Perrins 1979). However, supplementary foods (e.g. seeds, peanuts, fatballs and mealworms) from garden bird feeders have also make up a large proportion of the Blue Tit diet, particularly during the winter and in the lead up to the breeding season when the movement of pairs is not so constricted to breeding territories (e.g. see Shutt *et al*. 2021).

Blue Tits are almost exclusively insectivorous during the breeding season (Bańbura and Bańbura 2012) and large broods require a steady and plentiful supply of food (Perrins 1991). Caterpillars such as the Winter Moth (*Operophtera brumata*) and Oak Leaf Roller (*Tortrix* *viridana*) are a particularly rich source of proteins and nutrients, as well as being easily ingestible, and thus are a valuable, high quality food resource for provisioning nestlings (van Balen 1973; Blondel *et al*. 1991; Perrins 1991; Bańbura *et al*. 1994; Kaliński *et al*. 2009). However, caterpillars are only available during a very narrow phenological window when they exploit the newly emerged leaves of host deciduous trees, predominantly Oak (Quercus) species (Southwood *et al*. 2004; Marciniak *et al*. 2007; Kaliński *et al*. 2009). The availability of caterpillars (and other arthropod prey) is therefore largely dependent on bud burst date, which in turn varies yearly depending on local environmental conditions including spring temperature (e.g. Hunter and Lechowicz 1992; Buse *et al*. 1999; Nilsson and Källander 2006) as well as across different tree species (e.g. Blondel *et al*. 1993; Wesołowski and Rowiński 2006) and individual trees (Crawley and Akhteruzzaman 1988; Van Dongen *et al*. 1997; Hinks *et al*. 2015). This tri-trophic (deciduous tree – caterpillar – tit) food chain is a classic example of a seasonal ecological system (Perrins 1991; Visser *et al*. 1998; Buse *et al*. 1999), the phenology of which has been well studied at both the individual and population level (Visser and Both 2005; Visser *et al*. 2006; Hinks *et al*. 2015; Burgess *et al*. 2018).

Parents are therefore, heavily dependent on synchronising the peak energy demands of chicks (ages 10-11 days old; Perrins *et al*. 1965; van Balen 1975; Perrins 1991) with the transient spring peak in arboreal caterpillar productivity (Naef-Daenzer and Keller 1999; Tremblay *et al*. 2003). During this period of peak food demand, Blue and Great Tits may bring caterpillars to the nest at a rate of one per minute, with over 700 food items potentially delivered within a 16 hour foraging day (Gibb 1955; Perrins 1991).

Breeding timing in passerine song bird species such as Blue Tits is therefore under strong selection pressure (Visser and Both 2005; Hinks *et al*. 2015). First egg dates are on average approximately one month earlier than the peak in caterpillar availability in the UK (Burgess *et al*. 2018; Shutt *et al*. 2019), thus meaning pairs make decisions on when to begin breeding well in advance of the peak in nestling food demand (Visser *et al*. 1998; Cresswell and McCleery 2003; Hinks *et al*. 2015). Photoperiod is a fundamental cue for initiating reproductive phenology in insectivorous passerine species, (Murton and Westwood 1977; Wingfield and Farner 1980; Lambrechts *et al*. 1997; Dawson 2001), with other environmental cues including spring temperature (e.g. Caro *et al.* 2007; Charmantier *et al*. 2008; Visser *et al.* 2006, 2011; Schaper *et al*. 2012) and budburst phenology (e.g. Nilsson and Källander 2006; Hinks *et al.* 2015; Shutt *et al*. 2019) used to further refine the exact timing of breeding within each season.

The abundance and seasonal variation in caterpillar availability is therefore a key determinant of the trophic quality of the breeding habitat (Riddington and Gosler 1995; Tremblay *et al.* 2003) and can impact reproductive timing, early nutritional conditions for chicks, breeding performance and fitness (Marciniak et *al*. 2007; Amininasab *et al.* 2016a; Shutt *et al*. 2018).

1.4. STUDY AIMS AND OBJECTIVES

To address the knowledge gaps identified, this research utilises two distinct approaches to investigate how fine-scale variation in environmental conditions (i.e. urbanisation and weather) impact on breeding success in a population of birds living in a major city in the UK. Firstly, I used a nested (hierarchical) design, utilising study sites with *a priori* quantified degrees of urbanisation (i.e. urban density measured as the percentage of built landcover in the urban matrix within a 500m buffer of the centre of each site). Blue Tit breeding data were collected from a network of thirty one sites (each containing 10 nestboxes) strategically placed across a fine-scale, short, intra-city urban gradient in the city of Birmingham, UK. Sites encompassed a variety of greenspace forms, typically found in towns and cities, including remnant woodlands, parkland, amenity grasslands, cemeteries, canals and roadside verges. Using this free-living population as a case study, the primary aim of this thesis was to explore how environmental variation (at both the habitat and landscape scale) across a short, highly urbanised intra-city gradient impacts on different parameters of reproductive success during distinct phases of the breeding cycle.

Secondly, more recent advances in the statistical analyses of potential climate effects have enabled a more thorough and methodical approach to investigating the impacts of variation in temperature, rainfall and other weather variables in ecological studies (including on aspects of life history such as reproductive timing and breeding success in wildlife) both across complex environmental gradients (e.g. latitude, elevation and urbanisation) and within more biologically meaningful timeframes (Marques-Santos and Dingemanse 2020). Aligned with this, using the ‘critical time window approach’ (van de Pol *et al*. 2016), the second main aim of my thesis was to investigate how short-term variation in weather (namely temperature and precipitation) in the period immediately leading up to nesting and during the breeding season influence rates of hatching success, brood reduction and fledging success as well as individual nestling mass and survival.

More specifically the key objectives of my research were to:

1) Analyse variation in parameters of breeding occupancy and success during the pre-hatching (laying – hatching) and post-hatching (or brood rearing: hatching – fledging) phases of the reproductive cycle, using six years (2013 – 2018) of data collected from nestbox plots

and determine how data correlate with other pertinent biological and temporal variables (e.g. clutch size, brood size and laying date).

2) Identify the key habitat (site – level) and landscape-scale factors driving variation in breeding outcomes across the urban gradient and determine if the strength and direction of these effects vary across different phases of the reproductive cycle.

3) Ascertain if a particular phase of the reproductive cycle is more sensitive to environmental change and potentially driving overall reduced breeding success in the Blue Tit population.

4) Use critical time window analyses to explore the influence of variation in both temperature and rainfall across the urban gradient on a selection of breeding responses identified as key drivers in determining breeding success in this population.

5) Identify the key time periods and associated climate signals (i.e. the weather variable, statistic and relationship) that drive observed variation in breeding traits at the citywide scale and determine the reproductive stage when breeding birds appear most sensitive to changes in temperature and rainfall.

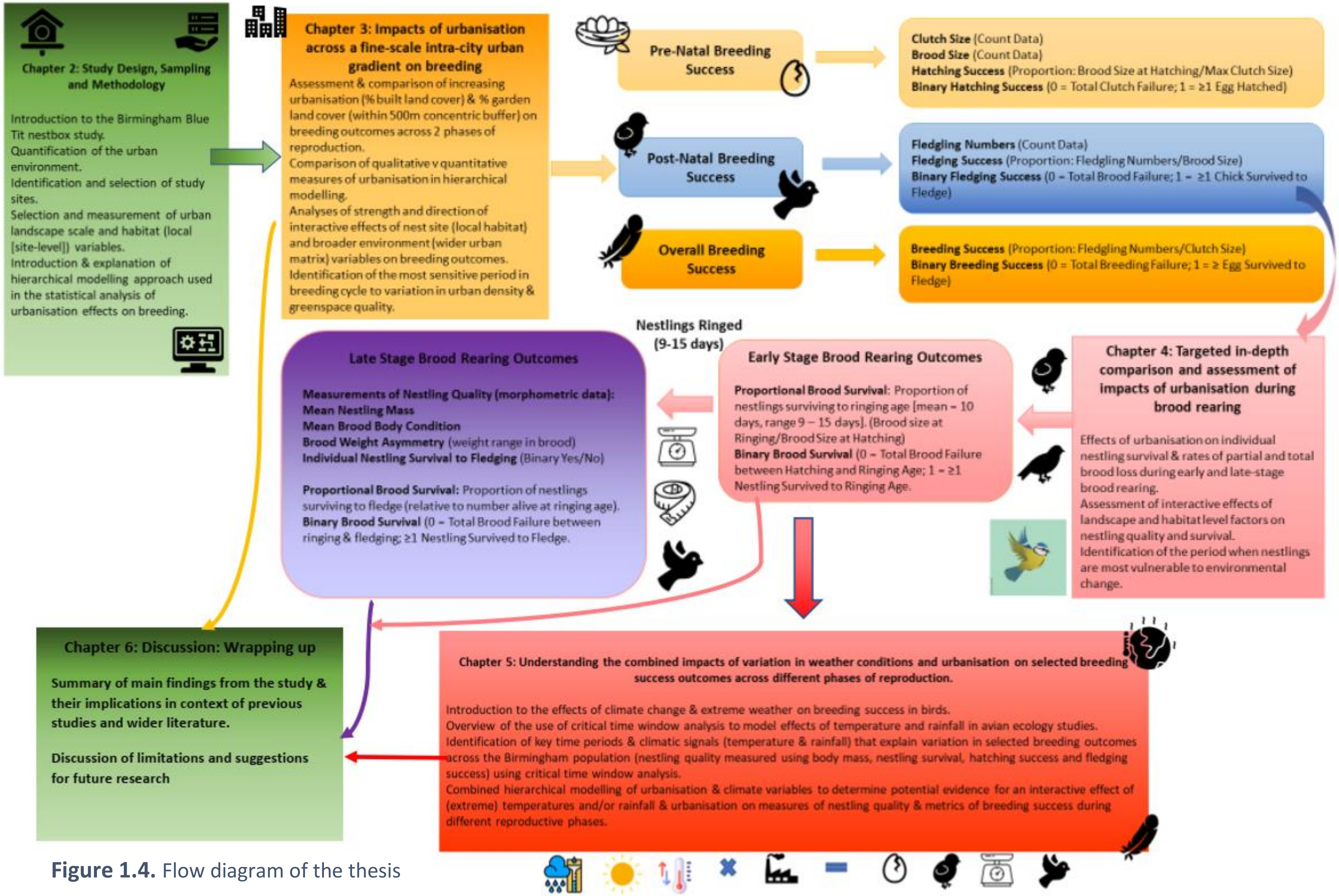
6) Investigate the potential for interactive effects between the urban gradient and variation in weather on breeding traits.

7) Determine the potential effects of current fluctuations and variation in temperature at the site-level on nestling mass.

Specific research hypotheses are specified within the relevant chapters but sit within the broader aims listed above.

1.5 THESIS STRUCTURE

The structure of the thesis is described below and is also visualised in the flow diagram (Fig. 1.4). In **Chapter Two** I provide a detailed explanation of the study design, field work, background biological information on the Blue Tit and the analytical methodology used to address the aims and objectives of Chapters 3 and 4 (pertaining to the effects of urbanisation on breeding). In **Chapter Three** I investigate how fine-scale variation in the characteristics of the urban environment at both the habitat- and landscape-scale influence the reproductive performance of birds nesting across the intra-city gradient of Birmingham using a systematic hierarchical modelling design. A comprehensive suite of breeding traits commonly studied in urban avian research are analysed to understand how the specification of the urban gradient, using a comparison of a qualitative (categorical) versus quantitative (linear) metric affects the sensitivity of models to predict the effects of urbanisation. The hierarchical modelling approach is simultaneously used to quantify and explore how the strength and direction of potential habitat- and landscape-scale correlational effects vary across the breeding season and if there is evidence for an interactive effect between variables across the two spatial scales investigated. Finally, I assess if particular breeding traits or phases of reproduction are potentially more sensitive to the environmental changes associated with urbanisation and may be driving lower reproductive success, as observed in other populations of city-dwelling birds. In **Chapter Four** I explore how variation in environmental characteristics across the urban gradient impact nestling quality and survival during the critical brood rearing phase. Rates of brood reduction and total brood loss across the intra-city urban gradient are analysed and compared for the early (0 – approximately 10 days) and late (approximately 10 – 20 days i.e. fledging) nestling developmental stages to understand the habitat and landscape scale factors driving breeding failure and to determine the period when chicks are most at risk of dying. Nestling mass, body condition and brood asymmetry are analysed to examine how nestling quality varies across the urban gradient and if there is evidence for covariation with nestling survival that may be linked to food availability and/or a brood reduction strategy. In **Chapter Five** I introduce how the recent advent of critical climatic time window analyses are currently being used to more reliably model and assess the influence of weather variables (including temperature and precipitation) on various aspects of avian ecology including measures of breeding success. Here I explore using the critical time window approach, how fine-scale temporal variation in temperature and rainfall at both the city- and site-scale impacts on response variables that were found in previous chapters to be potentially important drivers of reduced breeding success in the city. This information is used to estimate potential timeframes (either prior to or during breeding) when birds are likely most sensitive to variation in weather and the weather signals that have the strongest correlational effect on breeding success. Finally I explore the potential for an interactive effect between urbanisation and climate on breeding traits and discuss the potential implications for future reproductive success and long-term population stability in birds experiencing the ongoing multiple stresses of climate change in an increasingly urbanising world. Finally in **Chapter Six** I present a general discussion of the findings of this study and their implications within the wider context of avian urban and climate change research. I discuss how the results from this and other studies can help guide policy makers in the future planning, design and management of urban greenspace for the benefit of both wildlife and people. I also consider the potential limitations of the current study and propose a number of different avenues for future research that could help further elucidate the various factors and mechanisms driving reduced breeding success in urban areas and as a consequence of climate change.



Chapter 2: Study Design, Sampling and Methodology

Introduction to the Birmingham Blue Tit nestbox study.
Quantification of the urban environment.
Identification and selection of study sites.
Selection and measurement of urban landscape scale and habitat (local [site-level]) variables.
Introduction & explanation of hierarchical modelling approach used in the statistical analysis of urbanisation effects on breeding.

Chapter 3: Impacts of urbanisation across a fine-scale intra-city urban gradient on breeding

Assessment & comparison of increasing urbanisation (% built land cover) & % garden land cover (within 500m concentric buffer) on breeding outcomes across 2 phases of reproduction.
Comparison of qualitative v quantitative measures of urbanisation in hierarchical modelling.
Analyses of strength and direction of interactive effects of nest site (local habitat) and broader environment (wider urban matrix) variables on breeding outcomes.
Identification of the most sensitive period in breeding cycle to variation in urban density & greenspace quality.

Pre-Natal Breeding Success

Clutch Size (Count Data)
Brood Size (Count Data)
Hatching Success (Proportion: Brood Size at Hatching/Max Clutch Size)
Binary Hatching Success (0 = Total Clutch Failure; 1 = ≥1 Egg Hatched)

Post-Natal Breeding Success

Fledgling Numbers (Count Data)
Fledging Success (Proportion: Fledgling Numbers/Brood Size)
Binary Fledging Success (0 – Total Brood Failure; 1 – ≥1 Chick Survived to Fledge)

Overall Breeding Success

Breeding Success (Proportion: Fledgling Numbers/Clutch Size)
Binary Breeding Success (0 = Total Breeding Failure; 1 = ≥ Egg Survived to Fledge)

Chapter 4: Targeted in-depth comparison and assessment of impacts of urbanisation during brood rearing

Effects of urbanisation on individual nestling survival & rates of partial and total brood loss during early and late-stage brood rearing.
Assessment of interactive effects of landscape and habitat level factors on nestling quality and survival.
Identification of the period when nestlings are most vulnerable to environmental change.

Early Stage Brood Rearing Outcomes

Proportional Brood Survival: Proportion of nestlings surviving to ringing age [mean – 10 days, range 9 – 15 days]. (Brood size at Ringing/Brood Size at Hatching)
Binary Brood Survival (0 – Total Brood Failure between Hatching and Ringing Age; 1 – ≥1 Nestling Survived to Ringing Age.

Nestlings Ringed
(9-15 days)

Late Stage Brood Rearing Outcomes

Measurements of Nestling Quality (morphometric data):
Mean Nestling Mass
Mean Brood Body Condition
Brood Weight Asymmetry (weight range in brood)
Individual Nestling Survival to Fledging (Binary Yes/No)

Proportional Brood Survival: Proportion of nestlings surviving to fledge (relative to number alive at ringing age).
Binary Brood Survival (0 – Total Brood Failure between ringing & fledging; ≥1 Nestling Survived to Fledge.

Chapter 6: Discussion: Wrapping up

Summary of main findings from the study & their implications in context of previous studies and wider literature.

Discussion of limitations and suggestions for future research

Chapter 5: Understanding the combined impacts of variation in weather conditions and urbanisation on selected breeding success outcomes across different phases of reproduction.

Introduction to the effects of climate change & extreme weather on breeding success in birds.
Overview of the use of critical time window analysis to model effects of temperature and rainfall in avian ecology studies.
Identification of key time periods & climatic signals (temperature & rainfall) that explain variation in selected breeding outcomes across the Birmingham population (nestling quality measured using body mass, nestling survival, hatching success and fledging success) using critical time window analysis.
Combined hierarchical modelling of urbanisation & climate variables to determine potential evidence for an interactive effect of (extreme) temperatures and/or rainfall & urbanisation on measures of nestling quality & metrics of breeding success during different reproductive phases.

Figure 1.4. Flow diagram of the thesis

Chapter Two

Study design, sampling and methodology

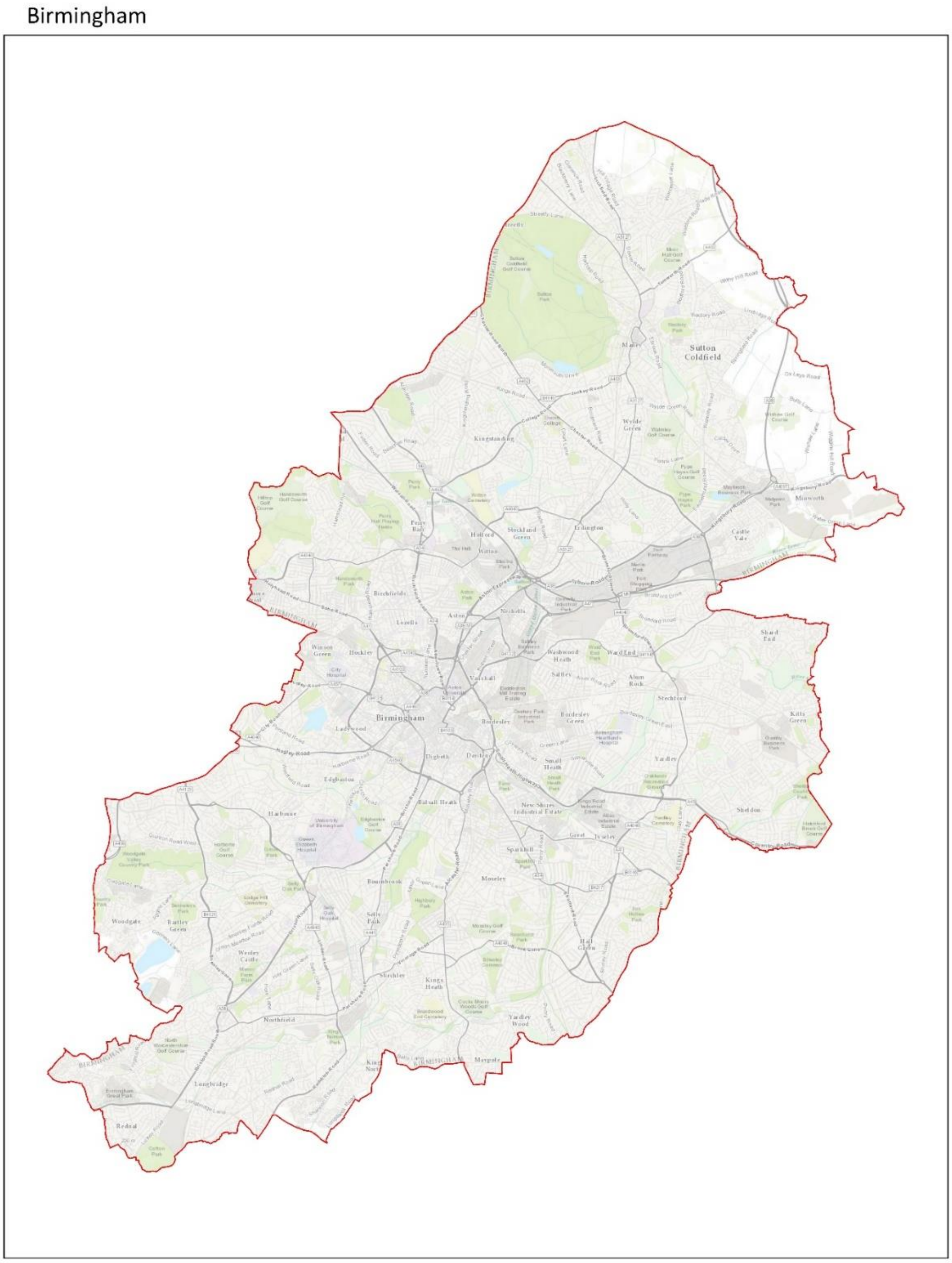
2.1. AIMS OF THE CHAPTER

This chapter lays the groundwork for the thesis by introducing and describing the key components of the Birmingham Blue Tit nestbox study and individual steps comprising the main study design and analysis as follows:

- background to Birmingham, the focal city for this project;
- initial quantification of the urban environment, and identification and selection of study sites;
- selection of urban landscape and site-level (habitat) covariates;
- outline of fieldwork and data collection; and
- an overview of the statistical modelling approach used in the analysis of breeding metrics.

2.2. STUDY AREA AND SITE SELECTION

2.2.1. Study area



Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 2.1. Map of the wider metropolitan Birmingham region showing areas of dense urbanisation, including the core of the city centre (shown in grey), and major parks and greenspaces (in green). (Source: Ordnance Survey and OpenStreetMap, 2022).

Birmingham, the focal city for this project (Fig. 2.1) is the UK's second city in both demographic and economic terms (Coulson and Ferrario 2007) and together with the wider region of the West Midlands is considered the traditional manufacturing heart of the UK (Coulson and Ferrario, 2007).

As the centre of the Industrial Revolution (Chinn and Dick 2016) and one of the UK's youngest, most ethnically diverse cities, it has a rich history of manufacturing, engineering, industrialisation, migration and development (McEwan *et al.* 2005; Abbas 2006; Barber and Hall 2008). Since the Industrial Revolution the city has undergone repeated cycles of industrial loss and decline, as well as periods of recovery, redevelopment and regeneration, resulting in distinct regions of pre- and post-war rejuvenation (McEwan *et al.* 2005; Coulson and Ferrario 2007; Barber and Hall 2008). Birmingham is currently undergoing another phase of extensive economic investment, regeneration and development and population growth (e.g. Barber and Hall 2008; Lombardi *et al.* 2011; van Meerkerk *et al*. 2013; Thorpe 2017). In 2021 the estimated population was 1,144,900, representing an increase of 6.7% from the last census conducted in 2011, when just over 1 million people were recorded (Birmingham City Council 2022; Office for National Statistics 2022).

In terms of grey space, the study area of the wider Birmingham metropolitan area (total area 598 km^2 (231.2 square miles) is characterised by a mix of different urban land uses and landcover of variable extents and densities including: sealed landcover (e.g. roads and pavements), canals, railways, motorways, residential areas, industrial zones and commercial parks (Hale *et al.* 2012).

Greenspace in the city is diverse in terms of the size, connectivity, structure and composition of patches. Habitat patches range from large highly managed parkland to small remnants of natural habitat, and from small grass verges, urban parks, allotments and gardens to heathland, woodlands, recreation grounds and nature reserves. This includes Sutton Park to the north of the city which at 2,400 acres (approx. 1,000 ha) in coverage is the UK's first Urban National Nature Reserve and Europe's largest urban park (source: https://www.birmingham.gov.uk). Altogether, Birmingham supports an extensive, albeit unevenly distributed, tree population, covering 23% of the city as well as 93 parks, 242 play areas, and 18 golf courses.

The city also has one of the most extensive and intricate canal networks in the world (with over 35 miles in total within the city itself) which were mainly built in the 1700s and 1800s and used intensively to transport goods for over 170 years. The use of the canal system for commercial traffic discontinued in the 1980s and the canals fell into disrepair. However, more recently many of them have been restored and improved to provide parkland, housing and other modern developments (source: https://canalrivertrust.org.uk/).

In total, there are > 3,500 ha of publicly accessible space including a network of over 400 km (> 250 miles) of streams brooks and canals. As of 2013 Birmingham was recognised as Britain's first Biophillic city (source: https://www.biophiliccities.org) and in 2017 was designated as one of the greenest cities in the country with 24.6% of the urban landscape devoted to greenspace (Table 2.1 source: ESRI UK, 2017).

Table 2.1. The UK's top-10 greenest cities ordered by the percentage of green landcover. Birmingham (ranked fourth) is highlighted in bold. (Source: ESRI UK 2017).

Ranking	City	Percentage greenspace (%)
1	Edinburgh	49.2
2	Glasgow	32.0
3	Bristol	29.0
4	**Birmingham**	**24.6**
5	Greater London	23.0
6	Sheffield	22.1
7	Leeds	21.7
8	Manchester	20.4
9	Bradford	18.4
10	Liverpool	16.4%

The University of Birmingham has been actively conducting urban ecology research in the wider Birmingham metropolitan area for over a decade, covering a wide variety of research areas including: urban land classification (Owen *et al.* 2006); biodiversity in urban habitat patches (including plants, carabid beetles, butterflies and mammals) (Angold *et al.* 2006); the impacts of urbanisation on the presence and activity of bats (Hale *et al.* 2012, 2015); bird species' abundance and diversity (Rosenfeld 2012), and the breeding ecology of Blue Tits (*Cyanistes caeruleus*) (Reynolds *et al.* 2016). These credentials, particularly the rapid and extensive ongoing development of the city, the balance of numerous green initiatives and its comparability in size to other European cities continue to make Birmingham an excellent and relevant site for urban ecology work.

2.2.2. Intra-city site selection

The Birmingham Blue Tit urban ecology project was initiated in the spring of 2013, with the initial project set-up, site selection and first three years of breeding data collection undertaken by former student Dan Hunt in conjunction with Professor Jon Sadler and Dr Jim

Reynolds. I joined the project in the autumn of 2015 and managed/conducted the collection of breeding data during the subsequent three breeding seasons (2016 – 2018). I was also responsible for the planning and collection of site level temperature data (2017-2018) and the weather data obtained from external sources for all years. All of the statistical analyses and the associated results described within each chapter were developed and conducted by myself using all six years of data. This is the first time the data from this project has been analysed.

The study design and methods employed during this project were developed from previous urban ecology research by Owen *et al*. (2006), Hale *et al*. (2012) and Rosenfeld (2012), who quantified landscape quality, composition and structure across the city using an urban gradient approach. Similarly to the previous studies undertaken, the current study considers solely on the urban gradient from the perspective of the degree of grey (built) and green landcover, whilst also considering additional covariates, specifically landscape connectivity and area of greenspace, to create a matrix for sample site selection.

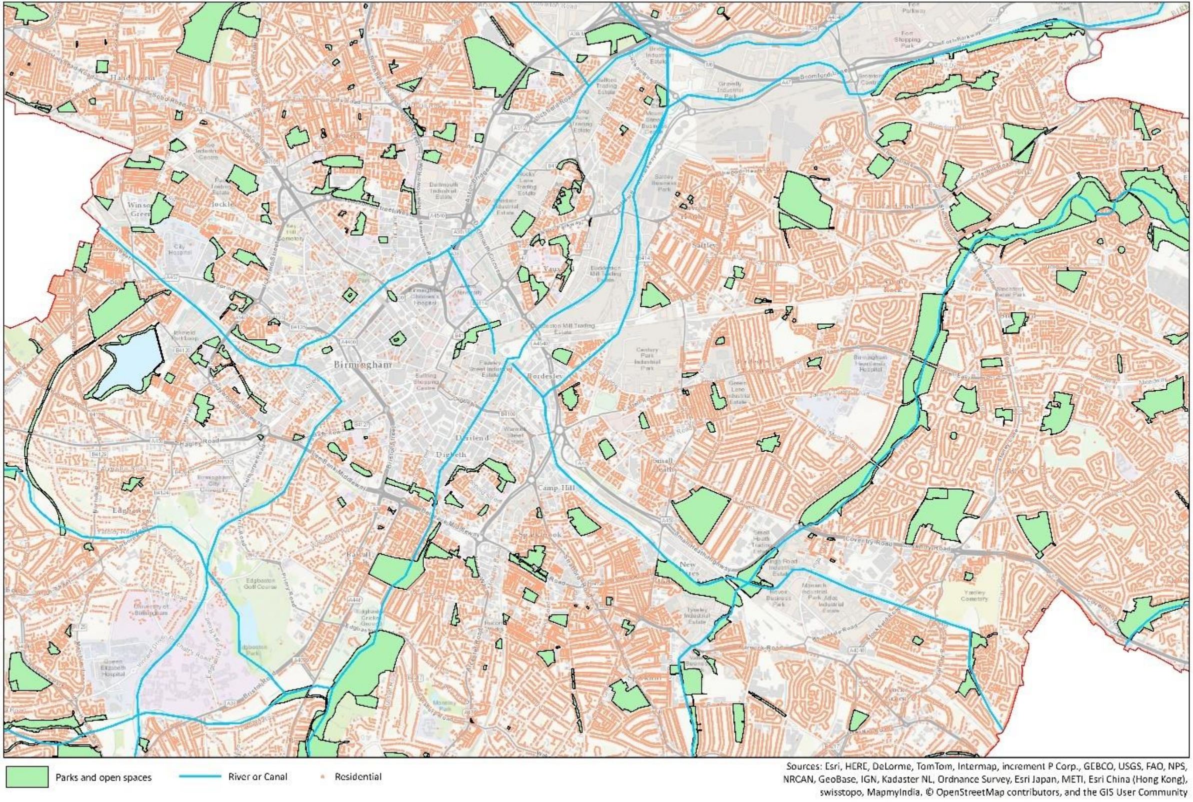
The site selection process involved two linked steps, using 1-km squares within the city boundary. First, digital data were used to create a synoptic urban gradient classification within the city. This dataset was then used to identify potential greenspace sites for demographic survey work. Secondly, remote sensing data derived from aerial photogrammetry were used to quantify variability in greenspace connectivity across the same gradient. Each step is described below.

2.2.2.1. Land-use and land-cover data extraction

OS Mastermap polygon data were converted to a 2-m resolution raster (Hale *et al.* 2012) and displayed in a GIS (ArcGIS 9.2, ESRI Redlands, USA) for this purpose. Values were assigned to differentiate between different types of land-use and aggregated into one of several different urban land-cover classes (e.g. ‘urban’, ‘motorway’) by Owen *et al.* (2006). From these, a set of two land-use and land-cover variables (LULC) – (i) built land-cover parcels (sealed surface) and (ii) greenspace (vegetated land-cover parcels) – were selected that provided a broad metric of urbanisation and that are known to be linked with the habitat and food resource requirements of Blue Tits during egg laying and incubation (e.g. Perrins 1979; Wilkin *et al.* 2007a; Plummer *et al.* 2013a; Amininasab *et al.* 2016a; Bailly *et al.* 2016; Vaugoyeau *et al.* 2016; Shutt *et al.* 2018; Reynolds *et al.* 2019*)* and brood rearing (e.g. Cowie and Hinsley 1988; Perrins 1991; Hinsley *et al.* 1999, 2002, 2008; Tremblay *et al.* 2003, 2005; Marciniak *et al.* 2007; Wilkin *et al*. 2009a; Sprau *et al.* 2017; Sepp *et al*. 2018; Dekeukeleire *et al*. 2019b): the two critical breeding periods investigated throughout my research.

To create the variable “built” all impervious surfaces including roads, houses, pavements and carparks were aggregated together as a single binary layer using the OS data, following Hale *et al*. (2012). Figure 2.2 provides an example of the output from this mapping process.

Birmingham - parks and open spaces/waterways/residential



Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 2.2. An example of the mapping data derived from the first phase of the land-use and land-cover variable identification and extraction process from OS Mastermap (OSM) (Ordnance Survey Mastermap, 2008) Here, parks and open space, residential areas and waterways including rivers and canals are displayed.

2.2.2.2. Landscape connectivity

Incorporating urban metrics such as measures of habitat connectivity are essential to capture mechanistic links and functional relationships operating between the presence and movement of volant species such as birds (Fernández-Juricic 2000a; Shanahan *et al.* 2011) and bats (Hale *et al.* 2012) within the urban environment. These are often missed or lost when using more traditional singular methods (e.g. proportion or density of green or grey space), as highlighted in Moll *et al.* (2019). As such, a separate remotely sensed vegetation layer and connectivity mask were created to provide an estimation of vegetation cover and, in particular, tree canopy connectivity. A separate raster layer for vegetation coverage (trees) at a 2-m pixel resolution was extracted using a combination of near Infra-Red and photographic data collected in 2007 by Bluesky International Ltd, Leicestershire, UK. Using a Lidar height layer, this tree layer was clipped to only include vegetation of ≥ 3 m in height and converted to a polygon class feature. This lower limit was specified to prevent errors in the dataset attributable, for example, to the misidentification of vegetation on roofs of buildings for trees by the classification algorithm (e.g. as explained by Hale *et al.* 2012). The vegetation layer was buffered (i.e. digitally expanded from the edge of the object) by a distance of 15 m, to create a connectivity mask (Fig. 2.3).

Figure 2.3. An example of the original vegetation layer and connectivity mask. The connectivity mask (light green) was created by expanding the vegetation layer (dark green) 15m in all directions, creating a buffer which incorporated all gaps ≤30m. (Source: Rosenfeld 2012).

Small insectivorous passerines such as tits will use multiple patches within their home ranges for foraging, especially in highly fragmented and heterogenous, food-poor habitats such as urban areas (Hinsley 2000; Creegan and Osborne 2005; Hinsley *et al*. 2008; Snell *et al.* 2020). However, gap crossing (i.e. movement of individuals between patches), incurs costs in terms of fitness, energy and time, as well as in productivity and survival due to the increased risk, for example, of predation (Matthysen and Currie 1996; Desrochers and Hannon 1997; Hinsley 2000; Stauss *et al*. 2005). Therefore, on the balance of the evidence a distance of 30 m was considered a conservative threshold for natural gap-crossing behaviour in passerines such as Blue Tits, whilst providing a robust estimate of the limit of functional connectivity in the urban environment (Bélisle and Desrochers 2002; Bélisle 2005; Desrochers *et al.* 2002; Creegan and Osborne 2005; Rosenfeld 2012). Therefore, the resulting layer, consisting of a contiguous network of trees (within which the maximum distance for gaps separating trees at any point was set at 30 m) was used to quantify the structural connectivity across sites and the surrounding landscape, thus providing a proxy for functional connectivity. This approach, which relied upon the assumption of limited gap crossing behaviour in passerines, provided a more accurate quantification of the habitat and landcover available to breeding Blue Tits (Marrot *et al*. 2017).

As Figure 2.4 demonstrates, at this scale, the tree network in the wider urban area is well connected, with the only significant breaks in cover evident for the dense urban core and Birmingham City airport located to the east of the city. The drop-off in connected tree cover towards the north-east authority boundary indicates the transition to agricultural land.

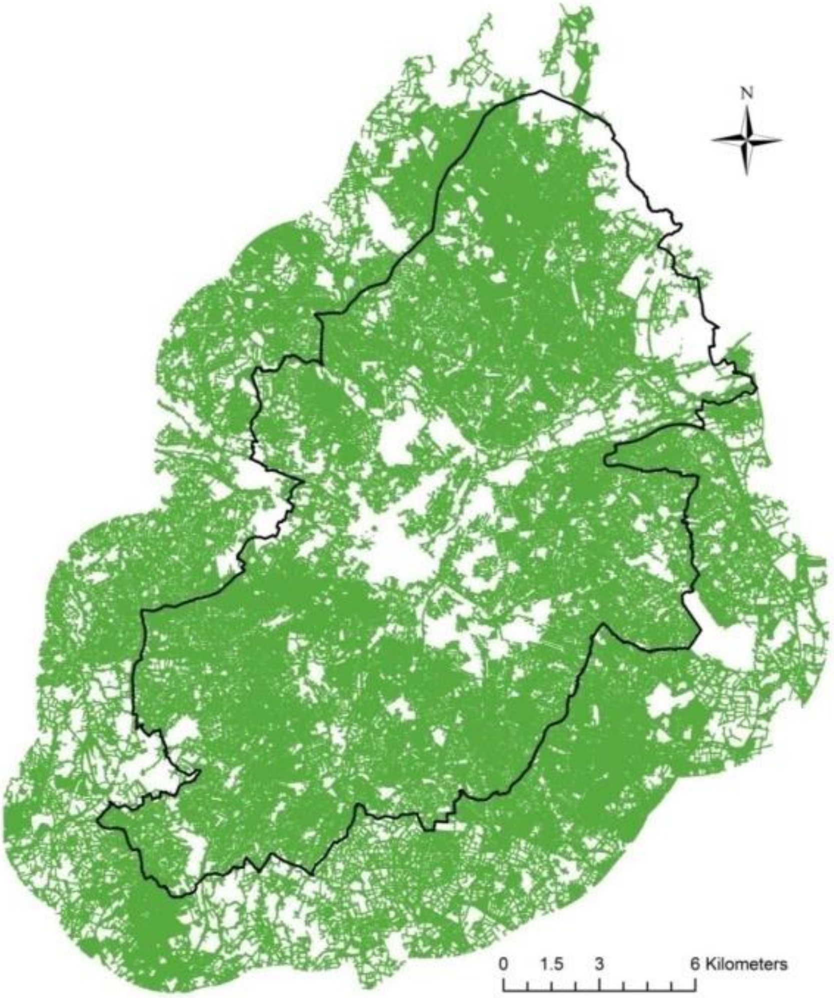


Figure 2.4. Map of landscape connectivity for the Birmingham study area. The tree network is shown in green and the local authority boundary in black. The original vegetation layer was expanded by 15m in either direction to create the connectivity mask. (Source: Rosenfeld 2012).

2.2.2.3. Study site selection

In 2013 the matrix derived from the four land-use and land-cover variables was used in the identification of potential greenspace (sites) for use in this study. This desk-based approach was combined with field visits to ensure that sites were selected that captured the variability in the size and types of greenspace that are commonly found in urbanised regions (including cemeteries, parks, recreation grounds, canal paths, remnant woodlands and grass verges). In total, 31 candidate sampling sites were ultimately selected (Fig. 2.5).

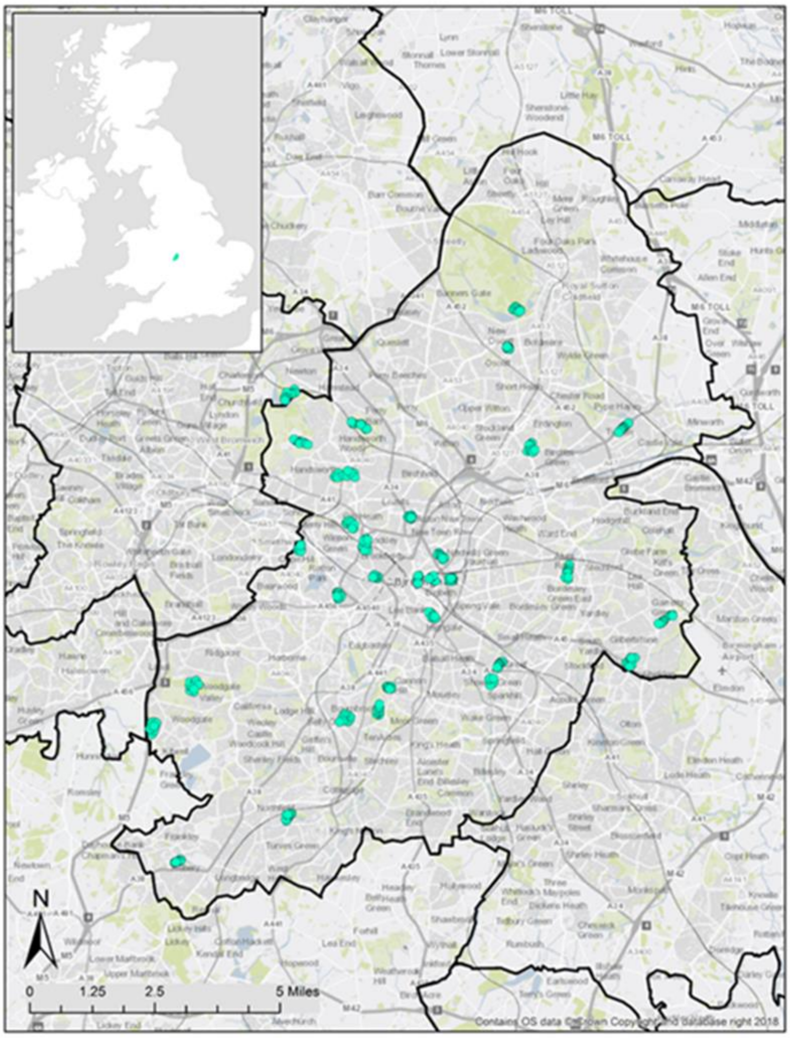


Figure 2.5. Map of the 31 selected study sites and their location within the Birmingham metropolitan area.

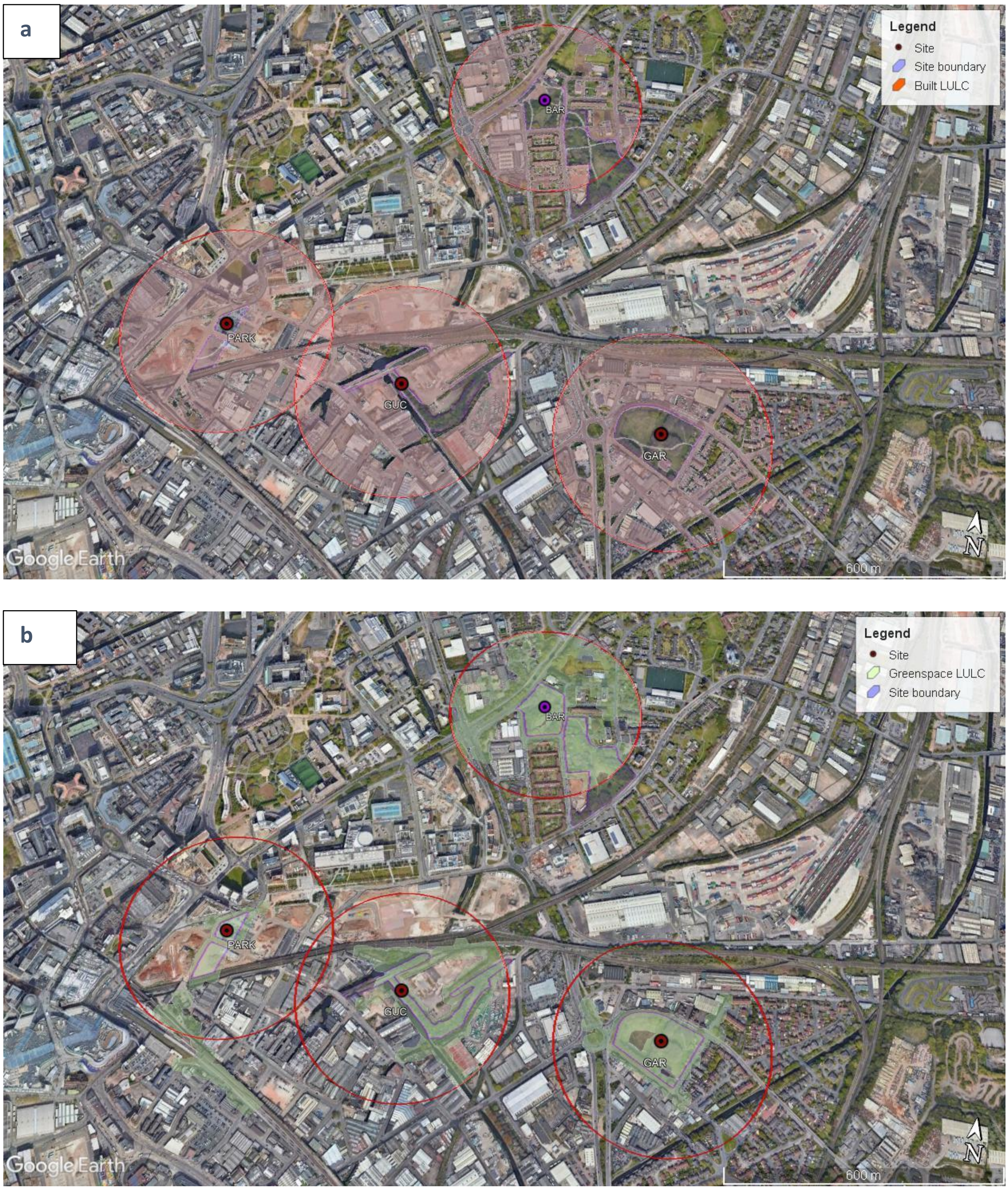
Sites were stratified across a 1-km^2 urban gradient (based on the degree of increasing built land-cover and connected landcover derived from the LULC data extraction above). Sites were then further categorised into three (low, medium, high) and five (1 = suburban to 5 = densely urbanised) classes of urban form to ensure a balanced design.

2.2.3. Landscape environmental covariates

Following the selection of sites, in the next step a multi-scale approach was used to extract landscape variable summary data for individual sites and their surrounding landscape, enabling a hierarchical measurement of change across the city. This was achieved using GIS to construct multiple concentric buffers at different radii from the centre of each site at distances of 100, 250, 500 and 1,000 m (Fig. 2.6). These are scales linked to aspects of the breeding biology, behaviour and life history of the focal species. The Thematic Raster Summary tool in Hawth's Tools (Beyer 2004) was used to extract the complete summary data of the underlying landscape for each site and its associated buffer zones. Landcover variables were quantified for both the area of the full circle generated from each of the radii and for each concentric ring (i.e. the area of the differenced circles), an example of which is shown in Figures 2.6a- 2.7b.

Two main landscape categories ('built landcover' and 'greenspace') were created, together with a subcategory for 'gardens'. All 'grey space' (including buildings, pavements, roads and railways etc.) were aggregated to create the category built landscape, providing a primary measurement of urbanisation. The greenspace category captured all greenspace patches (including urban parkland, remnant woodland, nature reserves, riparian corridors, grass verges, street trees, golf courses, allotments and gardens etc.). This measure was used to estimate the total potential habitat available to breeding pairs of birds. Thus, greenspace can be considered as contiguous areas of habitat which are fragmented by grey space.

Figures 2.6. An example of a city of Birmingham survey site (i.e. Cannon Hill) with extraction method. Concentric buffers were constructed at radial distances of 100, 250, 500 and 1000 m from the centre of the survey site (shown as red circles). These have been superimposed on the **(a)** built landscape and **(b)** connectivity mask. The extent of landcover was quantified for the two landcover types within each concentric ring and for each total circle area (in m^2 and as a percentage value of the total area available). Buffers also used for scale.



Figures 2.7. Expanded view of the mapping of the Birmingham city centre (moderately and highly urbanised) sites to demonstrate the capture of LULC data, using the example of a 250-m buffer (red outline). All **(a)** grey (built) and **(b)** greenspace LULC within the 250 m concentric buffer zone is highlighted.

A separate subcategory was created to determine if it was possible to differentiate between the potential impacts of garden landcover on variation in the different breeding responses used to measure reproductive performance of Blue Tits using this data extraction technique. This was undertaken on the basis that gardens comprise approximately a quarter of all urban landcover in UK cities and, as such, are a potentially significant component of the breeding habitat, providing corridors for movement between habitat patches and important resources of food (Loram *et al.* 2007; Plummer *et al.* 2019). Studies have established that the structure and composition of vegetation in suburban gardens significantly influences habitat quality and connectivity, with knock-on effects to the abundance and availability of natural prey including caterpillars (*Lepidoptera spp.*) (Cowie and Hinsley 1987; Narango *et al.* 2017, 2018). Concomitantly, the provisioning of supplemental food (e.g. at garden bird feeders) has also been shown to impact the breeding phenology and behaviour as well as reproductive success and survival of Blue Tits, with both positive and negative downstream effects (e.g. see Jones and Reynolds 2008; Robb *et al.* 2008b; Galbraith *et al.* 2015; Reynolds *et al.* 2017; Plummer *et al.* 2013b, 2019).

This first method of data extraction is ‘unrestricted’ in that it assumes that all habitat patches within the landscape are potentially available to and/or beneficial to Blue Tits (Rosenfeld 2012). However, the permeability of habitat and the movement of birds across greenspace is complex: for example the movement of individuals across areas of non-habitat (i.e. open or built landcover) might be limited due to the potential complex interactions operating between the characteristics of the landscape and biology of the species (for example see Greenberg 1989; Uezu *et al*. 2005; Cox *et al*. 2016). During the breeding season birds limit their movements: for example when provisioning nestlings foraging distances are a trade-off between the spatial distribution and quality of food patches and the energetic costs to breeding adults (Naef-Daenzer 2000; Stauss *et al.* 2005; Wilkin *et al.* 2009a). Therefore, individual birds will optimise the habitat available to them (MacArthur and Pianka 1966). The tree layer and connectivity mask data for each buffer zone (as described in Section 2.2.2.2) were therefore similarly extracted for each bufferzone, providing a second more refined quantification of greenspace and (tree) connectivity within the wider urban matrix surrounding breeding sites.

The degree of built landcover, greenspace, garden landcover and tree connectivity in the matrix surrounding sites was quantified using the 500 m concentric buffer for analytical purposes. This scale provided the best balance in capturing the extent, complexity and variation in urban density within the city, whilst also considering the potential maximum breeding home range and foraging territory of urban Blue Tits. Recent studies have highlighted that tits breeding in highly fragmented or sub-optimal habitats are less likely to remain bound to core foraging territories due to unsuitable conditions (Redhead *et al.* 2013; Dekeukeleire *et al.* 2019b). For example, tits have been shown to move 500 m from roost sites in suburban habitats to visit garden feeders during winter (Satgé *et al.* 2019). Breeding females have also been shown to expand foraging distances from 50 to 500 m to find richer food patches both during egg formation/laying (Wilkin *et al.* 2009a,b; Amininasab *et al.* 2016) and brood rearing (Tremblay *et al.* 2005; Stauss *et al.* 2005; Jarrett *et al.* 2020). Furthermore, 500 m was determined to capture the maximum breeding home ranges for passerine species in previous research investigating the effects of connectivity and urbanisation on bird abundance in Birmingham (Rosenfeld, 2012). Finally, it was anticipated that the quantification and analysis of urbanisation effects on bird breeding at this scale would facilitate future comparisons with other passerine species including Great Tit (*Parus* *major*) with similar life histories and other urban study systems (McDonnell and Hahs 2008; Seress *et al.* 2014; Moll *et al.* 2019).

The percentage landcover for each variable was calculated (relative to the total area of the 500 m buffer zone), creating a suite of landscape-scale metrics which were used to quantify the urban matrix surrounding each study site (Table 2.2). Sites were subsequently classified into one of five urbanisation classes on the basis of *a priori* determined percentage cut-off values of built landcover (Fig. 2.8 and Table 2.2).

Table 2.2. Core landscape-scale variables derived from original OS digital and remotely-sensed vegetation data that were considered for inclusion in statistical models to analyse how reproductive performance in a population of nestbox breeding Blue Tits varies across an urban gradient in Birmingham, UK over six years (2013-2018). Summary landscape variable data are provided for each of the 31 study sites initially included in the project. Values for each variable were calculated as the percentage of the total landcover within a 500m concentric buffer from the centre of each site. Sites were classified into one of five urban land class categories based on the percentage of built landcover. To aid visualisation ULC designations are colour coded to correspond with Fig. 2.8 below. **ULC1** (green) = least urbanised (suburban sites); **ULC2** (yellow) = dense-suburban; **ULC3** (orange) = moderately urbanised sites; **ULC4** (purple) = highly urbanised; **ULC5** (red) = most densely urbanised sites.

Site	Site ID	Greenspace Type	ULC	Built Landcover (%) (%BLC)	Garden Landcover (%) (%GLC)	Green Area (%)	Connected Landcover (%)
Hilltop and Manwood Public Open Space	**HILL**	Public open space/woodland	1	6.02	7.08	93.81	58.73
Sutton Park Nature Reserve	**SUTTON**	Nature Reserve	1	6.94	4.89	82.12	76.39
RSPB: Sandwell Valley Nature Reserve	**SAN**	Nature Reserve	1	6.96	8.02	80.29	75.99
Woodgate Valley Country Park	**WGVP**	Parkland/Woodland	1	15.59	14.95	84.14	72.65
Perry Hall Playing Fields	**PERRY**	Public Open Space	1	16.87	20.13	80.65	62.17
Holders Woods	**HOLD**	Woodland	1	18.95	25.44	80.08	80.21
RSPB: Cannon Hill Park	**CANNON**	Woodland	1	21.03	30.05	76.27	88.75
Woodgate Valley Country Park: The Pines	**PINES**	Public open space	2	24.08	23.05	75.86	59.64
Batchelors Farm Park	**BAT**	Parkland	2	26.91	33.72	72.10	74.09
Oakwood Road Coppice	**OAKW**	Woodland	2	31.81	60.17	68.12	88.35
Popes Lane POC	**POPES**	Public Open Space	2	34.66	29.77	64.76	79.74
Rookery Park	**ROOK**	Rec. Ground/Park	2	34.85	39.46	65.19	73.09
Selly Park Rec. Ground	**SELLY**	Recreation Ground	2	37.21	35.6	61.88	58.15
Handsworth Park	**HAN**	Rec. Ground/Park/Lake	3	37.32	24.33	60.04	73.18
Sheldon Country Park	**SHE**	Parkland	3	37.73	39.71	61.89	79.83
The Radleys	**RAD**	Residential/Public open space/river	3	42.35	29.39	57.29	59.05
Callow Brook	**CALL**	River/Woodland	3	44.66	17.98	53.16	72.45
Castle Vale Estate (Manby Road)	**MAN**	Residential/Verge/Public open space	3	46.91	23.4	45.61	43.69
Burbury Brickworks	**BUR**	Nature Reserve	3	54.36	21.02	44.74	21.59
Gib Heath Park	**SOHO**	Public open space/Heathland	4	55.69	21.79	43.89	50.01

(aka Soho Pool Wharf)							
Chamberlain Gardens	**CHAM**	Recreation Ground/Ornamental Public Gdns	**4**	57.25	24.48	42.62	67.39
Phillips Street Park	**PHIL**	Recreation Ground	**4**	59.43	20.4	40.48	49.32
Moilliett Street Park	**MOI**	Recreation Ground	**4**	61.72	20.91	36.60	19.87
Cowley Road	**COW**	Recreation Ground	**4**	62.9	10.16	35.68	24.91
Barrack Street Recreation Ground	**BAR**	Recreation Ground	**4**	64.78	7.78	34.29	55.91
Garrison Lane Park	**GAR**	Recreation Ground	**5**	67.9	9.02	30.36	5.14
Warstone Lane Cemetery	**WARS**	Cemetery	**5**	72.29	6.83	27.22	23.82
Highgate Park	**HIGH**	Park/Recreation Ground/Ornamental Public Gardens	**5**	73.6	7.14	26.04	29.80
City Centre Gardens	**CITY**	Ornamental Public Garden/Private Gardens/Canal	**5**	82.36	1.94	14.69	8.07
Grand Union Canal	**GUC**	Canal/Tow Path	**5**	83.23	1.3	14.61	13.01
Park Street Gardens	**PARK**	Park	**5**	86.16	0.66	12.88	2.07

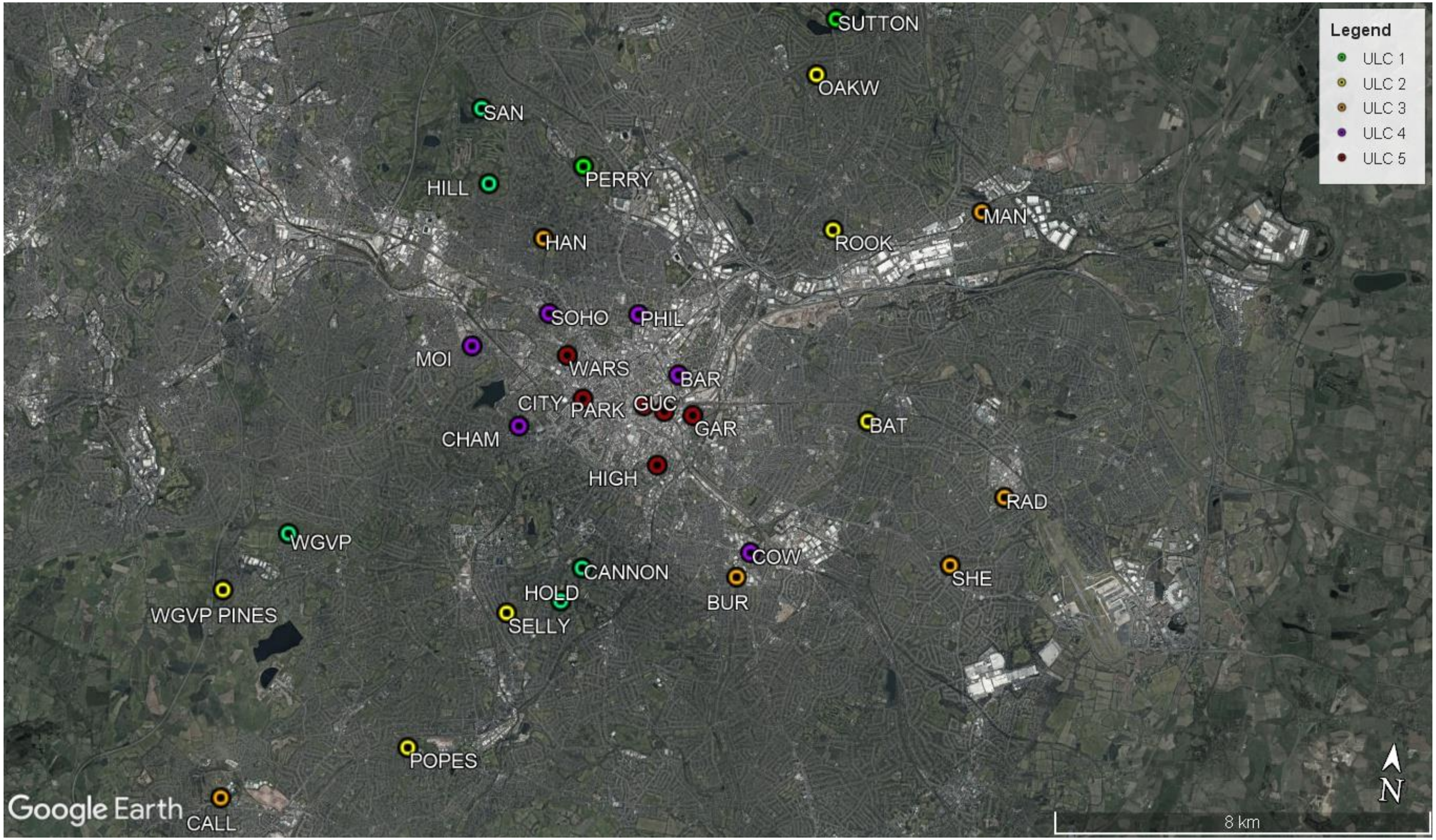


Figure 2.8. Map of the location of the original 31 study sites within the wider Birmingham metropolitan area. Sites were classified into one of five urban land class categories based on the percentage of built landcover within a 500m radius of the centre of each site. ULC designations are colour coded to correspond with Table 2.2 above. **ULC1** (green) = least urbanised (suburban sites); **ULC2** (yellow) = dense-suburban; **ULC3** (orange) = moderately urbanised sites; **ULC4** (purple) = highly urbanised; **ULC5** (red) = most densely urbanised sites.

2.3. HABITAT DATA COLLECTION

2.3.1. Vegetation structure and composition

Average habitat quality was estimated for each site by quantifying the structure and composition of breeding territories for a sample of nestboxes. Surveys were conducted to record the fine-scale habitat and vegetation characteristics of 30 sites during the summer of 2013, and for one site (i.e. Holders Wood) during February 2016. Four nestboxes were selected for surveying at each site, ensuring that the edge and interior of habitat patches in which nestboxes were located, were represented, thus enabling the effects of intra-site habitat variability on various breeding success traits to be captured.

The habitat within a 10-m radius of each nestbox was sampled, with the percentage area of different vegetation cover (including trees, herbaceous plants, shrubs and grasses and bare ground) estimated (see Appendix 1a for raw data). This radius was chosen following a thorough evaluation of the literature to determine both the estimated average breeding territory size of Blue Tits, distances covered during foraging trips during the breeding period in different habitats and circumference areas of habitat surveys used in other similar studies.

Estimating the area over which the structure and quality of vegetation within heterogenous landscape such as urban areas may be relevant to the movement of Blue Tits, however is not straightforward. The distances individual birds travel is dependent on a number of related factors including the availability and spatial distribution of food (Naef-Daenzer 2000; Hinsley *et al*. 2008; Telve *et al*. 2020), as well as individual fitness (including cognition, age, body condition and phenotype: Gustafsson 1988; Nooker *et al*. 2005; Stauss *et* al. 2005; Cole *et al*. 2012) and other temporal environmental factors such as weather conditions (Öberg *et* *al.* 2014) Consequently, the estimated average distance travelled by Blue Tits across different habitats varies widely across different populations and habitats, as extensively discussed in the literature. Concomitantly, the survey area and measurement of habitat characteristics are inconsistent across similar Blue and Great Tit nestbox breeding studies. Distances specified range from 10 m (Hedblom and Söderström 2012), 15 m (Shutt *et al.* 2018), 20 m (Arriero *et al.* 2006; Amininasab et al. 2016), 25 m (Glądalski *et al.* 2017) to 50 m (Bell *et al.* 2014; Demeyrier *et al.* 2016). As such, the final decision on the number of nestboxes to be sampled and the habitat survey area represented a compromise between biological relevance and the practicability of conducting fieldwork given the number and distance between individual sites, the quantity of trees to measure, and resource constraints.

Within the 10-m radius of each nestbox, all living trees were catalogued, identified to species or genus level and the girth at breast height (gbh) was measured (using the standard protocol of 1.5 m from the highest point of the ground at the base of the tree). In total 45 tree species were identified to the genus or species level, summing to a total of 1,470 individual trees identified and measured. Trees were assigned to different focal taxon categories. For example, the three species of willow (*Salix* spp.) that were identified (Common Osier *S. viminalis*, Goat Willow *S. caprea* and Crack Willow *S. fragilis*) were grouped under genus level *Salix*. Oaks (*Quercus* spp.) included both native species such as Pedunculate Oak *Q. robur* and Sessile Oak *Q. patraea*, with the Northern Red Oak *Q. rubra*, an ornamental and non-native species, classified separately.

The most dominant species of trees recorded across sites represented over 46% of the total number catalogued and included oaks (n = 179, 12.18% of all trees), European Ash *Fraxinus* *excelsior* (n = 167, 11.36%), Hawthorn *Crataegus monogyna* (n = 117, 7.96%), birches (*Betula* spp.) (n = 113, 7.69%) and Sycamore Maple *Acer pseudoplatanus* (n = 106, 7.21%).

Several different variables were generated from the raw tree data which were used to characterise the fine-scale composition and structure of an average breeding territory surrounding a nestbox at each site and which were considered as potential proxies for the availability of key natural food sources (Isaksson and Andersson 2007; Glądalski *et al.* 2015; Dekeukeleire *et al.* 2019; Wawrzyniak *et al.* 2020). For each variable the site level mean and standard deviation (SD) were calculated from the four individual nestbox survey values unless otherwise specified.

2.3.1.1. Tree density and identity

The total mean number of native deciduous broadleaved trees (NDB Trees) present at each site was calculated as a metric for site quality on the basis that native deciduous woodland is widely considered the optimal breeding habitat for secondary hole-nesting passerines including Blue Tits (van Balen 1973; Perrins 1991), providing abundant natural food (Dekeukeleire *et al.* 2019b). Oak trees, in particular, support a rich diversity and abundance of arthropods, the primary prey provisioned to nestlings (Perrins, 1979, 1991; Buse *et al.* 1999; Marciniak *et al*. 2007). As they are the preferred species of foraging adults during the peak nestling demand during brood-rearing, the density of oak trees is frequently used as a reliable indicator of breeding habitat quality (Wilkin *et al*. 2009a; Bell *et al*. 2014; Amininasab *et al.* 2016a). Shutt *et al.* (2018) also established that the availability of Birch and Sycamore trees within breeding territories across different types of woodland in Scotland were positive predictors of fledging success in Blue Tits. These three focal tree species (oak, birch and sycamore) therefore were initially selected for inclusion as variables in analyses on the basis that they are considered the most valuable tree species for breeding Blue Tits for food and in site surveys were found to be the most abundant tree species across Birmingham study sites. That said, due to the overall low number of trees throughout the study area, the total mean density (number) of all three species in the territory surrounding nestboxes was calculated for each site (Mean BOS Trees). However, this term was subsequently removed from the majority of analyses due to significant issues with model convergence and validation resulting from the consistent presence of preferred trees but low combined counts across sites (Table 2.3).

Table 2.3. The key habitat variables selected as indicators of breeding habitat quality and proxies for food availability for Blue Tits breeding in nestboxes located across 31 study sites stratified across an urban gradient in Birmingham, UK. Variables derived from site surveys and GIS. Longitude and latitude were specified as the centre point for each site. Altitude was calculated as the average value for each site from 10 nestbox measurements. (na measurements for three sites that were excluded later in the analyses).

Site ID	ULC	Mean Site Altitude	Lat (Centre Point)	Long (Centre Point)	Total Site Area (m^2)	Mean Edge Distance (m)	Mean NDB	Mean InvSI	Mean BOS Trees
HILL	**1**	145	52.51953	-1.94539	51948	24.96	7	4.74	4.25
SAN	**1**	113	52.53325	-1.95091	240904	35.84	8.5	6.95	2
WGVP	**1**	192	52.4492	-1.99603	460817	40.31	14.25	5.98	1.25
HOLD	**1**	143	52.44223	-1.90846	92674	55.39	28	4.95	16
CANNON	**1**	135	52.44847	-1.90362	25398	58.68	11.75	2.76	10
PINES	**2**	164	52.43708	-2.01547	99989	23.65	13.75	4.47	3.25
BAT	**2**	103	52.48169	-1.81883	192581	26.19	18.5	5.13	2.75
OAKW	**2**	149	52.54684	-1.84693	14451	54.26	7	4.18	6
ROOK	**2**	126	52.5176	-1.83613	64268	32.5	11.5	4.79	5
SELLY	**2**	146	52.43965	-1.92416	81017	23.88	1.25	1.61	6
HAN	**3**	123	52.51007	-1.92461	346267	40.51	4.25	5.38	1
SHE	**3**	103	52.45588	-1.78945	126081	30.7	7	4.59	6.5
RAD	**3**	95	52.46781	-1.77279	99424	37.96	12.5	2.29	1.25

CALL	**3**	187	52.39819	-2.00349	23628	42.9	19	2.66	2.5
MAN	**3**	91	52.52361	-1.79226	33891	22.88	13	4.7	4
BUR	**3**	116	52.45015	-1.85529	64306	39.01	9	4.58	8.25
SOHO	**4**	122	52.49589	-1.92188	49939	21.28	11.5	8.05	3
CHAM	**4**	163	52.4788	-1.92734	51009	24.57	2.75	7.33	0.5
PHIL	**4**	108	52.49778	-1.89331	17430	26.59	3.25	5.67	1.25
MOI	**4**	148	52.48876	-1.94577	34587	20.53	12.25	5.12	6.25
COW	**4**	115	52.45506	-1.85133	18165	24.86	13.5	8.32	3
BAR	**4**	121	52.48645	-1.87878	39208	29.18	12.75	7.02	0.75
GAR	**5**	115	52.45506	-1.85133	21394	17.88	0	2.68	0
WARS	**5**	138	52.48954	-1.91484	65097	27.969	1.25	3.6	0
HIGH	**5**	125	52.46934	-1.88315	33044	25.34	2	9.76	0.25
CITY	**5**	145	52.48044	-1.90979	15650	20.47	3	11.52	0.5
GUC	**5**	105	52.47995	-1.88282	14935	20.94	6	5.57	3
PARK	**5**	120	52.48032	-1.88972	6563	18.06	1.5	4.84	0.75
PERRY	**1**	100	52.52482	-1.91653	185109	34.57	na	na	na
SUTTON	**1**	128	52.55794	-1.84163	37381	84.46	na	na	na
POPES	**2**	147	52.41068	-1.95169	66975	41.58	na	na	na

2.3.1.2. Tree diversity

Tree diversity was quantified at the site level (pooling all tree records from across the four site surveys) using both Simpson's Diversity Index (SI) and the Inverse Simpson's Index (InvSI) calculated in the R package 'vegan' (Oksanen *et al.* 2020).

Simpson's Diversity Index was calculated for each site based on the Equation 2.1.

$$D = 1 - \frac{\Sigma\, \mathrm{n}(\mathrm{n}-\mathrm{N})}{N(N-1)} \qquad \text{(Eqn 2.1)}$$

where n is the number of individual trees of one species and N the total number of all individual trees. The value of SI ranges between 0 and 1, with the greater the value, the greater the sample diversity.

The Inverse Simpson's Index for each site was calculated as the reciprocal of D from Equation 1. The lowest possible value for this index is 1 (representing a habitat with one species). The maximum value which could be obtained is dependent on the number of species or genera present which varied between sites. Thus, the higher the value, the greater the diversity. Across all site surveys the highest mean Inverse Simpson's Index value recorded was 11.52 and the lowest 1.61 (Table 2.3).

The Diversity Indices were calculated using two approaches: the first utilised the complete tree dataset while the second excluded evergreen and coniferous species. The rationale for including the second calculation was two-fold. Firstly, coniferous species confer few benefits to Blue and Great Tits during the breeding season (Gibb 1954; Perrins *et al.* 1965; Van Balen 1973; Van Balen and Potting 1990) and constituted only a very small percentage (8% or 122 trees) of total species diversity and abundance across sites in Birmingham. Therefore, this approach allowed me to assess how much difference removing these species made to diversity scores. Secondly, and perhaps more importantly, whether higher species diversity is beneficial to breeding, particularly in urban environments, remains largely equivocal. For example, studies have highlighted that greater broadleaved tree diversity may be associated with temporal variation in the availability of prey during the breeding season, with both positive (Tremblay *et al.* 2003; Shutt *et al.* 2018; Dekeukeleire *et al.* 2019b) and negative (Hinsley *et al.* 2008; Batáry *et al.* 2014; Seress *et al*. 2018) knock-on effects on breeding performance. Therefore, a specific aim of my study was to explore if increasing broadleaved tree diversity within urban greenspace was associated with higher or lower breeding success of Blue Tits. Including coniferous species would inflate diversity scores, potentially obscuring any relationship between the diversity of these supposedly more beneficial species of trees in the urban environment and the breeding performance of birds contained therein. For the majority of sites, the two scores were found to be identical (i.e. no coniferous or evergreen trees present), whilst for the few sites where coniferous species were present the scores were only marginally different. For the purposes of analyses therefore InvSI for broadleaved species was used (Table 2.3).

2.3.2. Site area

The size and structure of parks are important characteristics that have been shown to influence urban bird assemblages (Jukka and Jokimäki 1988), species richness (Jokimäki and Suhonen 1993), diversity (Zhou and Chu 2012) and density (Jokimäki 1999). However, in comparison, the potential for similar such effects on breeding behaviour and success, has been much less studied. In my study, the perimeter and total area for each study site was estimated in Google Earth, to determine how the size of greenspace available to nestbox breeding Blue Tits varies across the urban gradient (Fig. 2.9 and Table 2.3).

Figure 2.9. An example of a city of Birmingham survey site (i.e. Gibs Heath) with the estimated perimeter of the park (dark purple line) and site area (light purple shading).

2.3.3. Edge effects

The distance of each nestbox to the nearest connected edge (within tree cover) was estimated from the connectivity mask (section 2.2.2.2.) to capture variation in edge effects both within- and between sites. The mean distance to the nearest connected edge was calculated for each site for inclusion as a covariate in models (Table 2.3).

2.3.4. Temporal change at the landscape and habitat scale

Landscape-scale mapping and site surveys were conducted only once during the six-year duration of my study. Our own observations during regular site visits assured us that with the exception of the loss of one site in 2018 (i.e. Park Street Gardens), very little substantial change to the land use or landcover surrounding sites or to the structure and composition of vegetation within sites had occurred or had affected sites directly. Although significant building work had been conducted in Birmingham during this period, the underlying landscape had not been altered or impacted extensively, as verified by the Corine Land Cover LCLU change map for 2012-2018 (Fig. 2.10).

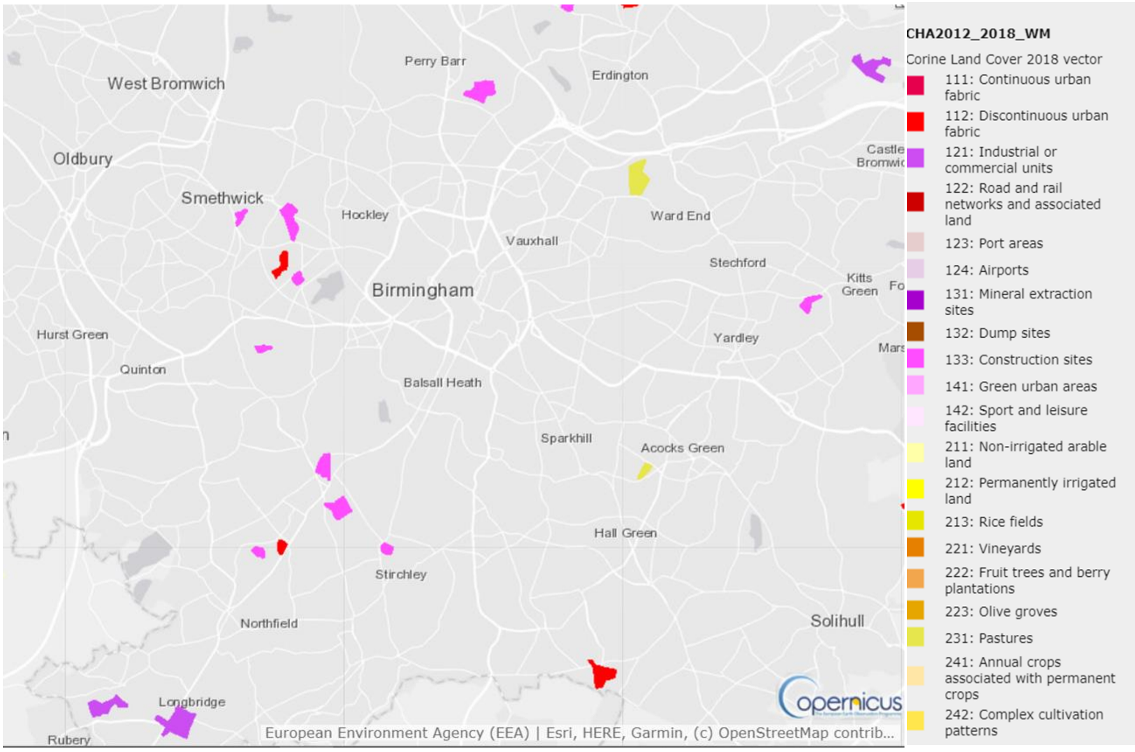


Figure 2.10: Changes in land-use and land-cover (LULC) in the wider metropolitan area of Birmingham during the period 2012-2018, derived from the datasets produced within the Corine Land Cover Programme (European Environment Agency). Data cover the project area and encapsulate the period during which reproductive performance in a population of Blue Tits breeding in nestboxes across 31 sites in the city of Birmingham was monitored (2013-2018). None of the study sites lie directly within highlighted areas of change.

Construction work to tower blocks and landscaping at Highgate Park in 2016, Chamberlain Gardens in 2016 and 2017, and tree felling within RSPB Sandwell Valley and Warstone Cemetery in 2018 required that six nestboxes be either moved to the nearest available tree from their original location or considered as unavailable for subsequent analyses. Moilliett Street Park was removed from inclusion in the study in 2017 due to safety concerns and continued vandalism of nestboxes. In 2018 Park Street Gardens was no longer accessible due to works associated with the HS2 development.

2.3.5. Final selection of habitat and landscape scale predictor variables

In total, over 50 different predictor variables were generated from the data extracted from LULC mapping from OS digital and remotely sensed data, and collected from on-the-ground habitat surveys. A subset of variables were consequently selected (Table 2.4) that it was felt could reliably be used to characterize the degree of urbanisation of each site and that related to the various measures of breeding timing and success considered in analyses.

Table 2.4. The final subset of habitat and landscape-scale covariates selected for inclusion in analyses to investigate reproductive performance in a population of Blue Tits breeding in 31 sites stratified across an urban gradient in Birmingham, UK over six consecutive years (2013-2018).

Variable	Method of collection	Tree survey	Habitat survey	Landscape 500 m
Built landcover	OSM LULC /GIS			✓
Greenspace	OSM LULC/GIS			✓
Garden coverage	OSM LULC/GIS			✓
Tree network	Remote Sensing/GIS			✓
Connectivity mask	OSM LULC/GIS			✓
Patch density	Fragstats/GIS			✓
% Trees	Site Survey		✓	
% shrubs	Site Survey		✓	
% herbaceous plants	Site Survey		✓	
% grasses	Site Survey		✓	
% bare ground	Site Survey		✓	
Park Perimeter/Area	Google Earth		✓	
Box – connected edge	RemoteSensing/GIS		✓	
Tree species count	Site Survey	✓		
Tree DBH/4 categories	Site Survey	✓		

Count & % mean NDB Trees	Site Survey	✓		
Count & % Non-Native Broadleaved Trees	Site Survey	✓		
Count & % Coniferous Trees	Site Survey	✓		
Most Common Tree Species	Site Survey	✓		
Mean Simpson Diversity Index	Site Survey	✓		
Mean Inverse Simpson Diversity	Site Survey	✓		

Selection was largely informed by the previous urban ecological work conducted in Birmingham by Hale *et al*. (2012) and Rosenfeld (2012) and a comprehensive review of the current literature to determine the best approaches to analyse associations of the urban environment with breeding in passerine species.

2.4. SITE BASED FIELDWORK

2.4.1. Nestbox monitoring and data collection

The study was established by former doctoral student Dan Hunt, between January and March 2013 with the provision of 10 identical Gardman© plywood nestboxes (22.5 [height] × 13.0 [width] × 12.0 [depth] cm) at each of the 31 study sites (N = 310 nestboxes). Nestboxes were positioned at least 40-50 m apart to reduce overlap and/or competition for territory space by Blue Tits and were located to ensure an even distribution across the interior and edges of the associated habitat enabling intra-site variation in breeding to be assessed (e.g. Fig. 2.9, Section 2.3.1). Nestbox entrance holes were 28 mm in diameter and each nestbox was fitted with a 28 mm (hole diameter) metal plate (CJ Wildlife, Shrewsbury, UK) as a reinforcement against predators and to encourage preferential use by Blue Tits (Fig. 2.11). All nestboxes were fixed at a height of between 2.0-3.0 m above the ground to reduce interference from the public and oriented as far as possible with entrance holes facing in a north-east direction (away from direct sunlight and prevailing south-west winds).

Figure 2.11. An example of the Gardman© nestboxes and their positioning, as used in the Blue Tit urban gradient study in Birmingham. UK. The nestbox in Holders Lane Woods is reinforced with a metal plate and attached to the tree using heavy-duty garden twine and staples. Nestboxes were regularly replaced to accommodate tree growth and prevent damage to tree trunks. (Photo: A. Mason).

Breeding data were collected over six consecutive years (2013-2018). Nestboxes were continuously monitored every week from early-March, which previous research in this region has established is the earliest point when females begin nesting (e.g. Smith *et al.* 2013). Nestboxes occupied by other species including Great Tits and Coal Tits (*Periparus ater*), missing, damaged or inaccessible (e.g. due to building works) were classed as unavailable to prospecting pairs of Blue Tits (representing <10% of overall nestbox availability over the six breeding seasons). At the end of each breeding season (August-September) all nesting material was removed from nestboxes to reduce parasitic loads and to ensure that they were ready for breeding the following year (Solonen 2001; Hedblom and Söderström 2012).

Nestboxes were considered active once the first nesting material was seen (Smith *et al.* 2013). During weekly nestbox checks (Fig 2.12) comprehensive data were collected on basic breeding traits including laying and hatching dates, clutch size, maximum brood size at hatching, final fledgling numbers, nestling deaths and breeding failures. Regular nestbox checks at each site were conducted until all offspring had fledged (by approximately mid-June).

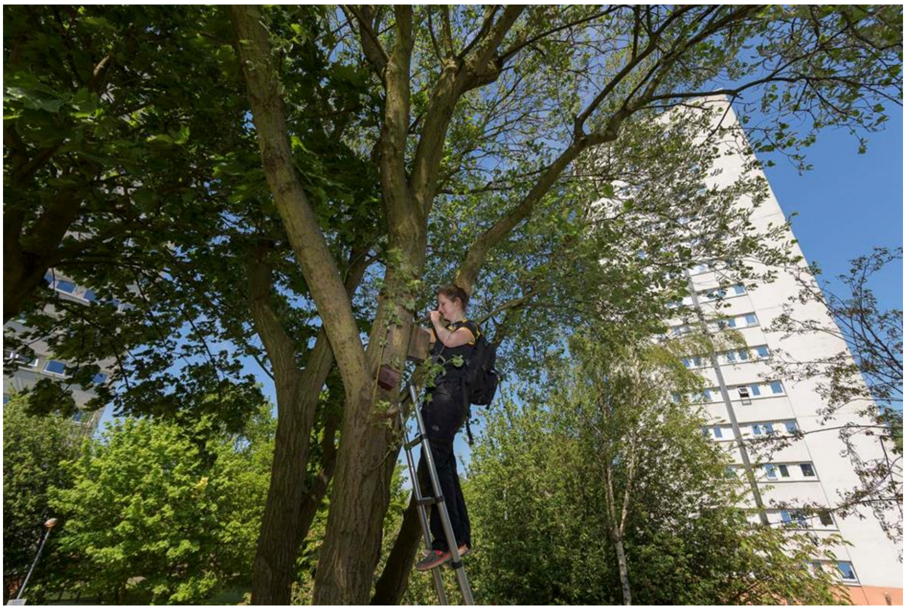


Figure 2.12. The author checking a nestbox at City Centre Gardens in 2018. All nestboxes were regularly checked throughout each of the six breeding seasons to collect Blue Tit breeding data. (Photo: A. Mason).

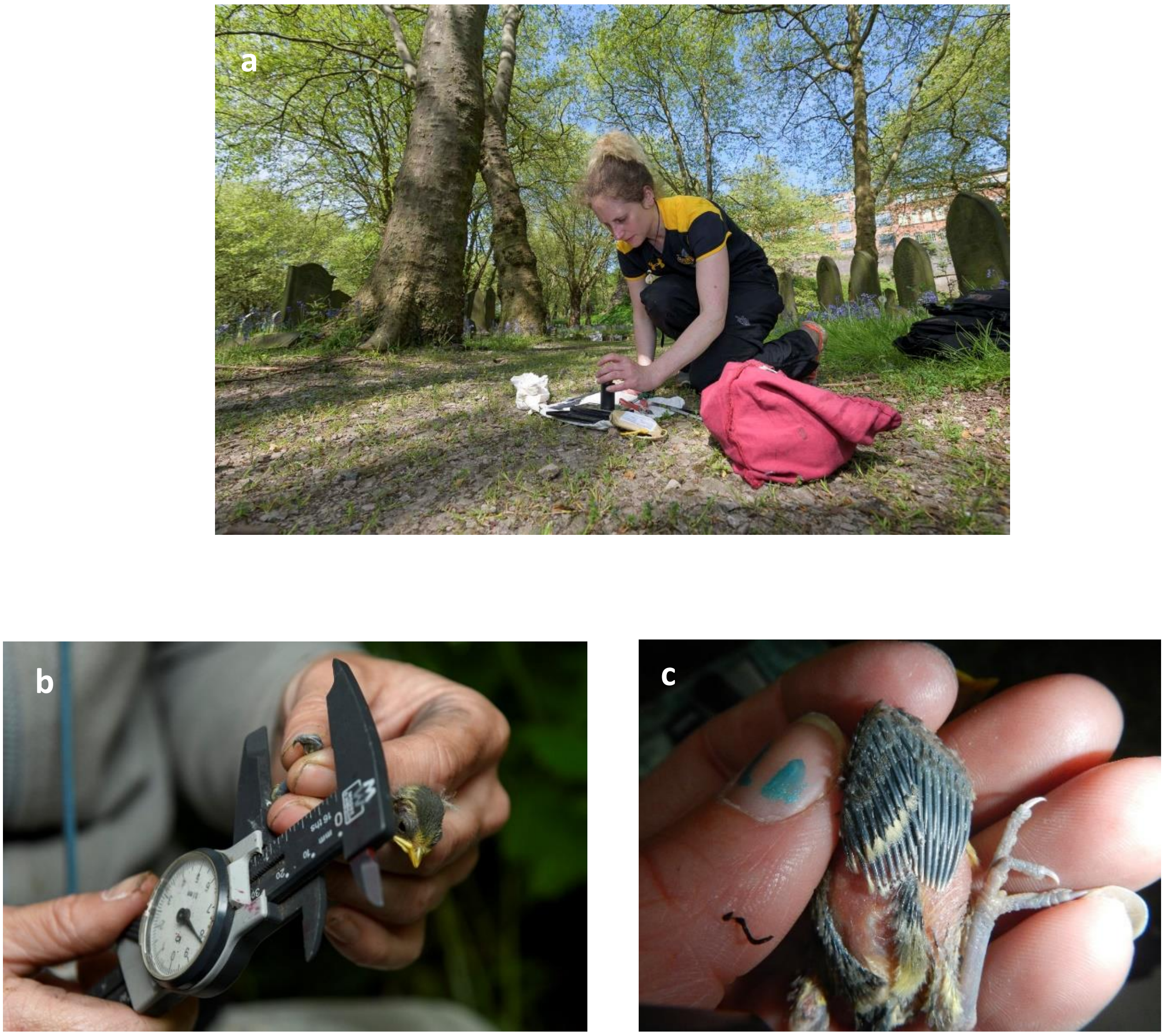
Clutch initiation dates (‘April Laying Date’) for each nest were determined from partial clutches using the standard method of back counting, which assumes one egg is laid per day (Perrins 1979). Incubation was estimated as beginning the day the penultimate egg was laid (specified as incubation day 0) (Bailly *et al.* 2016) and confirmed either by an attending female sitting tightly on the nest or the presence of uncovered but warm eggs.

To minimise the risk of nest abandonment by females, nests were checked 10-12 days after the onset of incubation, which is the earliest anticipated point of hatching (Perrins 1979). The date of hatching of the first egg (‘April Hatching Date’) was designated as nestling day 0 (Hinsley *et al.* 1999). Logistical and time constraints caused by the large spatial scale (Fig. 2.8 and Table 2.2) of the project meant it was not possible to visit nestboxes more regularly to generate more precise incubation and hatching dates, particularly in years in which hatching was highly synchronous across sites (e.g. 2018). Although rare, where nestlings were not observed within 48 hours of hatching, a photographic key was used to determine their approximate age and hatching date (Appendix 1b). All breeding dates were converted to ordinal dates, specified as days counted from April 1st.

Clutch size was recorded as the maximum number of eggs observed in the nest following the onset of incubation. Brood size (the maximum number of hatchlings per breeding attempt), was calculated as the total number of eggs laid minus evidence of unhatched eggs. Since tits rarely remove addled eggs from nests (Kempenaers *et al.* 1996, 1998), it is unlikely that in instances where nests were visited > 24 hours post-hatching, the maximum number of chicks hatched was underestimated. Nests were inspected for evidence of unhatched eggs during ringing of nestlings and then again post-fledging (> 20 days after hatching) when final nest checks were completed.

The total number of fledglings, (used as a measure of final brood-rearing productivity) was estimated based on the number of nestlings that survived until ringing age minus any chicks found dead during post-fledging checks (Tremblay *et al.* 2003).

With the exception of 2013 and 2016, all nestlings from each brood were ringed under licence from the British Trust for Ornithology (British Trust for Ornithology) (Fig. 2.13a-c).



Figures 2.13. (a) The author at Warstone Lane Cemetery in 2018 ringing nestlings and collecting morphometric data. Examples of the author **(b)** using dial callipers to measure the tarsus length of the nestling and **(c)** examining the growth and development of feathers on the wings which aids in ageing nestlings. (Photos: A. Mason and the author).

Broods were visited as close to 10-12 days post-hatching as possible to collect nestling morphometric data. The age (nestling days post-hatching) and number of chicks alive in the nest (brood size at ringing) were recorded. All nestlings in a brood were ringed with uniquely numbered metal BTO rings under licence from the British Trust for Ornithology (ringing permit C/6443) and individual morphometric measurements were taken. Individual nestlings were weighed to the nearest ± 0.1 g using an electronic balance (SA-500, SATRUE, Taiwan), and their minimum (right) tarsus length (± 0.1 mm) measurement was taken using a dial calliper (KWB, Switzerland), following the protocols of Svensson (1992) and Redfern and Clark (2001).

Attempts were made to capture breeding adults in all years during the same period, using a metal spring-loaded trap placed inside the nestbox, following the protocols of the Birmingham Centre for Ornithology research group (e.g. Smith 2010; Webber 2012). All adults that were successfully trapped were ringed with a uniquely numbered BTO metal ring, sexed and aged using moult limits as first year breeders or older, depending on plumage aging characteristics (Svensson 1992). Individuals were weighed to the nearest 0.1 g using an electronic balance (SA-500, SATRUE, Taiwan); their (left) tarsus length was recorded to the nearest 0.1 mm using analogue callipers (KWB, Switzerland) and maximum flattened wing chord measured to the nearest 1.0 mm with a stopped metal ruler (Redfern and Clark 2001).

Following ringing final nestbox checks were conducted no earlier than 20 days post-hatching to prevent the premature (forced) fledging of nestlings (Perrins 1979). During final checks the fate of individual nestlings and overall fledging success for each brood were determined. Fledgling numbers for each nestbox were estimated based on the number of chicks recorded during the previous (ringing) visit minus any chicks found dead in the nest (Tremblay *et al.* 2003). Where possible ring numbers of deceased chicks were recorded and used to establish the survival outcome of all individuals in each nestbox.

2.4.2. Site-level temperature data collection

During 2017 and 2018 air temperature at the centre and edge of each site was recorded at 5- and 10-minute intervals using Tinytag® dataloggers (Gemini Data Loggers, Chichester, UK) and Thermochron iButton® loggers (Maxim Integrated Products., Sunnyvale, CA, USA), respectively, from mid-March until the end of the breeding season each year of the study. The altitude and GPS co-ordinates of each nestbox were recorded using a handheld GPS unit (eTrex, Garmin, Southampton, UK) and later cross referenced with the application MilGPS v 6.8.2 on an iPhone 6s (Apple iOS Inc., USA). The centre-point for longitude and latitude and the mean altitude for each site were calculated for each site for use in subsequent analyses (Table 2.3).

2.5. OVERVIEW OF ANALYSES

2.5.1. Comparison of quantitative with categorical urban gradient metrics

In shifting their focus towards high-resolution, quantitative approaches, a number of more recent urban avian studies (e.g. Corsini *et al*. 2017, 2021; Satgé *et al*. 2019; Plummer *et al*. 2020; Strubbe *et al*. 2020) have highlighted the importance of selecting appropriate spatial scales and urbanisation metrics to define and capture the magnitude of urbanisation effects on life history and reproductive traits at population and individual levels. In my study a slightly different approach was undertaken, in which contrasting models containing either a categorical, qualitative (ULC) or linear, quantitative (%BLC) measure of urban landcover were evaluated to test how different urbanisation metrics influence the explanatory power/predictive capacity of models.

The %BLC was calculated as the percentage area of total built landcover (including buildings, infrastructure and other sealed surfaces) within a 500m concentric buffer around each site. For the ULC categorical factor, sites were assigned to one of five urban land classes based on the percentage of built up area following a similar method to Hale *et al.* (2012). The five urban land classes represented a gradient from the least urbanised (suburban) sites (ULC1) to the most densely built-up sites (ULC5).

2.5.2. Data cleaning and exploration

Data cleaning and exploration prior to analyses were undertaken following the protocols described in Zuur *et al*. (2007, 2010). Cleveland dotplots were used to identify the presence of outliers. Correlation matrices (using the panel.cor function in R) and VIFs were used to check for multi-collinearity between explanatory variables. Covariates with high levels of autocorrelation were removed sequentially on the basis of variance inflation factors (VIFs), using the function 'vif' from the car R package (v3.1.10; Fox and Weisberg 2019), using a cut-off value of 3 following Zuur *et al*. (2010, 2013).

2.5.3. The hierarchical modelling approach

Breeding responses were analysed using a hierarchical (nested) model structure, integrating variables from the habitat immediately surrounding nestboxes (habitat predictor block) and the wider urban matrix (landscape predictor block), together with biotic covariates (e.g. April laying date or clutch size) that are known to influence outcomes during subsequent stages of reproduction of birds (e.g. see also Biard *et al.* 2017; Shutt *et al.* 2018; Satgé *et al.* 2019).

Following Whittingham *et al.* (2006) and similar to approaches used in more recent studies (e.g. Pennington and Blair 2011; Seress *et al.* 2018; Shutt *et al.* 2018), full (global) models including all *a priori* selected fixed covariates were constructed for each response variable, with no further attempts to simplify these models. However, where the initial inspection of pair plots indicated potential non-linear relationships between fixed covariates and response variables, second order polynomial terms were included in models and retained if found to be significant.

Model parameterisation was individually revised for each response variable under investigation, taking into consideration the type and distribution of the raw data, and to deal with constraints related to issues of dispersion and zero-inflation which are commonly encountered with ecological data (Brooks *et al.* 2019). All statistical analyses were performed using linear mixed models (LMMs) in the R package "lme4" (v1.1-25; Bates *et al.*, 2015) or generalised linear mixed models (GLMMs) in the '*glmmTMB*' package version 1.0.1 (Brooks *et al.* 2017) in the R computing environment (versions 3.4.4 to 3.6.3, R Development Core Team 2018-2020). Intercept-only models were fitted with gls and/or glm. Default canonical link functions were specified for each error family in the model formulas for GLMM models unless otherwise specified. The Template Model Builder was used to fit GLMMs using the default maximum likelihood estimation (Brooks *et al*. 2017). All final global LMM models were specified with normal (Gaussian) family errors and fitted by restricted maximum likelihood estimation (REML) using the default Satterthwaite's method for comparison with nested models. For the purposes of reporting outputs, final models were fitted using maximum likelihood estimation (ML).

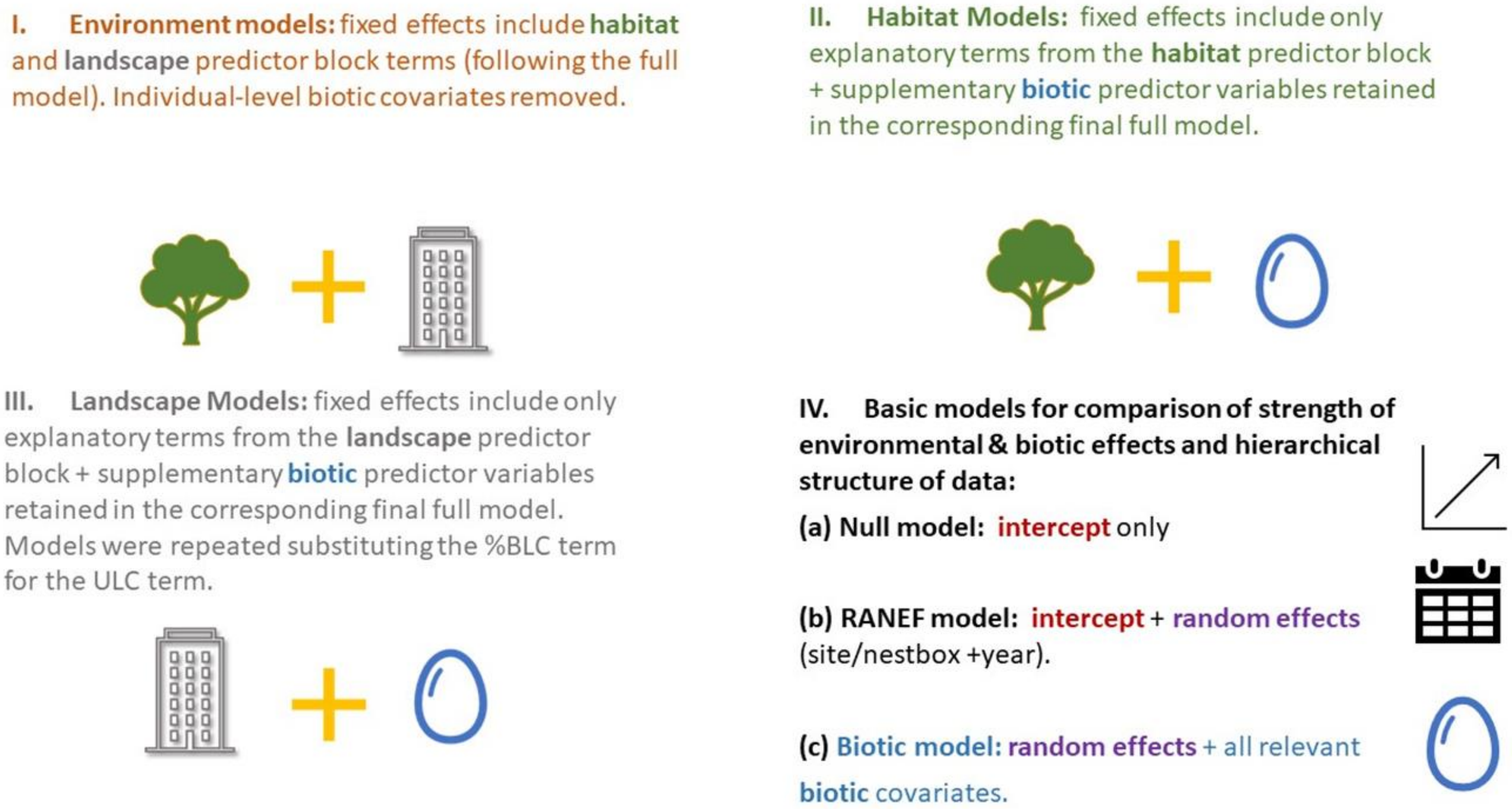
Full (global) models were fitted for each breeding response variable. Models were built by regressing the response variable against all covariates from both environmental (habitat and landscape) predictor blocks, together with parameters from the biotic predictor block. Alternate versions for each breeding model were built, with the categorical fixed effect (ULC) substituted with the linear, continuous variable %BLC. Model structure was otherwise kept as identical as possible to ensure meaningful comparisons.

Global built and ULC models were subsequently tested against a set of four 'nested' (biotic, habitat, landscape and environmental) models (Fig. 2.14), using summary statistics and likelihood ratio tests (ANOVA function) to determine which model(s) provide the best fit.

This approach can help determine if specific habitat and landscape level effects are better detected when considered together in a multi-spatial scale framework using hierarchical modelling rather than when analysed independently. It also enables the identification of potential additive or synergistic (i.e. interlinked) effects that may be operating among variables (Hostetler 2001; Mayor *et al.* 2009; Goddard *et al.* 2010; Pennington and Blair 2011; McGarigal *et al.* 2016; Seress *et al.* 2018). The comparison of global models against 'no biotic covariate' models was undertaken to assess if environmental variable impacts were potentially mediated or masked by the effects of other biotic traits (Satgé *et al.* 2019).

Finally, each model set was further assessed against two null models (i.e. an intercept-only model and a model including random effects terms) to determine how much of the variability in breeding responses may be explained by the hierarchical structure of the data.

For all nested and global models an *a priori* random effects structure was specified (*Year* crossed with the nested term: *Site Identity | Nestbox Identity*) to control statistically for between-year idiosyncratic variation in field season conditions (e.g. weather effects) and the potential spatial non-independence of nestboxes within the same site. Some models failed to converge or could not be validated and random effect structures were modified to account for this.



I. Environment models: fixed effects include **habitat** and **landscape** predictor block terms (following the full model). Individual-level biotic covariates removed.

II. Habitat Models: fixed effects include only explanatory terms from the **habitat** predictor block + supplementary **biotic** predictor variables retained in the corresponding final full model.

III. Landscape Models: fixed effects include only explanatory terms from the **landscape** predictor block + supplementary **biotic** predictor variables retained in the corresponding final full model. Models were repeated substituting the %BLC term for the ULC term.

IV. Basic models for comparison of strength of environmental & biotic effects and hierarchical structure of data:

(a) Null model: intercept only

(b) RANEF model: intercept + **random effects** (site/nestbox +year).

(c) Biotic model: random effects + all relevant **biotic** covariates.

Figure 2.14. Schematic of the set of four models used in analyses to compare against full ULC and built models for the analysis of variation in reproductive performance of a population of Blue Tits breeding across 31 sites stratified along an urban gradient in Birmingham, UK over six years (2013-2018). Habitat and Landscape models were also run with the biotic variables removed. Model structures I-III also included random effects structures. Terms used in the *a priori* RANEF structure were only deleted when issues with model convergence were encountered. The inclusion/exclusion of fixed and random covariates and factors followed the full model. Intercept-only models were fitted with gls and/or glm.

2.5.4. Model validation

The DHARMa: residual diagnostics for hierarchical (multilevel/mixed regression models) package for R (v0.3.3.0; Hartig and Lohse 2020, Hartig 2022) was used to check the validity of statistical assumptions for each model. Scaled residuals were visually inspected using the package's plot functions including Quantile-Quantile plots to detect deviations from the expected distribution for each model and plots of residuals against predicted values. Scaled residuals were plotted against each of the fixed predictors and random effects in the model (and dropped predictors) to detect possible model misspecifications. A suite of 'goodness of fit tests' was used to check for outliers, over/under dispersion and zero inflation. Finally, residuals were assessed for potential spatial dependency against data for individual years and all years combined using bubble plots (e.g. Fig. 2.15) from the *ggplot2* package (v3.1.0 - 3.3.2; Wickham 2011, 2016), and Moran's I analysis using the *spdep* package (v0.7-9 - 1.1-3; Bivand and Wong 2018).

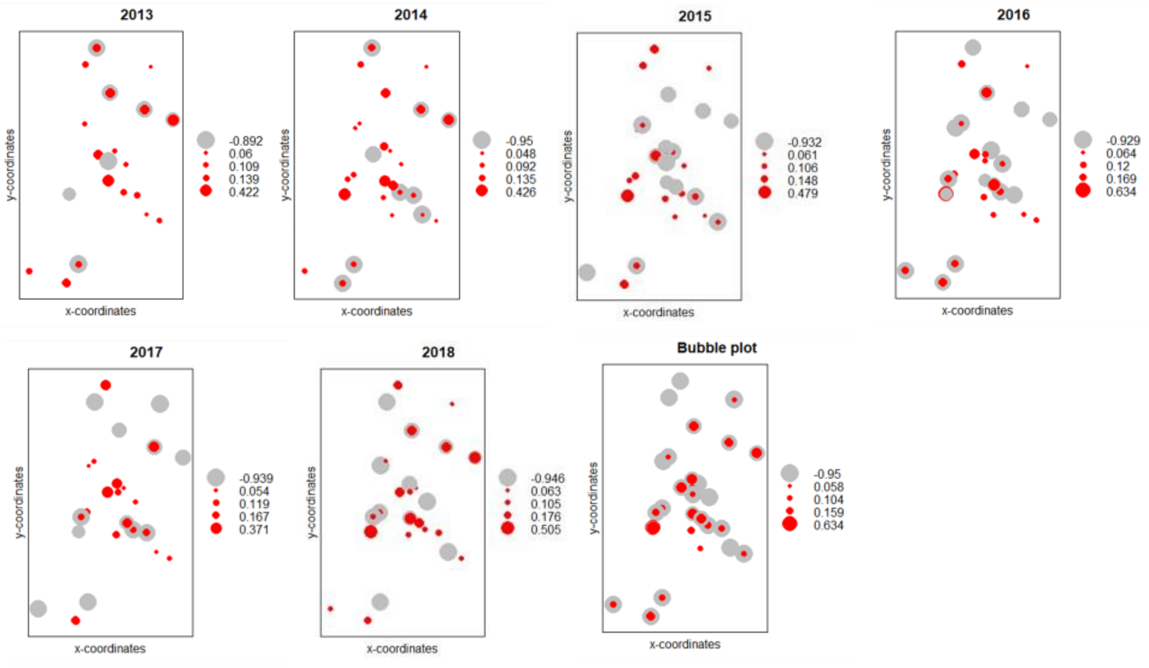


Figure 2.15. Example of the bubbleplots generated of residuals for each individual year and across all six years of a candidate best-fit GLMM model for Blue Tit breeding success demonstrating low levels of spatial autocorrelation.

Chapter Three

The influence of increasing urbanisation on Blue Tit (*Cyanistes caeruleus*) breeding success across a short high resolution urban gradient in the city of Birmingham, UK.

3.1. INTRODUCTION

Urbanisation is an increasing global phenomenon and a major driver of environmental change (Marzluff 2001; Grimm *et al.* 2008; Gaston *et al*. 2015). Urban areas are novel ecosystems (*sensu* Gilbert 1989; Rebele 1994*;* Hobbs *et al.* 2006) characterised by a myriad of different biotic and abiotic changes including fragmented and disturbed habitats (Marzluff 2001; McKinney 2006) increased impervious surfaces (Rebele 1994; Aronson *et al.* 2014), anthropogenic-induced changes in temperature, humidity, light and noise (Marzluff 2001, 2008; Fuller *et al.* 2007; Isaksson 2010; Dominoni *et al*. 2013; Gaston *et al.* 2013; Alberti 2015; Diamond and Martin 2020), high human densities (Evans *et al*. 2006; Seress and Liker 2015) and isolated patches of intensively managed greenspace dominated by non-native and invasive plant species (Pyšek 1998; McKinney 2008; Hahs *et al.* 2009). As such, compared with natural and semi-natural environments, urban landscapes impose novel selective pressures on wildlife (Marzluff 2001; Seto *et al*. 2011; Bailly *et al*. 2016) with potentially long-term fitness consequences to organisms that live and breed in these areas (Alberti *et al.* 2017; Corsini *et al*. 2021).

3.1.1. Defining the urban landscape

The urban landscape can be considered in the context of island biogeography theory (*sensu* MacArthur and Wilson 1967) with isolated greenspace (patches) a parallel to wildlife refugia or habitat islands, surrounded by a matrix of built landform dominated by sealed surfaces (Matthews 2015; Leveau *et al.* 2019; Snell *et al.* 2020).

The urbanisation gradient approach, originally established from traditional models of ecological theory (*sensu* Whittaker 1967 and reviewed by ter Braak and Prentice 1988) was first introduced as a concept and methodology by McDonnell and Pickett (1990). It is now one of the most well-established and recognised frameworks applied in the field of urban ecology and is widely used to examine the response patterns of plants and animals at individual, population and community levels (e.g. as discussed by Marzluff *et al*. 2001; Blair 2004; Pennington and Blair 2013; Aronson *et al.* 2013; Lepczyk *et al.* 2017). Notwithstanding its traction in the scientific literature, the methods used to define and quantify the urban gradient vary considerably, making the comparison and replication of studies difficult (Marzluff *et al.* 2001; Seress *et al.* 2014; Beninde 2015). Indeed, urban landscapes are by their very nature heterogenous and there is no definitive measure that can be employed in urban avian ecological research (McDonnell *et al.* 1993; Blair 2004; Pennington and Blair 2012). Further complicating matters, different aspects of bird demography, behaviour, physiology and morphology respond to the environment at different temporal and spatial scales (McCaffrey and Mannan 2012; Marzluff 2016). Consequently, there are a multitude of potential covariates available for inclusion in the measurement, modelling and assessment of urbanisation impacts (Seress *et al.* 2014). Moll *et al.* (2019) identified 1,177 different urban metrics (mean number of covariates per study: 4.8 ± 7.1 [SD]), from a total of 244 urban ecology studies published between 2012 and 2016. They found that most studies used simple, singular methodological approaches and were spatially variable and/or temporally static. Furthermore, the majority of studies have evaluated urbanisation effects at coarse grained scales (e.g. using whole species' distributions or individual home ranges) and used categorical dichotomous urban-rural comparisons (e.g. Clergeau *et al.* 1998; Björklund *et al*. 2010; Capilla-Lasheras *et al.* 2017; Glądalski *et al.* 2017; Pollock *et al*. 2017; Wawrzyniak *et al.* 2020). Concomitantly, the majority of urban metrics used focus on quantifying the structural components of the urban landscape (e.g. the proportion of area covered by impervious surface; Marzluff *et al.* 2001; MacGregor-Fors *et al.* 2009; MacGregor-Fors 2011).

Furthermore, compared with our knowledge of the affects of habitat features on urban bird communities (e.g. see MacGregor-Fors and Schondube 2011 and references contained therein) few urban breeding ecology studies have explicitly considered the impacts of urban-driven environmental change at the habitat-level including the structure and composition of vegetation (except see e.g. Hinsley *et al.* 2008; Mackenzie *et al.* 2014). Moreover, even fewer studies have simultaneously investigated between site variation in habitat quality together with the wider influence of the urban matrix to identify the effects of anthropogenic environmental change at different spatial scales, or to determine the potential for additive or interactive effects on breeding success (e.g. see de Satgé *et al*. 2019; Strubbe *et al*. 2020).

3.1.2. Urban greenspace as valuable habitats for breeding

For a limited number of urban adapted species, green spaces, particularly parks and gardens, provide an alternative habitat for breeding, in what is an otherwise largely inhospitable matrix, (Solonen and Hildén 2014) and can even support nationally significant wild bird populations (Chamberlain *et al.* 2009). However, evidence increasing suggests that many urban avian populations are experiencing reduced breeding productivity and failure, (Chamberlain *et al*. 2009; Seress and Liker 2015; Bailly *et al*. 2016; Glądalski *et al*. 2016; Pollock *et al*. 2017) leading many researchers to hypothesise cities may be acting as ecological traps (e.g. Sumasgutner *et al*. 2014; Glądalski *et al*. 2015; de Satgé *et al* 2019) and/or habitat sinks (Stracey and Robinson 2012). However, although, widely-studied, the key underlying environmental factors that drive the altered variation in breeding life-history traits and behavioural characteristics of avian species colonising urban landscapes remain poorly understood (Wawrzyniak *et al*. 2015; Corsini *et al.* 2017; Sprau *et al.* 2017). Variation in reproductive performance is likely, at least in part, the direct result of phenotypic or behavioural plasticity associated with learning (Sol *et al*. 2013). In particular, studies have attributed the capacity of individuals to adjust specific traits as a response to changes in (and the interaction between) population/breeding density, inter- and intra-specific competition and the quality, quantity and availability of food as predicted by the food limitation hypothesis (Anderies *et al*. 2007; Robb *et al*. 2008; Amininasab *et al*. 2016; Demeyrier *et al*. 2017; Seress *et al*. 2018, 2020). Alternatively, other authors have more recently proposed that adaptive differences in life history traits across landscape gradients may exist due to the "pace of life" theory and the "adult survival hypothesis" (Sepp *et al*. 2018; Wawrzyniak *et al*. 2020). Yet reproductive success is fundamental to the long-term stability of populations and the survival of species', particularly in areas that have already experienced extensive population declines, biodiversity loss and change due to human-mediated disturbance (Peach *et al*. 2008; Stracey and Robinson 2012; Seress *et al*. 2020). Consequently, the impacts of urbanisation on reproduction have become an increasingly important focus for urban ornithological research and in particular for assessing the adaptability of small insectivorous passerines including Blue and Great Tits, that are predicted to be among the species most likely to disappear (Chace and Walsh, 2006; Mackenzie *et al.* 2014).

Furthermore, there have been growing calls to shift the focus of urban ecological research to a more multi-scale and species-centric approach, and for the incorporation of more standardised, quantitative metrics to measure the urban gradient, as utilised for example by Biard *et al.* (2017), Sprau *et al*, (2017), Satgé *et al.* (2019) and Corsini *et al.* (2021). This shift in methodology takes into consideration the scale at which species experience their environment and the complexity of responses to rapidly changing environments, recognising that the landscape is not simply a mosaic of habitat and non-habitat (Pennington and Blair 2013; Cole *et al.* 2015; Moll *et al.* 2019).

3.1.3. Identification of indicators of habitat heterogeneity and quality for assessing breeding success

Local (i.e. breeding territory) habitat varies both spatially and temporally with respect to both resource availability and prevailing environmental conditions, as reviewed by Johnson (2007) and Piersma (2012) and therefore generates strong selective pressures on wildlife (Cody 1985; Chalfoun and Schmidt 2012). The quality of natural breeding habitat is, therefore, widely recognised as a major predictor of avian fitness (Dhondt *et al*. 1992; Germain and Arcese 2014; Shutt *et al.* 2018) and has been shown to impact many aspects of the reproductive cycle (Tremblay *et al.* 2004) including breeding phenology (Wilkin *et al.* 2007b), clutch size (Tremblay *et al.* 2003), chick growth and development (Sánchez *et al.* 2007), nestling survival to fledging (Dekeukeleire *et al.* 2019) and adult breeding condition (Atiénzar *et al.* 2010).

Habitat quality, estimated using various indices of vegetation structure and composition (Germain and Arcese 2014; Amininasab *et al.* 2016) affects temporal and spatial resource availability, including the abundance of caterpillars (*Lepidoptera spp.*) which are the preferred prey of Blue Tits during the energy-intensive breeding season (Perrins 1991; Blondel *et al.* 1993; Dias and Blondel 1996; Tremblay *et al.* 2003). Previous studies investigating breeding productivity in tits in more natural woodland habitats have shown that the composition of the dominant vegetation is key in driving spatial-temporal variation in breeding phenology and breeding success (e.g. Perrins *et al.* 1965; Van Balen 1973; Blondel *et al.* 1991, 1993; Tremblay *et al.* 2005). In particular the diversity and density of native species including Oak (*Quercus* spp.) that support rich and abundant caterpillar communities are important indicators of breeding habitat quality and reproductive success (Perrins 1991; Shutt *et al.* 2018; Dekeukeleire *et al.* 2019). Other structural features of the habitat including the size and density of woodland patches (Hinsley *et al.* 2002), as well as the age, height and size of individual trees (Hinsley *et al.* 2008; Arriero *et al*. 2006) also influence the trophic quality and therefore the availability of prey.

Site area (Fernández-Juricic 2000; Murgui 2007; Oliver *et al.* 2011; Huang *et al.* 2015) and habitat edges (Murcia, 1995; Fernández-Juricic 2001; Zurita *et al*. 2012) are also important determinants of habitat heterogeneity and quality. The size of greenspace may influence breeding behaviour and success due to variation in the amounts of protective cover, predation, natural food availability and levels of human disturbance (e.g. Fernández-Juricic and Tellería, 2000; Glądalski *et al.* 2016; Corsini *et al.* 2017). Habitat edges represent the transition between the more stable, higher quality interior of greenspaces and the lower quality, highly complex and variable urban matrix (e.g. see Hedblom and Söderström 2012). Edge effects typically reduce habitat quality and further reduce the functional size of greenspaces, and thus may influence reproductive performance and the movement of individuals within sites and across the wider landscape (Hinsley, 2000; Hinsley *et al.* 2008).

To address the current data gaps identified, in this chapter I investigate how different parameters of breeding success vary across a short, highly urbanised intra-city gradient in a population of Blue Tits nesting within the city of Birmingham, UK. I explore how the magnitude and direction of urban-driven habitat and landscape scale effects vary within and between two distinctive phases of the reproductive cycle using a suite of breeding success metrics widely used in avian reproductive research. The multi-spatial scale and nested design employed within this study also allows for the exploration of cumulative and interactive environmental effects that may be operating across different hierarchical levels of the urban environment.

3.1.4. Study aims hypotheses

I aim to identify key habitat and landscape characteristics of the urban environment that influence reproductive performance during two distinct periods of the breeding season: pre-hatching (from laying through to hatching) and post-hatching (from hatching through to fledging). I also aim to determine how the specification of the urban gradient affects the sensitivity of statistical models to detect and predict urban-driven environmental effects by comparing and evaluating analyses for each breeding response using two contrasting measures ("spatial grains") of urbanisation: a qualitative categorical (five level) factor and a quantitative (linear percentage) fixed effect.

My working hypotheses for this study are that:

(1) With the exception of clutch size, a pervasive negative effect of increasing urbanisation will be observed for all measures of reproductive success. However, clutch size across sites within the city are predicted to be on average smaller compared with the average clutch size commonly documented for Blue Tits breeding in rural oak woodlands (e.g. Perrins, 1979), as a potential adaptive response to lower habitat quality and the availability of food resources (e.g. see Cowie and Hinsley 1987; Solonen 2001; Chamberlain *et al.*, 2009; Bailly *et al.*, 2016)

(2) Variation in all successive breeding outcomes (i.e. hatching through to fledging) will be influenced by environmental effects operating at both habitat and landscape scales.

(3) More specifically breeding metrics will be negatively correlated with the size (area) of greenspace due to potentially increased levels of intra- and inter-species competition for resources.

(4) Measures of breeding success across both phases of reproduction considered will be positively correlated with the density of native broadleaved trees including Oak (*Quercus spp.*) and Birch *(Betula spp.*) and the diversity of vegetation (used as proxy measures of habitat quality).

(5) Overall the availability of gardens, (hypothesised to be linked to potential variation in supplemental bird feeding) will have a negative impact on breeding outcomes.

(6) Pairs breeding in nestboxes nearer to the edge of connected tree cover will produce smaller broods and fewer fledglings and suffer greater brood reduction and loss compared with their conspecifics nesting towards the centre of habitat patches.

(7) The quantitative measure of urbanisation is predicted to be a more reliable and sensitive predictor of variation in breeding responses compared with the traditional categorical approach to defining the urban gradient.

3.2. METHODS

3.2.1. Study site and focal species

Full details of the focal species, background of the study design and field data collection are described in Chapter Two.

3.2.2. Breeding success response variables

Variation in breeding performance across the urban gradient was evaluated using the suite of breeding response variables derived from the raw data collected during nestbox checks as described in section 2.4.1 and illustrated in Fig. 3.1.

Pre-hatching success was analysed using clutch size, proportional hatching success, binary hatching success and brood size metrics, whilst post-hatching success was analysed using fledgling numbers, proportional fledging success and binary fledging success metrics. Total variation in breeding success, measured across the entire laying-fledging period (hereafter referred to as breeding season or cycle) was assessed using overall breeding and binary success parameters.

Hatching success, used here to determine how hatching rates vary across the urban gradient, was calculated as the proportion of all eggs laid in a clutch that hatched (Bailly *et al.* 2016). Fledging success was calculated as the number of chicks estimated to have fledged as a proportion of brood size (Pollock *et al.* 2017) and was used to compare rates of brood reduction across the urban gradient. The comparison of hatching and fledging rates for each nesting attempt was used to determine how failure and loss varies both across different stages of the breeding season and the urban gradient. Breeding success, expressed as the number of chicks that fledged as a proportion of clutch size (Hinsley *et al*. 1999; Lambrechts *et al.* 2004), was used to determine how rates of success vary across the urban gradient, taking into consideration all nesting attempts that reached incubation, and all failures that occurred during both pre-hatching and post-hatching.

Binary (probabilistic) metrics were used to assess variation in nesting failure rates across the urban gradient for each breeding stage. Nesting attempts, for example, were defined as successful (i.e. binary outcome: 1) if ≥ 1 egg hatched or ≥ 1 chick fledged and failed (i.e. binary outcome: 0) if no eggs hatched or chicks fledged.

Evidence e.g. remains of chicks used to estimate fledging and breeding success after 20 days (post-hatch date)

Evidence of total brood failure due to starvation

Image shows an example of complete hatching failure due to predation

Figure 3.1. Graphical illustration of the pre-hatching (highlighted in yellow) and post-hatching (highlighted in pink and blue) breeding response variables derived from field data (2013-2018) and used in analyses to investigate how reproductive success in a population of Blue Tits varies along a fine-scale urban gradient in the city of Birmingham, UK.

3.2.3. Abiotic and biotic covariates

The selection, classification and measurement of environmental covariates are described fully in Chapter Two and summarised in Table 3.1.

Table 3.1. Details of the final variables selected from three predictor blocks for inclusion in full statistical models used to analyse breeding outcomes of Blue Tits nesting in Birmingham, UK between 2013 and 2018. Variables were generated from survey work, GIS and a literature review as described in Chapter 2. Habitat and landscape predictors are specified as site level means and breeding variables as individual-level covariates (with the exception of Occupancy Rate). Explanatory variables were fitted as fixed (numeric) covariates (FCs) with the exception of Urban Land Class (ULC: factor).

Variable name	Predictor block	Details
Mean NDB Trees (NDB Trees)	Habitat	FC: Mean number of native deciduous broadleaved trees recorded within a 10 m radius of an average nestbox (based on four within-site surveys).
Inverse Simpson's Diversity Index: (InvSI)	Habitat	FC: Site mean calculated from four nestbox surveys using total tree counts and species (excluding coniferous species). Value ranges: 1.615 - 11.524 (Simpson's Diversity Index = 0.381 - 0.913).
Mean Distance to a Connected Edge (Edge Distance)	Habitat	FC: Quantification of potential edge effects on breeding. Mean distance (m) of nestboxes to nearest connected edge. Average calculated from the measured distances of 10 nestboxes at each site.
$_{\log10}$Site Area (m^2)	Habitat	FC: Total area of greenspace (site) in which nestboxes were located.
% Built Landcover(%BLC)	Landscape	FC: Total % landcover within a 500 m concentric buffer of each site categorised as 'built' (including buildings, roads, railways, pavements and other sealed surfaces).
Urban Land Class (ULC)	Landscape	Categorical: Alternative measurement of urbanisation. Sites assigned to one of five urban classes based on % of built landcover.
% Garden Cover (%GLC)	Landscape	FC: Total % private garden landcover within a 500 m concentric buffer of each site.
Proportional Occupancy	Biotic	FC: Total number of nestboxes occupied within a site in a given breeding year specified as a proportion of the total number of available nestboxes (range in availability = 6 - 10). (Site level fixed effect).
April Laying Date	Biotic	FC: Ordinal date of clutch initiation (specified as number of days after April 1st in each breeding season).
April Hatching Date	Biotic	FC: Date on which the first chick of a brood hatched (specified as number of days after April 1st in each breeding season).
Clutch Size	Biotic	FC: Total number of eggs laid for each breeding attempt (attempts not reaching incubation excluded).
Brood Size	Biotic	FC: Hatchlings (the maximum number of chicks alive at hatching).

From the list of potential habitat and landscape variables identified for inclusion in analyses (Table 2.4), a total of seven covariates were *a priori* used in models of breeding success (Table 3.1). This final selection was primarily determined following checks for multi-collinearity between explanatory variables using VIFs (section 2.5.2), whilst taking into consideration constraints on the number of terms that can be included in models (associated with their limited power relative to the amount of data).

Precedence was given to retaining urbanisation metrics (%BLC and ULC): they directly relate to the urban gradient and best capture the important aspects of variability in landscape patterns and structure across the city (Riitters *et al.* 1995; Hahs and McDonnell 2006; Moll *et al.* 2019). Furthermore, these metrics provide a common element, which will help facilitate the integration of results from this study with those from research conducted on other Blue Tit populations and other passerine species with similar life histories (McDonnell and Hahs 2008).

The final selection of habitat variables was largely informed by previous research investigating the effects of habitat on breeding success in urban birds (e.g. Hinsley *et al.* 2008; Chamberlain *et al.* 2009; Hedblom and Söderström 2012; Mackenzie *et al.* 2014), whilst ensuring that variability in the structure, composition and quality of average breeding territories of Blue Tits across sites within the city was captured.

Individual-level breeding (biotic) covariates were selected based on their potential influence on subsequent breeding responses. April laying date was included in pre-hatching models to account for the well documented seasonal decline in early Blue Tit breeding success (Perrins 1979; Perrins and McCleery 1989; van Noordwijk *et al*. 1995; Visser *et al*. 2006). Hatching date was included in post-hatching models to control for seasonal declines in nestling survival associated with the progressive phenological mismatch between natural food availability and peak nestling nutritional demand (Naef-Daenzer *et al.* 2000; Thomas *et al.* 2001).

Other breeding parameters were also included in models as appropriate due to their potential influence on each other (Charmantier *et al.* 2017). Brood size, for example is known to be positively correlated with clutch size, whilst fledgling numbers and fledging success may be influenced by brood size, due to within-nest competition (de Satgé *et al.* 2019). The proportion of available nestboxes occupied in each site was *a priori* included as a fixed term in all statistical models to control for the potential negative effects of breeding density and competition on breeding success (Dhondt *et al.* 1992; Kempenaers *et al.* 1996).

Since binomial success measures assessed the overall productivity of nests and hence took into consideration other components of breeding (Satgé *et al.* 2019), only phenological and occupancy covariates were included in these statistical models.

3.2.4. Statistical analysis

3.2.4.1. Data Filtering

Studies investigating breeding ecology in passerines have previously routinely only focussed on successful nests by filtering out 'zero data' from each phase of the breeding cycle. For example, they have excluded total hatching failures from measures of hatching success or total brood failures from measures of fledging or overall breeding success when conducting statistical analyses (e.g. Hinsley *et al.* 1999; Glądalski *et al.* 2017; Satgé *et al.* 2019; but see Bailly *et al.* 2016; Seress *et al.* 2018). However, as suggested in more recent studies (e.g.

Charmantier *et al*. 2017; Wawrzyniak *et al*. 2020), it is important to consider that the ratio of total to partial losses may vary across urban gradients and/or total nest failures may be caused by different factors from those leading to partial losses (e.g. predation or extreme weather events (EWEs) versus temperature or food availability/quality).

Taking these points into consideration, my study adopted a conservative approach, which involved including: (1) total nesting failures in all measured outcomes and (2) a separate set of analyses to determine nest failure rates across the urban gradient for each breeding phase, following Bailly *et al.* (2016) and Seress *et al.* (2018).

Zero data for specific breeding periods were filtered out from the raw data, generating three distinct datasets which were used in this and subsequent sets of analyses (Appendix 2). The first, 'clutch-filtered' dataset (n = 752 observations) was limited to only nesting attempts in which incubation was confirmed, to exclude the effects of nest abandonment prior to clutch completion in subsequent analyses. This dataset retained all records of complete hatching failure that occurred post-incubation. To exclude the effects of nest abandonment during incubation, the second 'hatching-filtered' dataset (n = 662 observations) only included records in which at least one egg hatched successfully. This dataset retained breeding attempts which resulted in complete brood failure. The third ('fledging-filtered') dataset (n = 554 observations) only included records in which at least one chick successfully fledged.

3.2.4.2. Analytical framework and models

Data cleaning and exploration prior to analyses were undertaken as described in section 2.5.2. A total of three landscape- and four habitat-scale explanatory variables (VIFs <3; Table

3.1) were ultimately retained for inclusion in models, together with covariates from the biotic predictor block as appropriate.

Site area was linearised ($\log_{10}$ transformed) to improve its distributional properties. Quadratic terms for built landcover (%BLC), garden landcover (%GLC) and Inverse Simpson's Index (InvSI) were fitted and retained in models as required given the spread of the data. All fixed effect covariates were standardised using a z-score transformation (to obtain a mean of 0 and SD of 1) prior to modelling to prevent potential issues with model convergence and aid the interpretation of regression coefficients (Schielzeth 2010). Except for the main regression results tables, the non-transformed values for predictors are displayed in text and figures. Additional interaction terms were not considered for analyses since there were no specific *a priori* expectations for their inclusion and no attempt was made to simplify models using dredging or stepwise term deletion.

The final (global) model parameterisation used in the analysis of each breeding response variable is illustrated in Fig. 3.2, whilst details of the fixed and random effects structures for each model are provided in the accompanying Appendix 3. Analyses were conducted on each metric using the appropriate 'unfiltered' dataset (i.e. retaining true-zero data – Appendix 2).

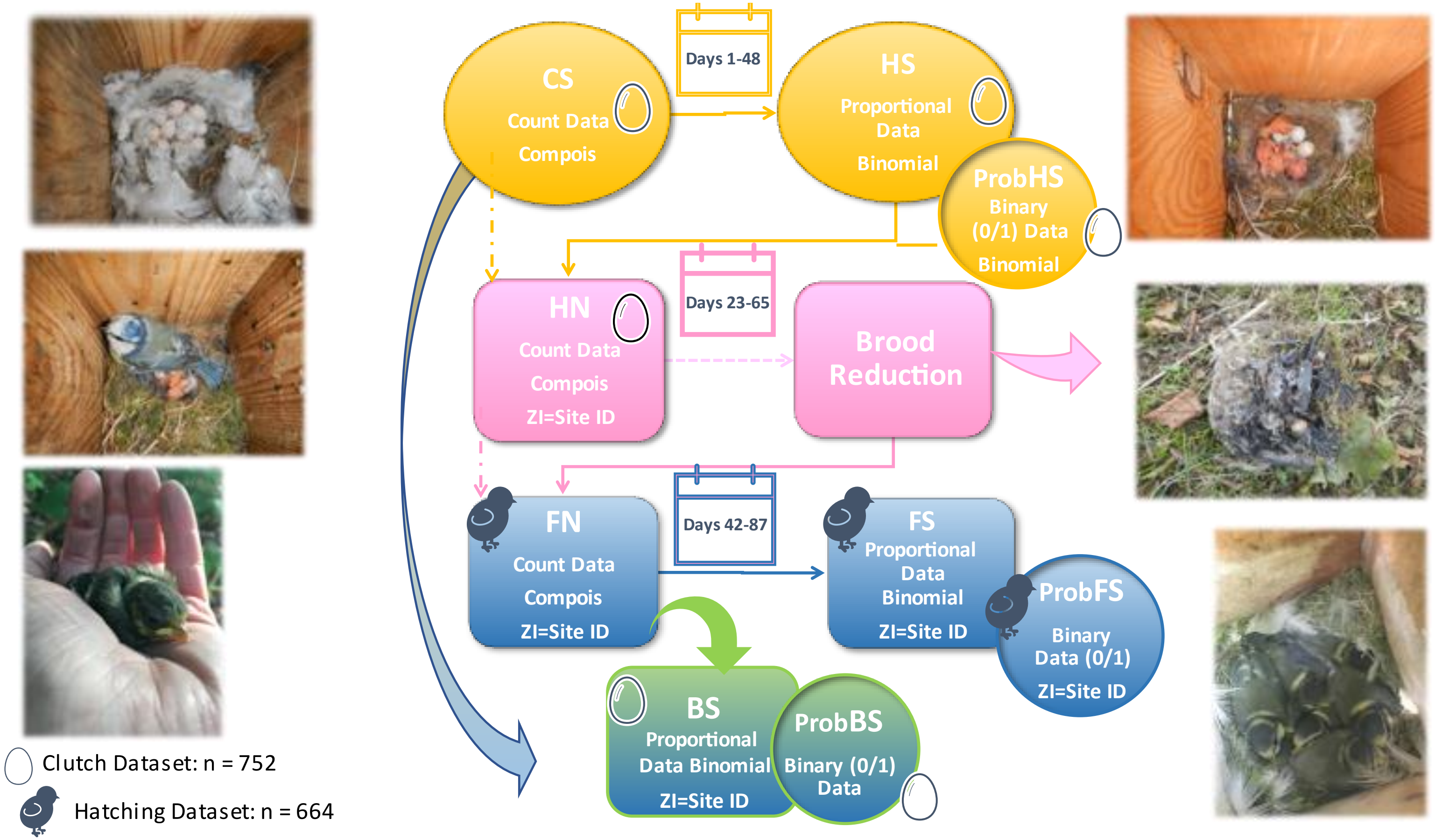


Figure 3.2. Schematic diagram of the analyses used to investigate the variation in Blue Tit breeding success across the intra-city urban gradient in the city of Birmingham, UK. Breeding performance was evaluated for two breeding phases using a total of nine response variables: pre-hatching (yellow and pink) and post-hatching (blue). Information for each response includes the dataset used in analyses, the type of data (i.e. count, proportional or binary), and the distribution of data/family used in model parameterisation (Conway-Maxwell Poisson [compois] or binomial). April days (April 1st = 1) are given for minimum and maximum laying, hatching and fledging dates (from across the six years of data collection). CS = clutch size; HN = brood size (total **n**umber of chicks **h**atched); HS = proportional hatching success; ProbHS = probability of hatching success (binary); FN = Fledgling numbers; FS = proportional fledging success; ProbFS = probability of fledging success (binary); BS = overall breeding success & ProbBS = overall binary success/failure of the nest.

Clutch size (CS), brood size (total number of chicks hatched; HN) and fledgling number (FN) models (Fig. 3.2) were measured using discrete count data and were specified with Poisson distributions. Models were parameterised using a Conway-Maxwell-Poisson (CMP) distribution (Shmueli *et al.* 2005; Barriga *et al.* 2014; Lynch *et al*. 2014) with the compois family (Brooks *et al.* 2017, 2019) to correct for the under-dispersed nature of the data. Hatching success (HS), fledging success (FS) and breeding success (BS) (proportional responses) and $_{\text{prob}}$HS, $_{\text{prob}}$FS and $_{\text{prob}}$BS (equivalent binary responses) models (Fig. 3.2) were fitted with binomial distributions (Zuur *et al.* 2009, 2013; Bolker 2017). Clutch size was dropped as a fixed biotic covariate from HN models and hatching date and brood size from FN models due to issues with Quantile-Quantile plots and the distribution of residuals. Proportional occupancy was dropped from the FS (ULC) model due to validation issues caused by co-correlation with landscape terms.

Zero-inflation models (Brooks *et al.* 2017, 2019) were fitted, with zi-formula specified as *Site Identity*, to account for the high number and unequal distribution of zeros across sites in HN, FN, FS, and BS (ULC and built) models. GLMMs were fitted using maximum likelihood estimation via the Template Model Builder (Brooks *et al*. 2017). The upper and lower bounds of the 95% confidence intervals (CIs) were computed using the confint function for all fixed parameters in each final model, using a comparison of wald, profile and boot-strapping methods.

Ideally, female identity would have been included as a random effect in analyses to control for non-independence of individuals breeding across multiple years (Cole *et al.* 2015; Demeyrier *et al.* 2017). Together with the inclusion of measures of individual fitness or social dominance (e.g. adult body size, condition and age) this would have captured potentially confounding effects of parental quality on variation in breeding traits (Przybylo *et al*. 2001; Lambrechts *et al.* 2004). However, trapping efforts at nestboxes were largely unsuccessful, with females in particular, exhibiting aggressive and neophobic behaviours (e.g. see also Miranda *et al.* 2013; Sepp *et al.* 2018), including a reluctance to re-enter nestboxes following the placement of traps inside them. This led to significant variation in adult trappability across sites and years, resulting in a total of only 297 captures ranging from six in 2013 to 98 in 2018. Therefore, due to small sample sizes and the potential for capture data to be biased towards certain sites and/or particular parental phenotypes (Cole *et al.* 2015), adult variables were excluded from analyses.

The urban gradient was defined using two different metrics in this study: a categorical effect (ULC) and linear, quantitative variable %BLC (section 2.2.3.). For each breeding response, models were tested by using both measures of urbanisation as illustrated in Fig 3.3 below. This comparative approach was undertaken to investigate which urban metric best predicted the effects of increasing urbanisation on different breeding outcomes and if the measurement used influenced the ability of models to predict the effects of other landscape and habitat level variables. Finally for each breeding response, the hierarchical modelling procedure was followed, as described in section 2.5.3 and illustrated in Fig. 3.3.

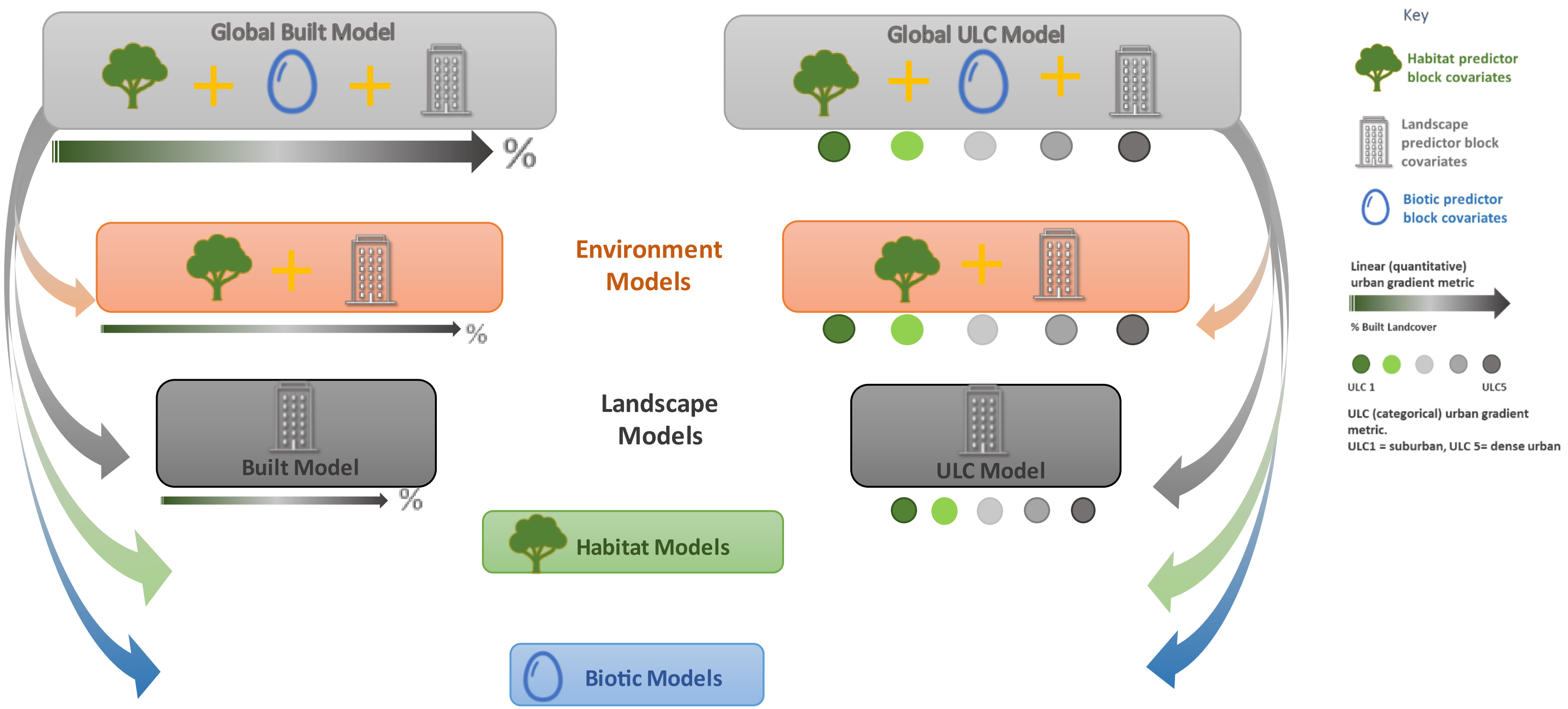


Figure 3.3. Schematic diagram of the hierarchical modelling framework used in the analysis of breeding response variables of Blue Tits nesting across an urban gradient in Birmingham, UK (2013-2018). Global ULC and %BLC models for each breeding trait were tested by removing each predictor block to determine the extent to which environmental parameters at different spatial scales explained variation in breeding performance across the urban gradient and ascertain if environmental effects on breeding were potentially being obscured or mediated by the influence of other breeding traits. Each model set was also assessed against two null models (an intercept only model and a model including random effects terms) to determine how much of the variability in breeding responses may be explained by the hierarchical structure of the data. Environment, landscape and habitat models for each response variable were run both with and without the associated biotic covariates included. All model structures (including random effects, zi formula and family) followed the global models. All models were compared against an intercept-only and random effects model (using glm).

All reported statistical inferences are for the final full models analysed, with all predictor variables retained unless otherwise specified. Predictors were considered of importance where z score values ≥ 1.5 (with the two-tailed statistical significance level defined as $P \leq 0.05$). Where CIs of β-estimates crossed zero, covariates were considered to have no effect. Reported predicted values for specific significant model terms and their effect on responses were generated by computing model-fitted terms. All other covariates were fixed at constant (mean) values, apart from ULC which was specified as a fixed categorical factor with base level ULC1. Accompanying plots were created using *ggplot2* (v3.1.0 - 3.3.2; Wickham 2016).

3.3. RESULTS

3.3.1. Summary of breeding success statistics

Of the 786 breeding attempts recorded over the six years of the study, a total of 752 (95.67%) reached the onset of incubation and were retained for analyses (Table 3.2). Twenty-eight breeding attempts were excluded from the dataset due to nest abandonment prior to incubation. A further six nest records were removed from the dataset, including: one instance of a double clutch laid by two separate females in the same nestbox; two cases of missing breeding data due to site access issues; vandalism resulting in the unknown outcome of one brood post-hatching, and two presumed second laying attempts by pairs late in the season (*sensu* Perrins 1979; Wilkin *et al.* 2006).

Table 3.2. Annual breeding records (2013-2018) for a population of Blue Tits nesting along a linear urban gradient within the city of Birmingham. Breeding data were collected from 280 nestboxes across 28 sites. For each year, the number of occupied nestboxes is provided, (total number available for breeding in parentheses), together with the total number of breeding attempts that reached each phase of the breeding season investigated (egg-laying to fledging).

	Total breeding attempts	**Number of breeding attempts reaching:**		
Year	**Number of nestboxes occupied (Max. N = 280)**	**Clutch completion**	**≥ 1 Chick hatched**	**≥ 1 Chick fledged**
2013	69 (279)	64	62	53
2014	138 (272)	129	110	99
2015	155 (276)	148	122	102
2016	136 (266)	134	126	99
2017	135 (253*)	129	115	91
2018	149 (240**)	148	127	110
Total	782 (1586)	752	662	554

*Moilliett Street removed from the study due to site safety issues and **Park Street Gardens due to HS2 works (see Chapter 2).

Data from three sites (Popes Lane, RSPB Sutton Park and Perry Hall Playing Fields: Table 2.2 and Fig. 2.8) were subsequently excluded from analyses due to persistent and high levels of predation resulting in high rates of complete breeding failure during egg laying. Consequently, for the rest of the thesis the remaining 28 sites only are considered. Furthermore, whilst Moilliett Street and Park Street Gardens were retained in analyses, data for these two sites were only available up to and including 2016 and 2017, respectively. Monitoring at Moilliett Street was discontinued during the 2017 breeding season due to ongoing safety concerns and continued vandalism of nestboxes. Data collection in Park Street Gardens ceased due to the commencement of works associated with the HS2 rail project which prevented access from winter/spring 2018.

3.3.2. Comparison of global with nested models

Across all breeding responses, global models performed better compared with null and random effects only models. Moreover, the results of ANOVA tests, comparisons of AIC values and model summary outputs suggest that global models were more likely to detect potential effects of habitat and landscape-scale covariates and provided stronger evidence for significant predictor-response relationships, compared with associated nested (habitat-only and landscape-only) model structures (models II-III as illustrated in Fig. 2.14 and Figs. 3.2-3.3). A comparison of global models with models retaining only environment predictors (habitat + landscape models) (model I in Fig. 2.14), confirmed that biotic covariates were unlikely mediating or concealing the effects of the environment at the habitat or landscape scale.

3.3.3. Pre-hatching breeding success

Pre-hatching (laying – hatching) breeding success parameters were best explained using the categorical ULC metric. Moreover, results from statistical models suggest that early breeding outcomes were more strongly impacted by breeding phenology (April laying date) and variation in the characteristics of the habitat surrounding nestboxes, rather than the degree of built or garden landcover within the wider urban matrix.

3.3.3.1. Clutch size

On average pairs breeding in the city laid 8.81 ± 1.82 eggs (mean ± SD, total range = 2-16 eggs, n = 752 clutches). As hypothesised, there was no discernible effect of increasing built landcover on clutch size (Fig. 3.4 and Table 3.3) using either the continuous fixed covariate or categorical urbanisation metric.

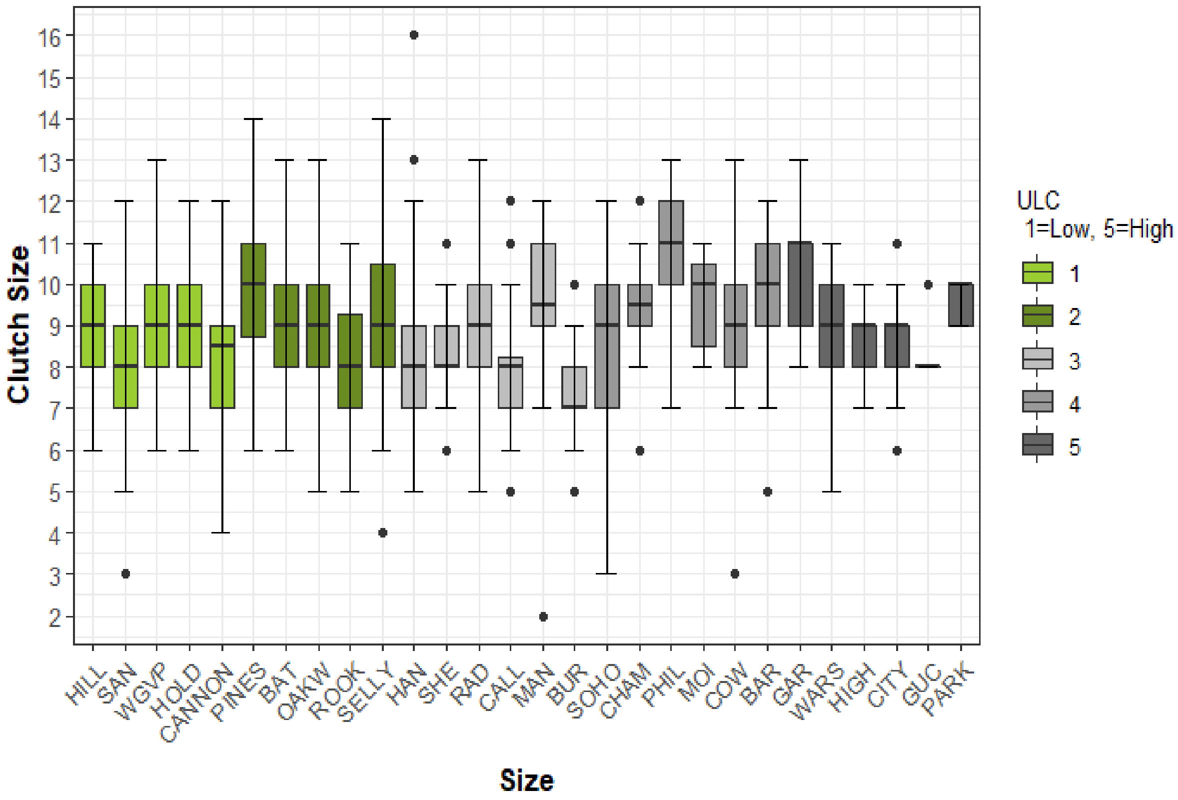


Figure 3.4. Boxplot summaries of clutch size in Blue Tits nesting across 28 sites along an urban gradient in Birmingham, UK over 6 breeding seasons (2013-2018). Black lines within boxes indicate the median number of eggs laid, upper hinges the 75th percentile and lower hinges the 25th percentile of the clutch data. The vertical lines ('whiskers') indicate the minimum and maximum number of eggs laid. For sites with outliers (represented by points), whiskers extend to 1.5 times the inter-quartile range. Sites are in order of increasing %BLC and categorized into one of five urban landcover classes (ULC1=least urbanised (suburban) sites and ULC5 = dense urban). Site acronyms (Table 2.2) and locations (Figs. 2.8) are provided in sections 2.2.3 (Chapter 2).

Table 3.3: Model summaries from a GLMM analysis of Clutch Size for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). $^{\bullet}$ indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Analyses based on data from 752 breeding attempts.

	Clutch Size (CS Built Model)			**Clutch Size (CS ULC) Model**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**
Intercept	2.348±0.028			2.196 ± 0.046		
Year: 2014	**-0.207 ± 0.032*** **	**-6.41**	**-0.270, -0.144**	N/A	N/A	N/A
2015	**-0.181 ± 0.029*** **	**-6.13**	**-0.238, -0.123**	N/A	N/A	N/A
2016	**-0.160 ± 0.028*** **	**-5.74**	**-0.215, -0.106**	N/A	N/A	N/A
2017	**-0.308 ± 0.034*** **	**-9.10**	**-0.374, -0.241**	N/A	N/A	N/A
2018	**-0.129 ± 0.030*** **	**-4.29**	**-0.188, -0.070**	N/A	N/A	N/A
Me NDB Trees	0.010 ± 0.014	0.67	-0.018, 0.037	0.019 ± 0.012	1.56	-0.005, 0.043
Inverse Simpson's Index	-0.009 ± 0.013	-0.70	-0.034, 0.016	-0.028 ± 0.012*	-2.43	-0.051, -0.006
Inverse Simpson's Index^2	N/A	N/A	N/A	-	-	-
Mean Edge Distance (m)	-0.0279 ± 0.015$^{\bullet}$	-1.83	-0.058, 0.002	-0.030 ± 0.017$^{\bullet}$	-1.80	-0.063, 0.003
Site Occupancy	0.011 ± 0.0117	0.96	-0.012, 0.034	0.014 ± 0.011	1.22	-0.008, 0.036
(log) Site Area (m^2)	-0.027 ± 0.016$^{\bullet}$	-1.67	-0.058, 0.005	-0.006 ± 0.013	-0.48	-0.032, 0.019
Garden Landcover (%)	-0.006 ± 0.014	-0.43	-0.033, 0.021	0.021 ± 0.020	1.05	-0.018, 0.060
Built Landcover (%)	0.001 ± 0.018	0.08	-0.034, 0.037	N/A	N/A	N/A
ULC Model: ULC 2	N/A	N/A	N/A	-0.054 ± 0.052	-1.06	-0.155, 0.047
ULC 3	N/A	N/A	N/A	-0.084 ± 0.035*	-2.41	-0.152,-0.016
ULC 4	N/A	N/A	N/A	0.066 ± 0.045	1.45	-0.023, 0.155
ULC 5	N/A	N/A	N/A	0.088 ± 0.053$^{\bullet}$	1.67	-0.016, 0.191

April Laying Date	-0.120 ± 0.009***	-13.64	-0.138, -0.103	-0.119 ± 0.009***	-13.20	-0.136, -0.101
Random Terms	Variance ± SD			Variance ± SD		
Box: Site ID	0.006 ± 0.075			0.006 ± 0.076		
Site ID	0.002 ± 0.045			0.001 ± 0.026		
Year	N/A	N/A	N/A	0.008±0.090		

The lack of any correlational effect of urbanisation on clutch size was likely compounded by the paucity of data from the most urbanised sites and the comparatively more pronounced variation observed in the number of eggs laid between females breeding within the same site (Fig. 3.4).

Both built and ULC models detected a strong seasonal effect of laying date on clutch size across urban greenspace (Table 3.3 and Fig. 3.5), with a significant decline in the number of eggs laid with later breeding. Model predictions suggest a reduction in clutch size with laying date from ~10.5 eggs at the beginning of the breeding season (around April 1st) to ~7.0 eggs by mid-May (Fig. 3.5).

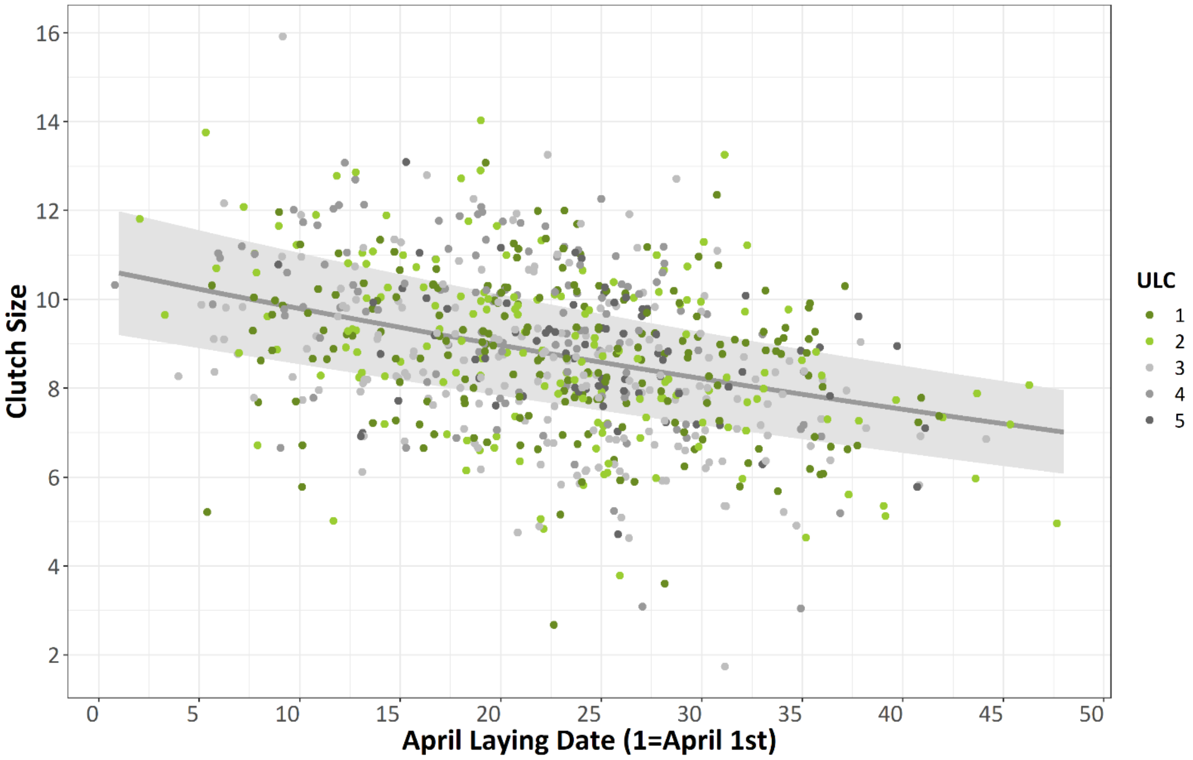


Figure 3.5. The negative correlational relationship between April laying date and clutch size of Blue Tits nesting along an urban gradient in the city of Birmingham, UK, over six breeding seasons (2013-2018). Raw data are represented by coloured points, categorized by urban land cover (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a zero inflated Conway Maxwell Poisson Model.

Mean clutch size across urban greenspace in Birmingham was very similar over the six breeding seasons, except for 2016 when an overall drop in the number of eggs laid per breeding attempt was observed (mean = 8.36 ± 1.69 eggs). In contrast to between-year variability, there was a greater degree of variation in clutch size between breeding females within individual years (e.g. clutch size standard deviations ranged between ± 1.62 eggs in 2013 to ± 1.94 eggs in 2014).

There was very little difference between the outputs of the final ULC and built models. Notwithstanding a moderate negative effect of broadleaved tree diversity (ULC model; Table 3.3), variation in clutch size was not explained by any covariates associated with the habitat surrounding nestboxes, the availability of garden landcover or the occupancy rate of sites.

3.3.3.2. Hatching Success

Hatching success was best explained using the ULC model (Table 3.4), and was significantly correlated with several habitat and landscape variables. Including total clutch failures, the average proportion of eggs surviving to hatch per nest varied across years and sites, from a mean of 0.46 ± 0.51 (mean ± SD; n = 5 nests from five breeding seasons) in Park Street Gardens to 0.97 ± 0.06 (n = 16 nests from six breeding seasons) in Chamberlain Gardens (Fig. 3.6). When total nesting failures were excluded from the data, this resulted in an increase in hatching success statistics for most sites. The mean hatching success rate in Park Street Gardens, which remained the lowest performing site using this dataset, for example, increased to 0.77 ± 0.40 (n = 3 nests).

Table 3.4. Model summaries from a GLMM analysis of Hatching Success for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: P ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Analyses based on data from 752 breeding attempts.

	Hatching Success (HS Built Model)			**Hatching Success (HS ULC) Model**		
Fixed Terms	**Coefficient ± SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ± SE**	**z value**	**CI (2.5/97.5%)**
Intercept	2.524 ± 0.105			3.164 ± 0.207		
Me NDB Trees	**0.297 ± 0.098****	**3.032**	**0.105, 0.489**	**0.357 ± 0.088*****	**4.054**	**0.184, 0.530**
Inverse Simpson's Index	0.152 ± 0.087•	1.755	-0.018, 0.323	**0.187 ± 0.083***	**2.249**	**0.024, 0.349**
Inverse Simpson's Index^2	-	-	-	-	-	-
Mean Edge Distance (m)	**-0.235 ± 0.104***	**-2.261**	**-0.439, -0.031**	**-0.506 ± 0.123*****	**-4.120**	**-0.747, -0.265**
Site Occupancy	**-0.194 ± 0.091***	**-2.138**	**-0.371, -0.016**	-0.115 ± 0.087	-1.326	-0.285, -0.055
(log) Site Area (m^2)	0.035 ± 0.106	0.329	-0.173, 0.243	-0.019 ± 0.092	-0.209	-0.201, 0.162
Garden Landcover (%)	0.070 ± 0.094	0.737	-0.115, 0.254	**0.412 ± 0.147****	**2.807**	**0.124, 0.699**
Built Landcover (%)	-0.227 ± 0.121•	-1.870	**-0**.465, 0.011	-	-	-
ULC Model: ULC 2	N/A	N/A	N/A	**-1.223 ± 0.373****	**-3.278**	**-1.955, - 0.492**
ULC 3	N/A	N/A	N/A	**-0.504 ± 0.234***	**-2.154**	**-0.963, -0.045**
ULC 4	N/A	N/A	N/A	**-1.074 ± 0.320 *****	**-3.359**	**-1.700, - 0.447**
ULC 5	N/A	N/A	N/A	-0.692 ± 0.355•	-1.947	-1.389, 0.0045
April Laying Date	-0.027 ± 0.060	-0.449	-0.146, 0.091	-0.030 ± 0.059	-0.517	-0.145, 0.085
Random Terms	**Variance ± SD**			**Variance ± SD**		
Box: Site ID	**-**			-		
Site ID	0.097 ± 0.312			0.041 ± 0.202		
Year	0.024 ± 0.156			0.017 ± 0.129		

Whilst no significant effect of the linear urban gradient (built model, Table 3.4) was detected, the ULC model (Table 3.4; Fig. 3.6) established that compared with the least urbanised (suburban; ULC1) sites, rates of hatching success were significantly lower across dense-suburban (ULC2) to highly urbanised (ULC4) sites. Although hatching success was on average comparatively lower in the most densely urbanised sites (ULC5), any difference detected was borderline significant (z = -1.947, resid. d.f = 710, *P* = 0.052).

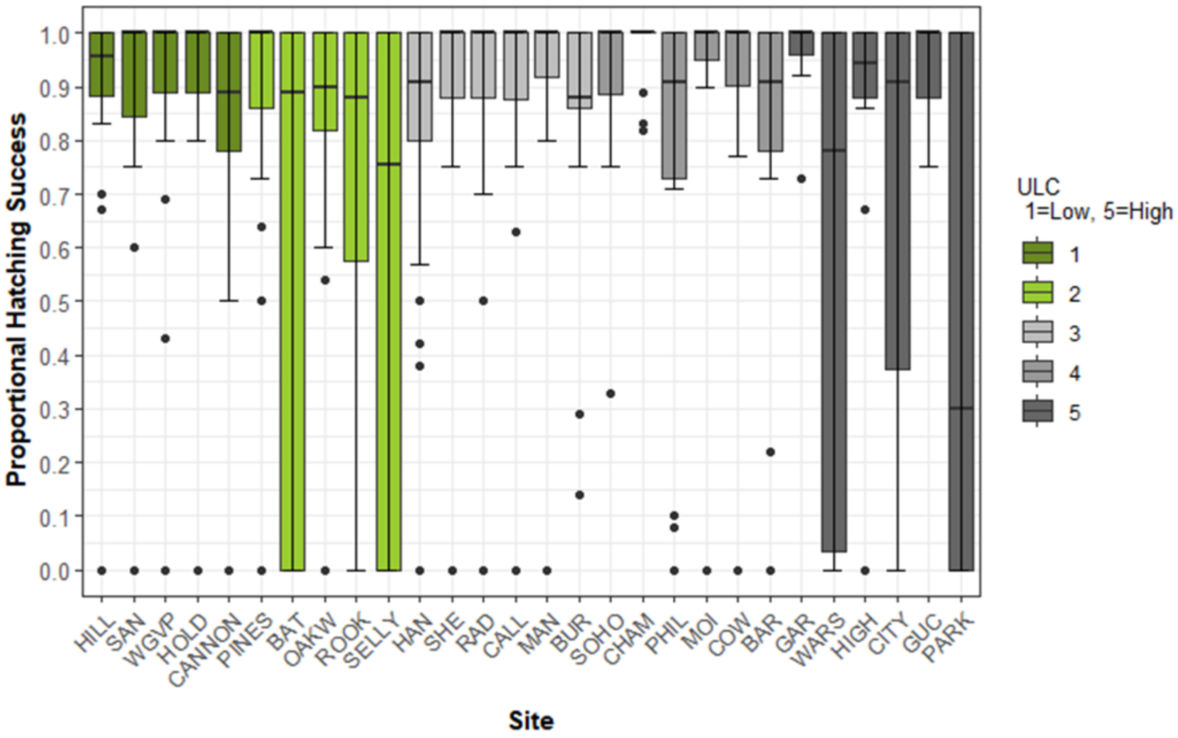


Figure 3.6. Boxplot summaries of hatching success in Blue Tits nesting across 28 sites in Birmingham, UK over six breeding seasons (2013-2018). Black lines within boxes indicate the median proportion of eggs hatched within sites over the six years, upper hinges the 75th percentile and lower hinges the 25th percentile of the data. The vertical lines ('whiskers') indicate the minimum (0) and maximum (1.0) proportion of eggs hatched. For sites with outliers (represented by points), whiskers extend to 1.5 times the inter-quartile range. Sites are in order of increasing %BLC and categorized into one of five urban landcover classes (ULC1=least urbanised (suburban) sites and ULC = dense urban). Site acronyms (Table 2.2) and locations (Figs. 2.8) are provided in sections 2.2.3. (Chapter 2).

At the individual nest level, hatching success was highly variable, both within individual sites and urban land-class categories, as well as across years, with sites categorised as dense-suburban (ULC2) or densely urbanised (ULC5) found to have the most variable rates of hatching success (Fig. 3.6). This variation was likely driven by the low number of breeding attempts recorded within certain sites, particularly within the most densely urbanised sites (ULC5), coupled with the disparity between overall high rates of complete nesting failure, but high hatching success values in the few rare cases where females successfully hatched chicks.

Hatching success declined with increasing nestbox occupancy rates (built model only). However, whilst hatching success also declined with April laying date (both built and ULC models) as expected, this correlation was not significant. This was surprising considering the strong and consistent seasonal effect of advancing lay date observed on both clutch and brood size.

Both built and ULC models predicted a significant positive correlational effect of native broadleaved tree density (me NDB trees) on rates of hatching success, with this relationship showing a stronger response using the ULC model (Table 3.4 and Fig. 3.7).

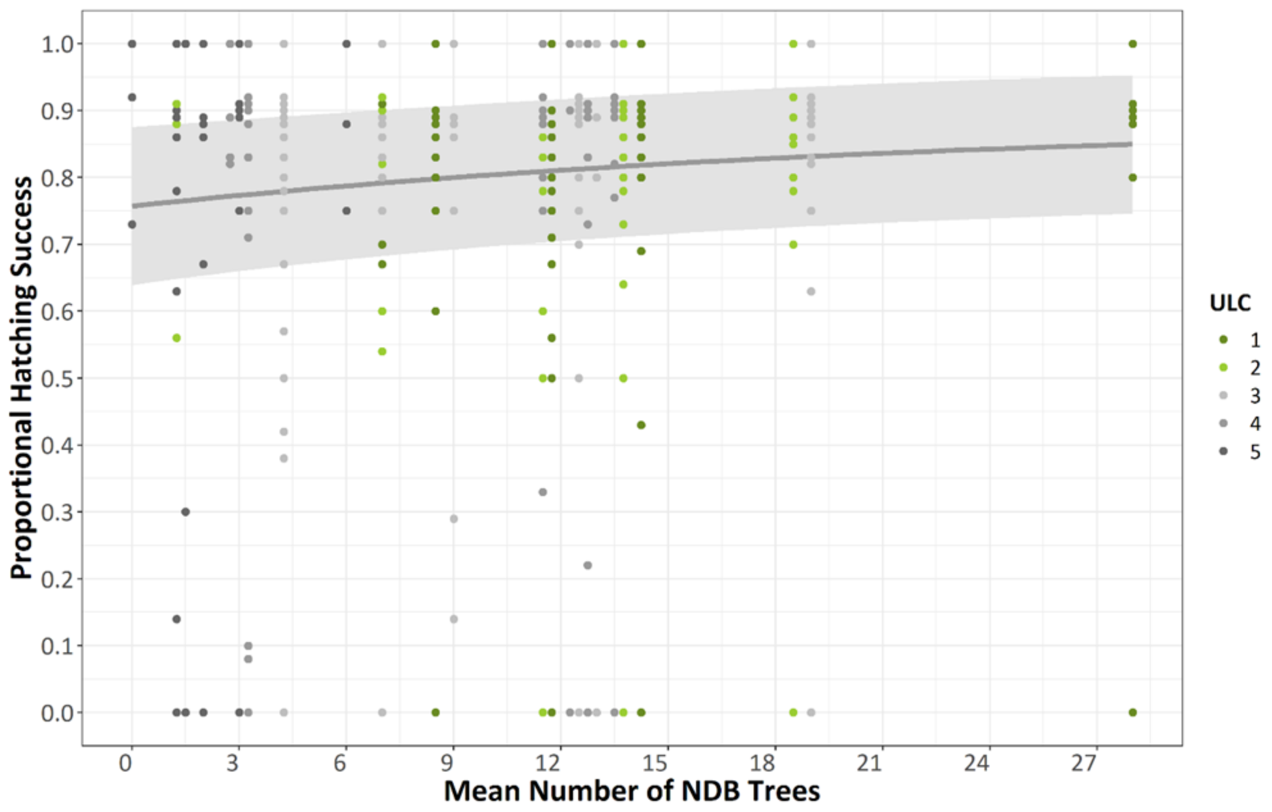


Figure 3.7. The correlational relationship between the mean number of native broadleaved deciduous trees within a 10m radius of nestboxes and hatching success in Blue Tits nesting along an urban gradient in the city of Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points, categorised by urban land cover (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a binomial model of maximum brood size (successes) and unhatched eggs (failures). The model included urban class as a fixed factor (base = ULC 1) and all other variables were kept at their mean. (n = 752 observations).

The ULC model further established that hatching success was also positively influenced by higher broadleaved (native and non-native) tree diversity (as measured using the Inverse Simpson’s Index) and also by the increased availability of gardens (percentage of landcover) within a 500m concentric buffer of sites. With respect to the latter, the ULC model predicted an increase in the proportion of eggs successfully hatching from 0.75 (few gardens) to 0.88 (≥ 50% garden landcover) (Fig. 3.8). Interestingly, the correlational effect was similar in direction and strength to the relationship observed between hatching success and mean native deciduous broadleaved trees.

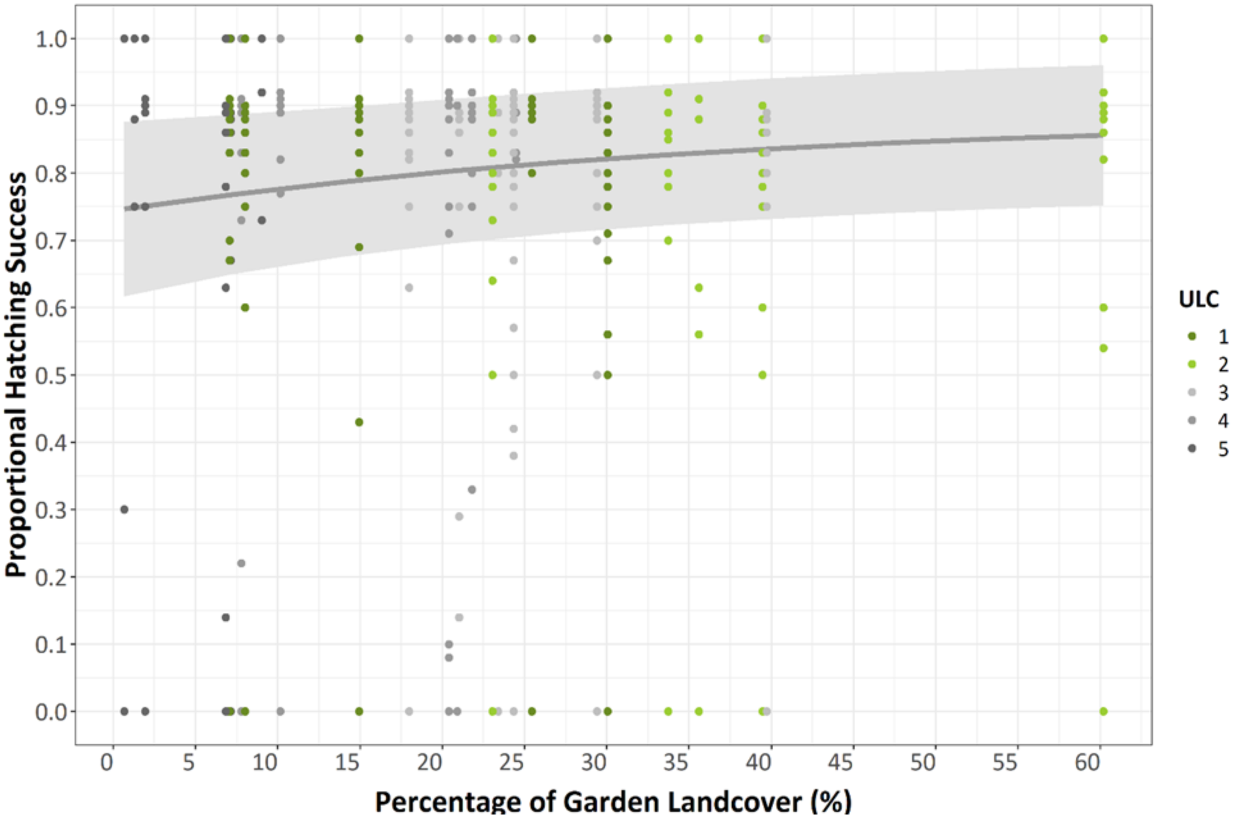


Figure 3.8. The positive correlational relationship between the percentage of garden landcover within a 500m radius of the centre of each site and proportional hatching success in Blue Tits nesting along an urban gradient in the city of Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points, categorised by urban land cover (ULC). ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a binomial model of maximum brood size (successes) and unhatched eggs (failures). The model included urban class as a fixed factor (base = ULC 1) and all other variables were kept at their mean. (n = 752 observations).

Contrary to predictions, both built and ULC models identified a highly significant negative effect of the distance of nestboxes to a connected edge (z = -0.506, res. d.f. = 710, *P* = <0.0001; ULC model, Table 3.4). Thus, suggesting that pairs in nestboxes within patch interiors (i.e. areas of connected tree cover within sites) suffered higher rates of partial clutch loss during incubation, compared with their conspecifics breeding in nestboxes nearer to connected patch edges.

3.3.3.3. Brood size

The mean brood size calculated from all breeding attempts across the six years was 7.18 ± 3.25 nestlings (mean ± SD, total range: 0-14 nestlings, n = 752 clutches), increasing to 8.16 ± 2.01 nestlings (n = 662 broods) when total hatching failure data were excluded. Brood size was highly variable both between and within years, ranging from an average of 6.61 ± 3.55 nestlings (n = 148 clutches) in 2015 to 7.94 ± 2.35 nestlings (n = 64 clutches) in 2013.

The ULC model was determined to be a marginally better predictor of brood size compared with the built model (Table 3.5). However, both models were consistent in indicating a potentially stronger and more significant effect of the composition and structure of the habitat surrounding nests compared with variables associated with the wider urban matrix.

	Brood Size (HN Built Model)			Brood Size (HN ULC) Model		
Fixed Terms	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**
Intercept	2.099 ± 0.031			2.162 ± 0.045		
Me NDB Trees	**0.039 ± 0.016***	2.42	**0.007, 0.0699**	**0.048 ± 0.015****	**3.23**	**0.019, 0.077**
Inverse Simpson's Index	0.007 ± 0.015	0.49	-0.022, 0.036	-0.011 ± 0.015	-0.74	-0.0407, 0.018
Inverse Simpson's Index^2	N/A	N/A	N/A	N/A	N/A	N/A
Mean Edge Distance (m)	**-0.050 ± 0.017****	**-2.91**	**-0.084, -0.016**	**-0.070 ± 0.021*****	**-3.43**	**-0.111, -0.030**
Site Occupancy	-0.013 ± 0.016	-0.84	-0.044, 0.0178	0.001 ± 0.016	-0.08	-0.0318, 0.029
(log) Site Area (m^2)	-0.020 ± 0.018	-1.12	-0.058, 0.0152	-0.007 ± 0.016	-0.41	-0.0381, 0.025
Garden Landcover (%)	-0.001 ± 0.016	-0.06	-0.032, 0.030	0.043 ± 0.024•	1.77	-0.005, 0.091
Built Landcover (%)	-0.024 ± 0.021	-1.16	-0.0641, 0.017	N/A	N/A	N/A
ULC Model: ULC 2	N/A	N/A	N/A	**-0.133 ± 0.062***	**-2.15**	**-0.255, -0.117**
ULC 3	N/A	N/A	N/A	**-0.119 ± 0.041****	**-2.87**	**-0.200, -0.037**
ULC 4	N/A	N/A	N/A	-0.028 ± 0.055	-0.50	-0.138, 0.082
ULC 5	N/A	N/A	N/A	0.009 ± 0.066	0.14	-0.121, 0.139
April Laying Date	**-0.109 ± 0.013*****	**-8.46**	**-0.1346, -0.084**	**-0.112 ± 0.013*****	**-8.62**	**-0.137, -0.0865**
Clutch Size	-	-	-	N/A	N/A	N/A
Random Terms	**Variance ± SD**			**Variance ± SD**		
Box: Site ID	0.004±0.066			0.004 ± 0.066		
Site ID	0.002±0.045			0.001 ± 0.029		
Year	0.005±0.069			0.006 ± 0.075		

Table 3.5. Model summaries from a GLMM analysis of Brood Size for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Clutch size was removed from both built and ULC models due to issues with model validation. Analyses based on data from 752 breeding attempts.

The observed large standard deviations, suggested that brood size varied considerably both between and within sites and thus at the level of individual nests. This translated into very little correlational effect predicted from either urban gradient metric. Indeed, the only significant changes in nestling numbers observed were in the ULC model, in which brood size was found to be smaller in both dense-suburban (ULC2) and moderately urbanised sites (ULC3), compared with suburban (ULC1) sites (ULC model, Table 3.5). Such high variation at the nestbox level was further substantiated by the relatively low random effects variance (and concomitant high standard deviation values) observed for both the site and nested spatial terms. Whilst variance values remained high enough for random effects to be retained in analyses, they suggest greater variation in brood size across nests (between broods) within the same site than might be expected, particularly when compared with differences in brood size between sites.

Aligned with results from clutch size analyses, there was, as expected, a significant gradual decline in brood size with advancing laying date, which was consistent across all years and sites. Models predicted that delayed breeding led to an almost 50% decrease in the mean predicted number of chicks hatching per nest, with the earliest laying pairs producing an average brood of 9.5 compared to ~5 hatchlings for the most delayed breeders. Clutch size was removed from both built and ULC models due to issues with model validation.

Overall, both built and ULC models predicted a positive correlation between brood size and the average number of native deciduous broadleaved trees, with a marginally stronger effect detected in the ULC model (Fig. 3.9).

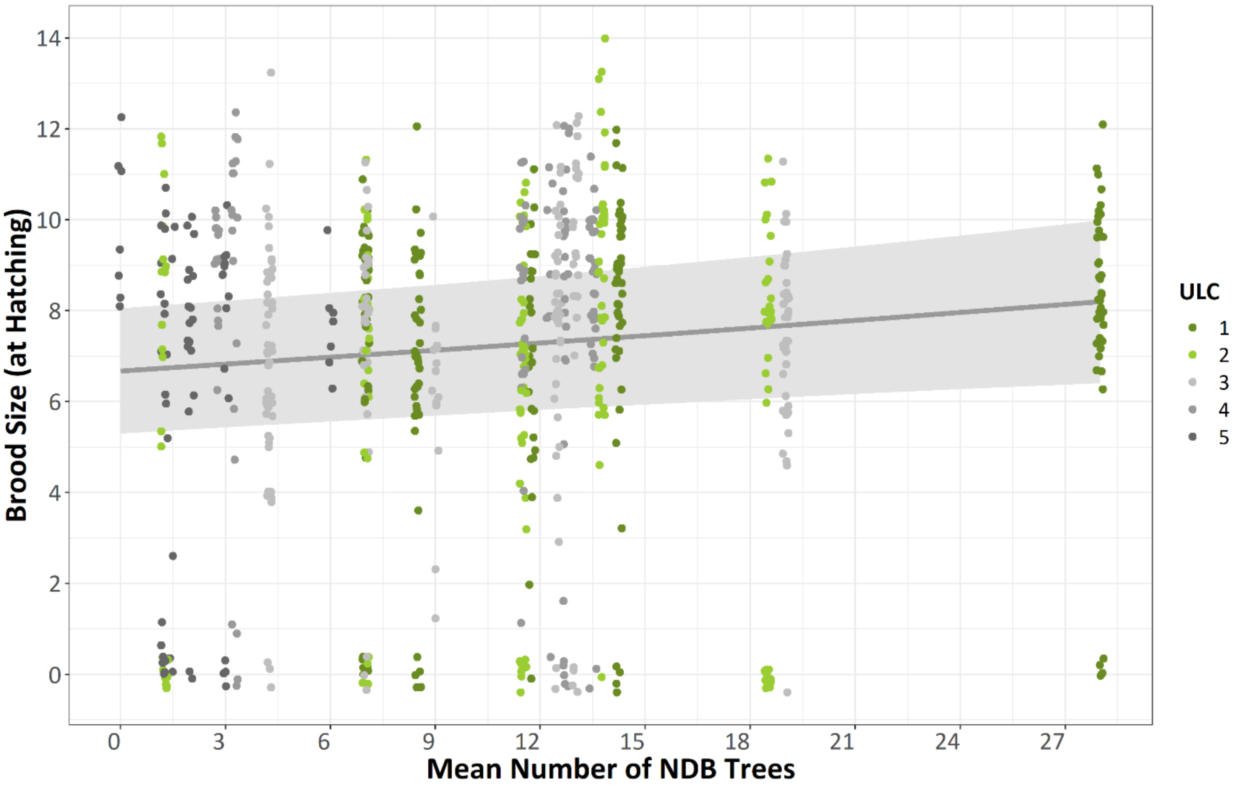


Figure 3.9. The positive correlational relationship between the mean number of native deciduous broadleaved trees within a 10m radius of nestboxes and brood size in Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a zero inflated Conway Maxwell Poisson (glmmTMB family = compois) Model. The model included urban class as a fixed factor (base = ULC 1) and all other variables were kept at their mean (n = 752).

Model estimates predicted that pairs breeding in nestboxes surrounded by few or no native broadleaved deciduous trees hatched an average of 6.75 chicks compared with ~8 nestlings for pairs breeding in sites with the highest mean density of native trees in Birmingham. Contrary to predictions, but consistent with the model outcomes of hatching success, brood size was found to be significantly negatively correlated with the mean distance of nestboxes to a connected tree edge, with a stronger response detected from the ULC model (Table 3.5). Model predictions suggested that pairs hatched up to two fewer chicks in nests located deeper within connected tree cover, compared with their conspecifics nesting nearer to patch edges (Fig. 3.10).

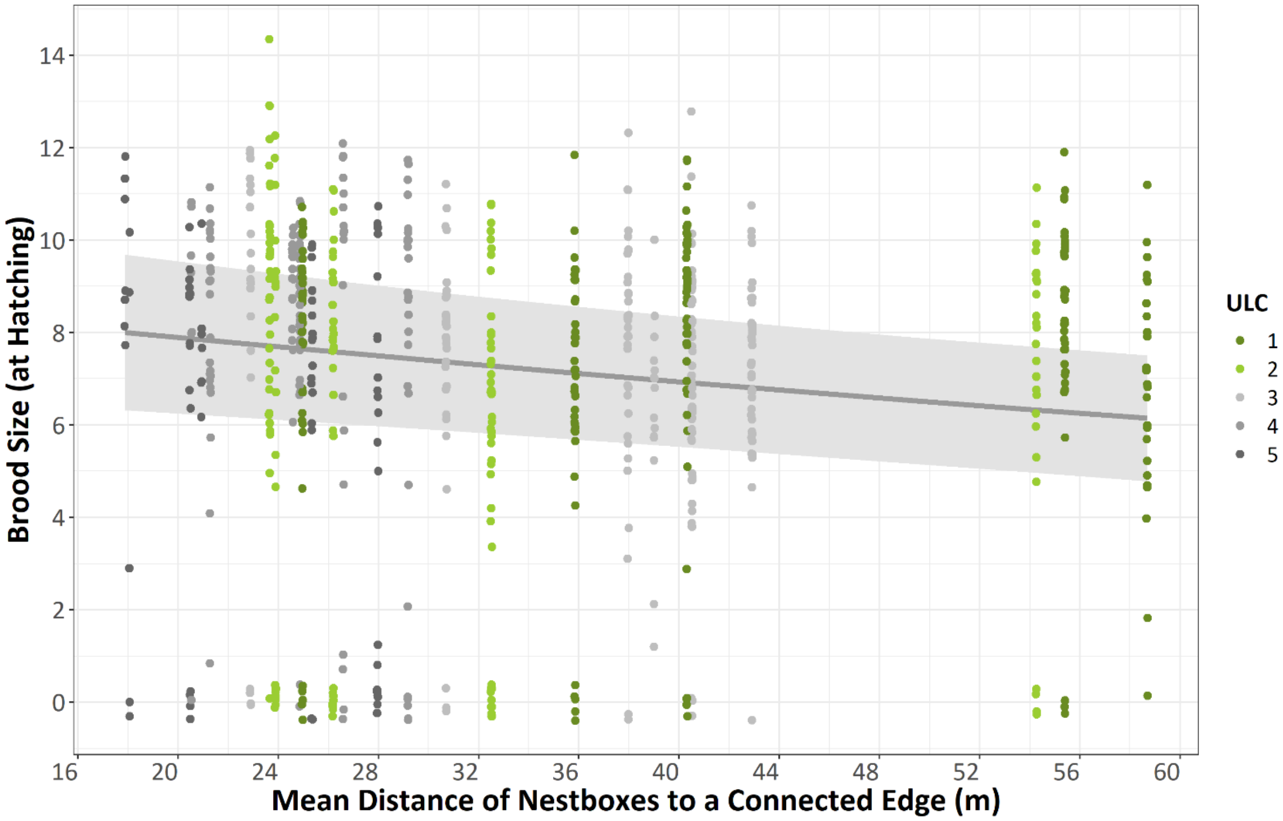


Figure 3.10. The negative correlational relationship between the mean distance of nests from the edge of connected tree cover (mean "edge distance") and brood size in Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a zero inflated Conway Maxwell Poisson (glmmTMB family = compois) Model. The model included urban class as a fixed factor (base = ULC 1) and all other variables were kept at their mean (n = 752).

3.3.4. Post-hatching breeding success

In contrast to pre-hatching and hatching outcomes, fledgling numbers, fledging success and breeding success response variables were more strongly impacted by variables measuring variation in the environment at both habitat and landscape scales. Furthermore, response variables were better explained using the linear urban gradient and associated built models.

Overall, of the 662 Blue Tit pairs that successfully hatched at least one chick over the six years of the study, 554 pairs (83.69%) produced at least one fledgling, (73.67% of the total 752 breeding attempts that reached incubation). Of the 544 nests that fledged at least one chick, 424 (77.94%) experienced the partial loss of eggs and/or nestlings, with 57.35% of those losses incurred during chick-rearing. Overall, 36.56% of breeding attempts that hatched at least one nestling resulted in total fledging success.

3.3.4.1. Fledging success and overall breeding success

Over the six years of the study, the average proportion of nestlings that survived to fledging was 0.66 ± 0.39, whilst the overall mean breeding success ratio was 0.54 ± 0.39. Selly Park was the poorest performing site overall, with only 13 breeding attempts out of 22 producing nestlings. Furthermore, very few nestlings survived the brood-rearing period, resulting in very low fledging success (0.20 ± 0.37) and overall breeding success (0.11 ± 0.2) rates. In comparison, RSPB Sandwell Valley had the highest fledging success rates, with a mean of 0.89 ± 0.24 fledglings per chick (n = 34 nests). With respect to overall breeding success, Chamberlain Gardens was the most successful site over the six years, with pairs producing an average 0.80 ± 0.21 fledglings for every initial egg laid (n = 16 nests).

Table 3.6. Model summaries from a GLMM analysis of Fledging Success for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Analyses based on data from 752 breeding attempts.

	Fledging Success (FS Built Model)			**Fledging Success (FS ULC) Model**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**
Intercept	1.854 ± 0.221			2.326 ± 0.358		
Me NDB Trees	**-0.262 ± 0.132***	**-1.988**	**-0.520, -0.0037**	**-0.374 ± 0.135****	**-2.774**	**-0.638, -0.110**
Inverse Simpson's Index	0.155 ± 0.132	1.169	-0.105, 0.415	0.063 ± 0.148	0.428	-0.227, 0.353
Inverse Simpson's Index^2	**-0.263 ± 0.073*****	**-3.587**	**-0.407, -0.119**	**-0.210 ± 0.076****	**-2.765**	**-0.358, -0.0610**
Mean Edge Distance (m)	0.092±0.144	0. 644	-0.189,0.374	0.010 ± 0.179	0.054	-0.341, 0.360
Site Occupancy	-0.118 ± 0.090	-1.308	-0.295, 0.059	-	-	-
(log) Site Area (m^2)	-0.243 ± 0.152	-1.604	-0.5409, -0.054	-0.227 ± 0.145	-1.568	-0.512, 0.0568
Garden Landcover (%)	**-0.273 ± 0.129***	**-2.107**	**-0.526, -0.019**	-0.252 ± 0.204	-1.234	-0.651, 0.148
Built Landcover (%)	**-0.433 ± 0.170***	**-2.553**	**-0.765, -0.101**	N/A	N/A	N/A
ULC Model: ULC 2	N/A	N/A	N/A	-0.680 ± 0.551	-1.236	-1.759, 0.399
ULC 3	N/A	N/A	N/A	-0.418 ± 0.379	-1.101	-1.161, 0.326
ULC 4	N/A	N/A	N/A	-0.621 ± 0.498	-1.247	-1.597, 0.355
ULC 5	N/A	N/A	N/A	**-1.730 ± 0.564****	**-3.065**	**-2.836, -0.624**
April Hatching Date	**-0.466 ± 0.075*****	**-6.176**	**-0.613, -0.318**	**-0.456 ± 0.075*****	**-6.051**	**-0.604, -0.309**
Random Terms	**Variance ± SD**			**Variance ± SD**		
Box: Site ID	0.872 ± 0.934			0.866 ± 0.931		
Site ID	0.140 ± 0.374			0.098 ± 0.313		
Year	0.178 ± 0.422			0.198 ± 0.445		

Table 3.7. Model summaries from a GLMM analysis of Breeding Success for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Analyses based on data from 752 breeding attempts.

	Overall Breeding Success (BS Built Model)			**Overall Breeding Success (BS ULC) Model**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**
Intercept	1.309±0.150			1.809 ± 0.272		
Me NDB Trees	-0.088 ± 0.113	-0.781	-0.310, 0.133	-0.150 ± 0.112	-1.342	-0.370, 0.069
Inverse Simpson's Index	0.138 ± 0.115	1.199	-0.088, 0.363	0.068 ± 0.127	0.535	-0.181, 0.317
Inverse Simpson's Index^2	**-0.195 ± 0.066****	**-2.961**	**-0.325, -0.066**	**-0.151 ± 0.067***	**-2.244**	**-0.283, -0.019**
Mean Edge Distance (m)	-0.035 ± 0.121	-0.289	-0.273, 0.203	-0.153 ± 0.148	-1.034	-0.442, 0.137
Site Occupancy	-0.140 ± 0.076•	-1.856	-0.289, 0.008	-0.119 ± 0.075	-1.580	-0.266, 0.029
(log) Site Area (m^2)	-0.118 ± 0.127	-0.927	-0.367, 0.131	-0.084 ± 0.122	-0.686	-0.322, 0.155
Garden Landcover (%)	-0.183 ± 0.113	-1.610	-0.405, 0.0396	-0.091 ± 0.175	-0.518	-0.433, 0.252
Built Landcover (%)	**-0.337 ± 0.144***	**-2.345**	**-0.619, -0.055**	N/A	N/A	N/A
ULC Model: ULC 2	N/A	N/A	N/A	-0.836 ± 0.457•	-1.828	-1.732, 0.060
ULC 3	N/A	N/A	N/A	-0.448 ± 0.310	-1.446	-1.055, 0.159
ULC 4	N/A	N/A	N/A	-0.662 ± 0.412	-1.605	-1.470, 0.146
ULC 5	N/A	N/A	N/A	**-1.507 ± 0.475****	**-3.170**	**-2.439, -0.575**
April Laying Date	**-0.215 ± 0.059*****	**-3.632**	**-0.331, -0.099**	**-0.203 ± 0.059*****	**-3.442**	**-0.319, -0.088**
Random Terms	**Variance ± SD**			**Variance ± SD**		
Box: Site ID	0.636 ± 0.798			0.641 ± 0.801		
Site ID	0.104 ± 0.322			0.061 ± 0.246		
Year	0.548 ± 0.234			0.055 ± 0.234		

Variation in both fledging and breeding success were best predicted by built models (Table 3.6 and 3.7), with results suggesting that both measures of success rates were influenced by the timing of breeding, and variables associated with habitat quality and features of the wider urban matrix. Consistent with the seasonal effects of April laying date on pre-hatching breeding outcomes, pairs that bred later in the season had lower rates of fledging and ultimately lower overall breeding success, with a consistent and strong negative correlational effect observed across all four final fledging and breeding success models (Tables 3.6 and 3.7).

A significant quadratic effect of mean broadleaved tree diversity was also observed across the set of four global fledging and breeding success models analysed. Whilst the strongest correlational relationship was detected for fledging success, all four models consistently predicted that the proportion of fledglings produced initially increased with increasing broadleaved tree diversity, from 0.50 to 0.65 (built FS model) and 0.44 to 0.56 (built BS model; Fig. 3.11), but only up to moderate Inverse Simpson's Index values of ~5.5-6.5 species. Any further increases in diversity values were associated with reduced fledging and breeding success, with sites with the highest broadleaved tree diversity exhibiting even poorer breeding success (proportion of fledglings produced per egg <0.35) compared with sites with the lowest moderate Inverse Simpson's Index scores.

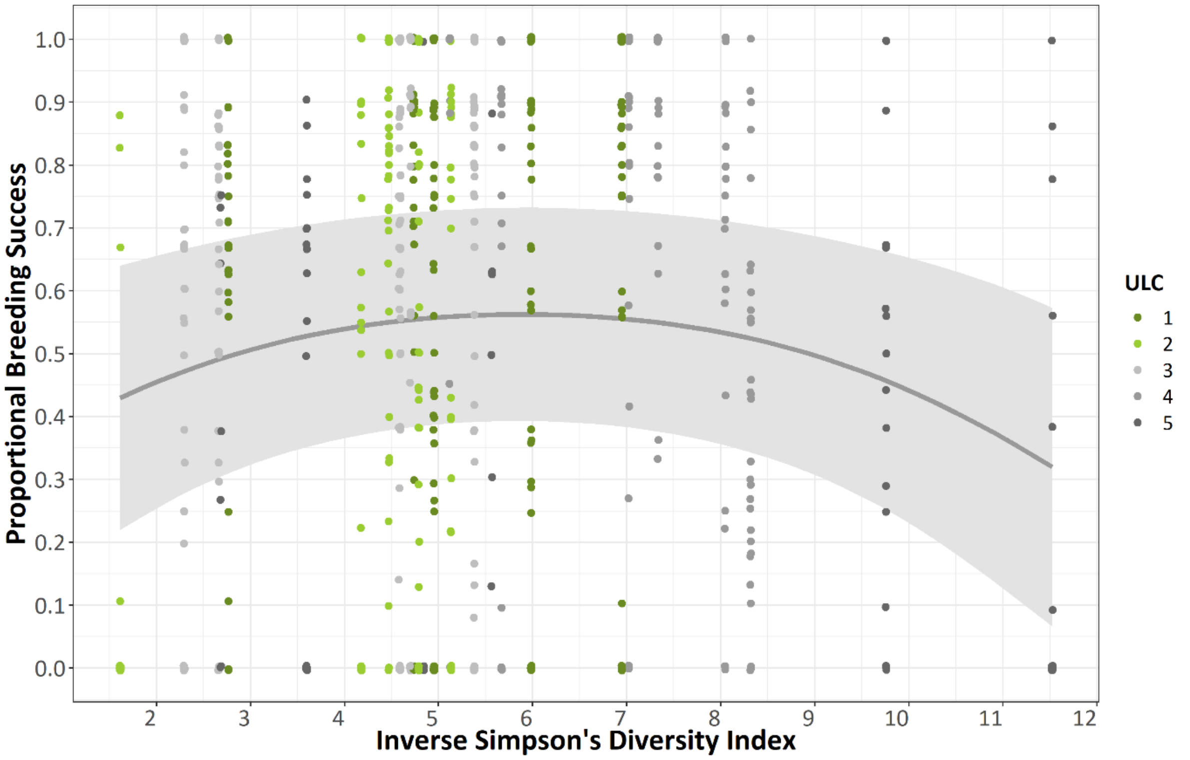


Figure 3.11. The non-linear relationship between broadleaved tree diversity (including native and non-native tree species) measured using Inverse Simpson's Index and overall breeding success for Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points, categorised by urban land cover (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a binomial (built) model of fledglings (successes) and failures (including un-hatched eggs and dead nestlings). All other fixed covariates were kept at their mean. (n = 752 observations).

In contrast to the positive effect of increasing native deciduous broadleaved tree density on pre-hatching and hatching parameters, a consistent negative correlation was observed between fledging success and NDB trees (but not breeding success), with the strongest effect detected in the ULC model (z = -0.374, res. d.f. = 619, *P* = 0.0055).

As hypothesised, models predicted a significant decline in both fledging and overall breeding success with increasing urbanisation using the quantitative metric (%BLC) (built models; Tables 3.6 and 3.7). Pairs breeding in the 'greenest' (i.e. least built-up) sites were predicted to fledge an average of 0.63 chicks from all eggs laid (BS model), with this rate falling to 0.46 in highly urbanised sites (> 90% BLC). The equivalent estimated figures for the FS model (Fig. 3.12) were slightly higher but with very similar rates of change observed. In contrast, the two equivalent ULC models only detected a significant difference in success rates between the two extreme classes of urbanisation.

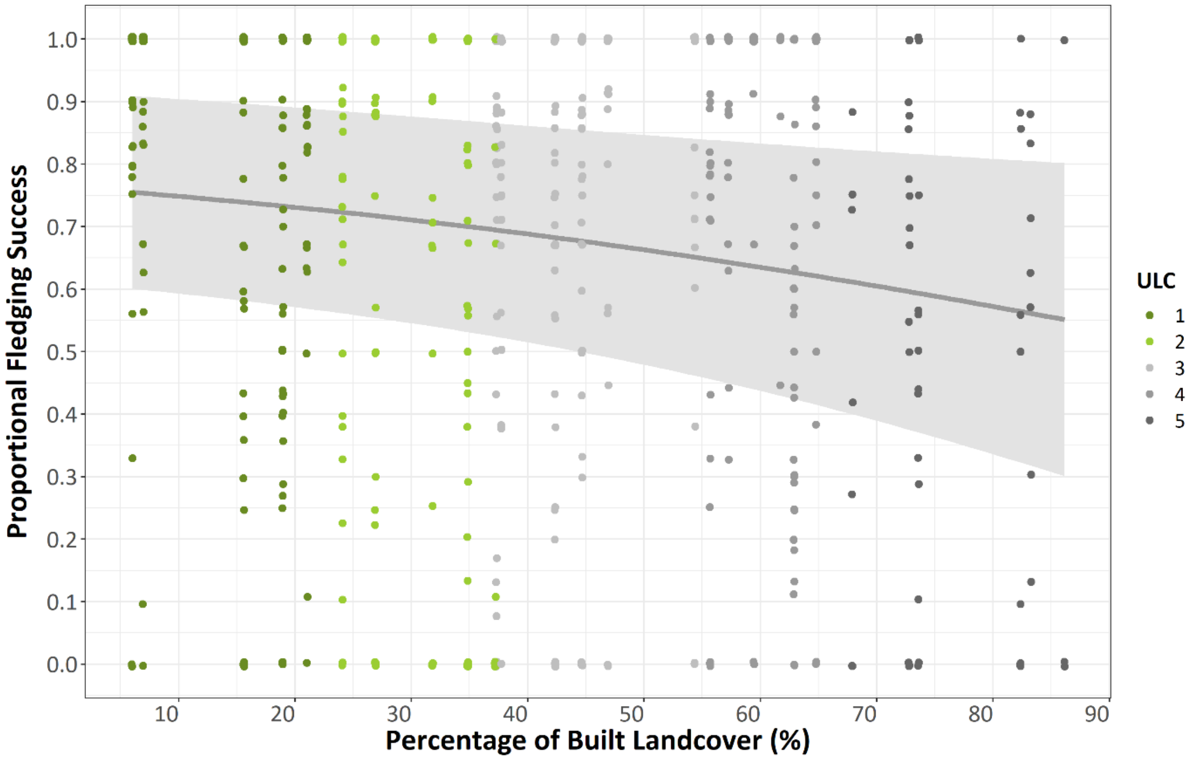


Figure 3.12. The negative correlational relationship between the urban gradient (measured using the quantitative metric; %BLC) and proportional fledging success for Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018).. Raw data are represented by coloured points, categorised by urban land cover (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a binomial model of fledglings (successes) and hatchling deaths (failures). All other fixed covariates were kept at their mean. (n = 662 observations). The plot demonstrates the high levels of noise in the data, with the width of CIs increasing with increasing %BLC likely in part due to the lower numbers of breeding attempts.

Finally, the built FS model (Table 3.6) revealed a significant negative correlation between fledging success and the percentage of garden landcover within the 500m bufferzone of sites (z = -0.273, res. d.f. = 621, *P* = 0.035). However, when plotted, model predictions, revealed a relatively shallow, negative trend, particularly compared with the stronger, positive correlational relationship of garden landcover and hatching success predicted from the ULC HS model.

3.3.4.2. Fledgling numbers

Including cases of total breeding failure (equating to 16.31% of nests across all years), pairs across the city on average produced 5.37 ± 3.32 fledglings per breeding attempt (range: 0-12 fledglings, n = 662 nests), increasing to an average of 6.42 ± 2.54 fledglings (n = 554 nests) when complete brood failures were removed from the raw data.

Variation in fledgling numbers across sites was influenced by environmental variables at both habitat and landscape scales, with the linear quantitative gradient proving a better predictor of urbanisation effects (Table 3.8).

April hatching date and brood size were removed from the final models to improve model validation. However, when retained in analyses, models demonstrated that, as expected fledgling numbers increased with brood size and declined with the progression of the breeding season.

Table 3.8. Model summaries from a GLMM analysis of Fledgling Numbers for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against *a priori* selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Results are provided for both built (left columns) and ULC (right columns) models which use the quantitative (%BLC) and categorical (five-level urban land class) gradient metrics respectively. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates *a priori* not included. Analyses based on data from 662 breeding attempts.

	Fledgling Numbers (FN Built Model)			**Fledgling Numbers (FN ULC) Model**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CI (2.5/97.5%)**
Intercept	1.891 ± 0.048			2.021±0.084		
Me NDB Trees	-0.012 ± 0.037	-0.33	-0.084, 0.060	-0.025 ± 0.036	-0.694	-0.096, 0.0459
Inverse Simpson's Index	0.017 ± 0.038	0.44	-0.057, 0.091	-0.033 ± 0.042	-0.775	-0.116, 0.0501
Inverse Simpson's Index^2	**-0.052 ± 0.022***	**-2.36**	**-0.094, -0.009**	-0.033 ± 0.022	-1.504	-0.0767, 0.010
Mean Edge Distance (m)	-0.069 ± 0.040•	-1.71	-0.148, 0.010	**-0.095 ± 0.048***	**-1.974**	**-0.189, -0.0006**
Site Occupancy	-0.036 ± 0.029	-1.22	-0.093, 0.022	-0.026 ± 0.029	-0.902	-0.083, 0.031
(log) Site Area (m^2)	-0.042 ± 0.042	-0.99	-0.124, 0.041	-0.010 ± 0.040	-0.253	-0.089, 0.068
Garden Landcover (%)	-0.013 ± 0.036	-0.35	-0.083, 0.057	-0.017 ± 0.055	-0.311	-0.091, 0.125
Built Landcover (%)	**-0.091 ± 0.046***	**-1.97**	**-0.181, -0.0004**	N/A	N/A	N/A
ULC Model: ULC 2	N/A	N/A	N/A	-0.236 ± 0.148	-1.595	-0.526, 0.054
ULC 3	N/A	N/A	N/A	**-0.200 ± 0.101***	**-1.974**	**-0.399, -0.0001**
ULC 4	N/A	N/A	N/A	-0.095 ± 0.132	-0.719	-0.353, 0.163
ULC 5	N/A	N/A	N/A	**-0.371 ± 0.156***	**-2.380**	**-0.677, -0.065**
April Hatching Date	-	-	-	-	-	-
Brood Size	-	-	-	-	-	-
Random Terms	**Variance ± SD**			**Variance ± SD**		
Box: Site ID	-			0.001 ± 0.038		
Site ID	0.016±0.128			0.012 ± 0.107		
Year	0.005±0.074			0.006 ± 0.075		

The built model detected a moderate but significant quadratic effect of mean broadleaved tree diversity (z = -0.052, res. d.f. = 622, *P* = 0.018; Table 3.8). Pairs were predicted to produce more fledglings as Inverse Simpson's Index values initially increased, from a projected low of 4.5-5.5 to a peak of 5.5-6.5 (±1.0 CIs) fledglings (Fig. 3.12). Consistent with the results reported across other response variables, this final best model indicated a threshold Inverse Simpson's Index value of ~ 5.5-6.5, beyond which greater broadleaved tree diversity within city greenspaces was associated with lower fledgling numbers.

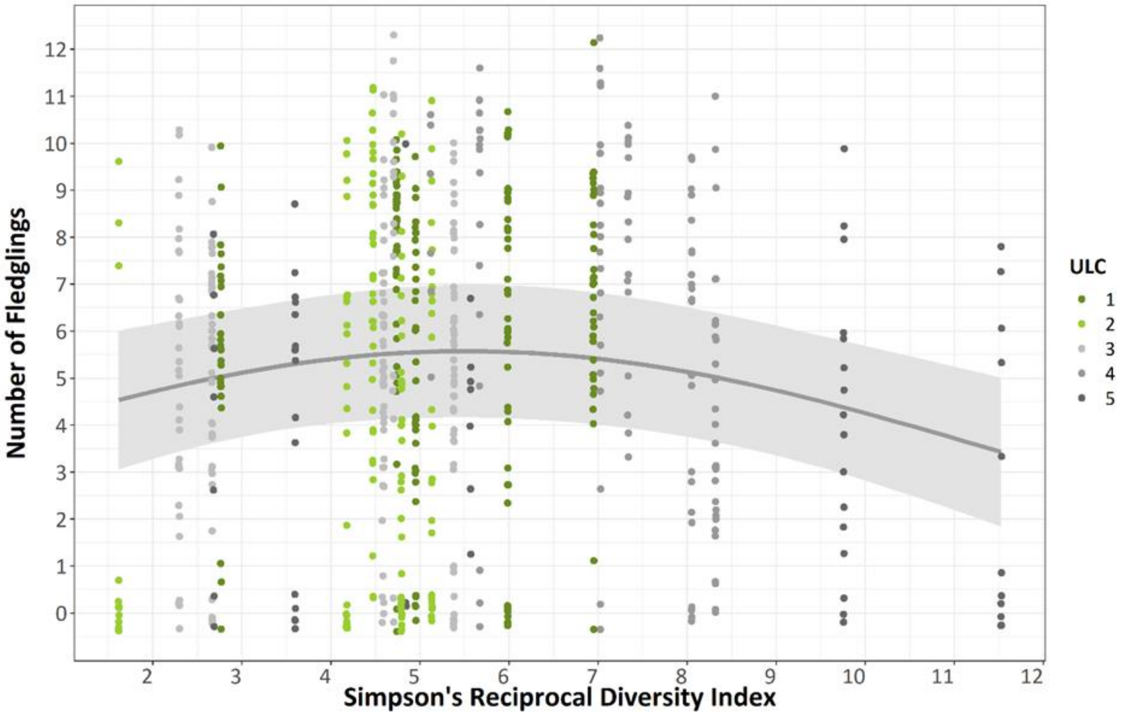


Figure 3.13. The non-linear relationship between broadleaved tree diversity (including native and non-native species) measured using Inverse Simpson's Index and fledgling numbers for Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a zero-inflated Conway Maxwell Poisson Model (family = compois). The urban gradient was specified using %BLC. All fixed covariates were kept at their mean (n = 662).

Whilst the ULC model did not detect an effect of increasing tree diversity on fledgling numbers, it did predict an equally significant negative effect of the mean distance of nests to a connected edge (z = -0.095, res. d.f. = 618, P = 0.048; Table 3.8).

Finally, the built model predicted a significant decline in fledgling numbers as the percentage of built landcover increased (z = -0.091, res. d.f. = 622, *P* = 0.0489; Table 3.8). Pairs nesting in the greenest (suburban) sites were predicted to produce 6.5 ± 1.5 fledglings, compared with 4.5 ± 1.5 fledglings produced by conspecifics breeding in the most heavily built-up sites (Fig. 3.14).

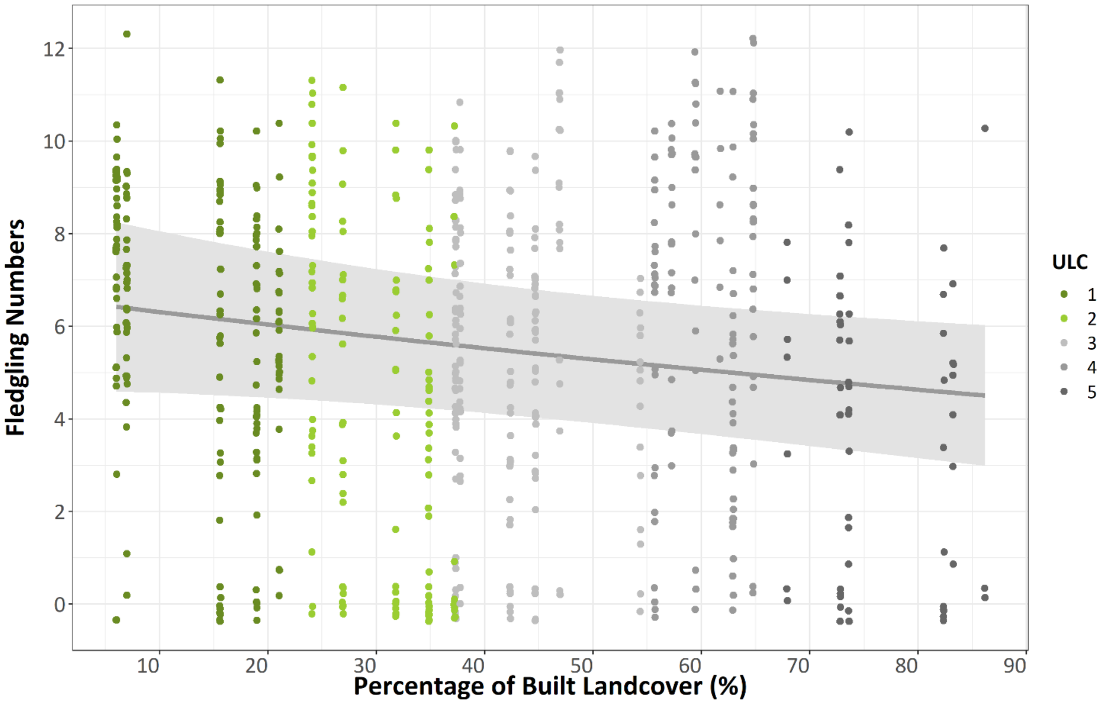


Figure 3.14. The negative correlational relationship between the urban gradient (%BLC) and fledgling numbers for Blue Tits nesting along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points (categorised by urban land cover (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a zero-inflated Conway Maxwell Poisson Model (family = compois). The urban gradient was specified using %BLC. All fixed covariates were kept at their mean. (n = 662).

The ULC model (Table 3.8) also demonstrated variation in fledgling numbers albeit only between the least urbanised sites (ULC1) and sites with moderate or very high levels of urban density (ULC 3 and 5, respectively).

3.3.5. Probability of total nesting failure

A total of 26.33% of all breeding attempts failed over the six breeding seasons, with the number of failures fluctuating across sites (Fig. 3.15).

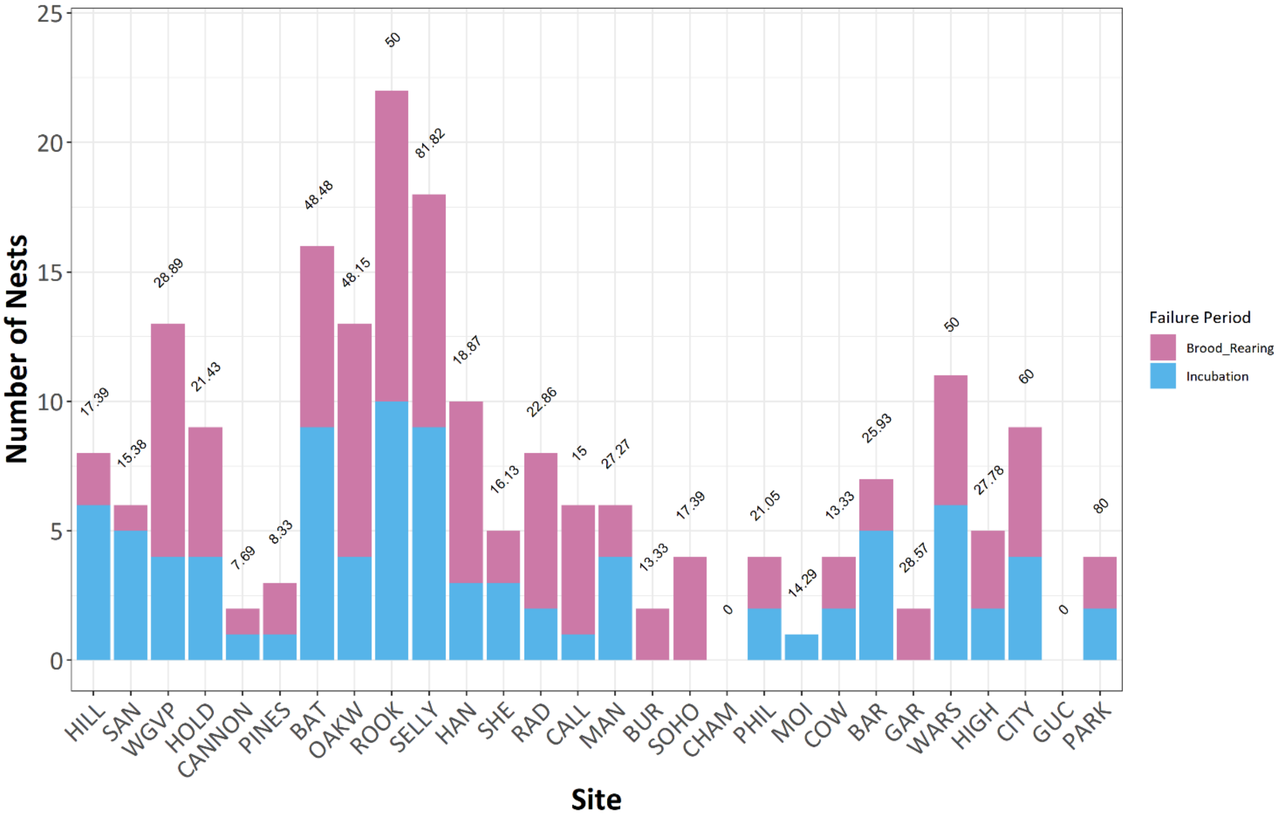


Figure 3.15. Bar plot of total nesting failures for Blue Tits breeding across an urban gradient in the city of Birmingham, UK over six breeding seasons (2013-2018). Failures are broken down for each site across two breeding phases (incubation and brood-rearing). Values above bars denote breeding failures as a percentage of the total number of breeding attempts for each site across all six years. Sites are ordered by %BLC. Sites (i.e. Chamberlain and GUC) recording 0% failure rates did not suffer complete losses during either incubation or brood-rearing. Note that for GUC (a highly urbanised site) only 7 nesting attempts were recorded but all were successful with at least one chick hatching and fledging from each attempt.

Table 3.9. Model summaries from GLMM analyses of the effects of habitat and landscape parameters on measures of the probability of breeding success/failure (binary HS, FS and BS) for Blue Tits breeding along an urban gradient within the city of Birmingham, UK between 2013-2018 using built models. Response variables were regressed against a priori selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: P ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates a priori not included.

	Hatching Success (Built Model) (n = 752)			**Fledging Success (Built Model) (n = 662)**			**Breeding Success (Built Model) (n = 752)**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CIs (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CIs (2.5/97.5%)**	**Coefficient ±SE**	**z value**	**CIs (2.5/97.5%)**
Intercept	3.072± 0.355			2.834±0.347			2.112±0.269		
Me NDB Trees	-0.034 ±0.169	-0.200	-0.365,0.297	-0.129±0.170	-0.756	-0.462,0.205	-0.098±0.159	-0.615	-0.409,0.214
Inverse Simpson's Index	0.251 ±0.153	1.640	-0.049,0.550	**0.435±0.166****	**2.621**	**0.110,0.760**	**0.440±0.153****	**2.875**	**0.140,0.740**
Inverse Simpson's Index^2	-	-	**-**	**-0.256±0.084****	**-3.050**	**-0.421, -0.091**	**-0.203±0.077****	**-2.622**	**-0.355, -0.051**
Mean Edge Distance (m)	**0.523 ± 0.174****	**3.001**	**0.181,0.864**	0.226±0.175	1.296	-0.116,0.568	**0.366±0.160***	**2.280**	**0.051,0.679**
Site Occupancy	**-0.429±0.203***	**-2.114**	-0.827, -0.031	-0.263±0.187	-1.407	-0.630,0.104	**-0.373±0.149***	**-2.496**	**-0.665, -0.080**
(log) Site Area (m^2)	-0.160 ±0.195	-0.817	-0.543,0.223	**-0.407±0.202***	**-2.010**	**-0.804, -0.010**	-0.283±0.178	-1.595	-0.631,0.065
Garden Landcover (%)	**-0.885±0.232*****	**-3.821**	**-1.339, -0.431**	**-1.015±0.228*****	**-4.442**	**-1.463, -0.567**	**-0.975±0.214*****	**-4.546**	**-1.395, -0.555**
Built Landcover (%)	-0.191±0.199	-0.959	-0.580,0.199	**-0.488±0.227***	**-2.150**	**-0.932, -0.043**	-0.353±0.190•	-1.858	-0.726,0.019
Built Landcover (%) (%BLC)^2	**-0.782±0.214*****	**-3.647**	**-1.202, -0.361**	**-0.630±0.217****	**-2.898**	**-1.055, -0.204**	**-0.736±0.196*****	**-3.754**	**-1.120, -0.352**
April Laying Date	-0.183±0.151	-1.213	-0.478,0.112	N/A	N/A	N/A	-0.079±0.099	-0.806	-0.273,0.114
April Hatching Date	N/A	N/A	N/A	-0.223±0.136	-1.644	-0.489,0.043	N/A	N/A	N/A
Random Term	**Variance ± SD**			**Variance ± SD**			**Variance ± SD**		
Box:Site ID	-			0.310±0.557			0.054±0.232		
Site ID	0.071±0.267			0.057±0.239			0.153±0.392		
Year	0.205±0.453			0.064±0.254			0.007±0.083		

	Hatching Success (ULC Model) (n = 752)			**Fledging Success (ULC Model) (n = 662)**			**Breeding Success (ULC Model) (n = 752)**		
Fixed Terms	**Coefficient ±SE**	**z value**	**CIs (2.5,97.5%)**	**Coefficient ±SE**	**z value**	**CIs (2.5,97.5%)**	**Coefficient ±SE**	**z value**	**CIs (2.5,97.5%)**
Intercept	2.155±0.460			2.508±0.420			1.808±0.402		
Me NDB Trees	0.099±0.183	0.543	-0.259,0.457	-0.007±0.152	-0.047	-0.304,0.290	-0.106±0.177	-0.601	-0.454,0.241
Inverse Simpson's Index	0.070±0.164	0.428	-0.251,0.391	0.292±0.156$^{\bullet}$	1.879	**-0.013,0.597**	**0.415±0.184***	**2.258**	**0.055,0.774**
Inverse Simpson's Index^2	-	-	**-**	**-0.249±0.083****	**-2.984**	**-0.412, -0.085**	**-0.225±0.085****	**-2.639**	**-0.392, -0.058**
Me Distance CE	0.442±0.260$^{\bullet}$	1.700	-0.068,0.952	-0.040±0.235	-0.169	-0.501,0.421	0.324±0.224	1.445	-0.115,0.763
Site Occupancy	-0.315±0.213	-1.482	-0.732,0.102	-0.146±0.183	-0.799	-0.506,0.213	-0.266±0.148	-1.797	-0.557,0.024
(log) Site Area (m^2)	0.067±0.196	0.340	-0.318,0.451	-0.289±0.190	-1.523	-0.660,0.083	-0.265±0.201	-1.318	-0.658,0.129
Garden Landcover (%)	-0.309±0.330	-0.937	-0.957,0.338	-0.412±0.265	-1.556	-0.931,0.107	-0.177±0.275	-0.645	-0.716,0.361
Garden Landcover (%^{2})	**-**	**-**	**-**	**-**	**-**	-	-0.222±0.125	-1.772	-0.468,0.024
ULC 2	-0.070±0.795	-0.089	-1.628,1.488	-0.880±0.691	-1.273	-2.234,0.475	-0.432±0.656	-0.658	-1.717,0.853
ULC 3	0.853±0.559	1.525	-0.243,1.949	0.103±0.464	0.222	-0.806,1.012	0.270±0.458	0.590	-0.627,1.166
ULC 4	0.522±0.670	0.779	-0.791,1.835	-0.654±0.697	-0.938	-2.019,0.712	-0.381±0.597	-0.639	-1.551,0.788
ULC 5	-0.630±0.746	-0.844	-2.093,0.833	**-1.823±0.709***	**-2.571**	**-3.214, -0.433**	-1.213±0.635	-1.911	-2.457,0.031
April Lay Date	-0.167±0.160	-1.039	-0.481,0.148	n/a	n/a	n/a	-0.069±0.099	-0.702	-0.263,0.125
April Hatch Date	n/a	n/a	n/a	-0.176±0.128	-1.372	-0.427,0.075	n/a	n/a	n/a
Random Term	**Variance ± SD**			**Variance ± SD**			**Variance ± SD**		
Box:Site ID	0.318±0.564			-			0.029±0.171		
Site ID	0.555±0.236			0.021±0.145			0.119±0.344		
Year	0.212±0.460			0.059±0.242			0.008±0.870		

Table 3.10. Model summaries from GLMM analyses of the effects of habitat and landscape parameters on measures of the probability of breeding success/failure (binary HS, FS and BS) for Blue Tits breeding along an urban gradient within the city of Birmingham, UK between 2013-2018 using ULC models. Response variables were regressed against a priori selected covariates (Fixed Effects) from three predictor blocks: habitat and landscape (abiotic) and biotic. Intercept = ULC1 (suburban sites). Intercept Year = 2013 where specified as a fixed factor. All significant slopes (using CIs) are indicated in bold (significance codes: P ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero); '-' values denote covariates initially included in models but subsequently removed; 'n/a' values indicate covariates a priori not included.

Of the breeding attempts that reached incubation, 11.97% (n = 90 clutches) resulted in total hatching failure, whilst 14.38% (n = 108 broods) failed during the chick-rearing phase. Although the probability of breeding failure remained low, where it did occur, there were consistent correlational relationships with several different environmental variables at both habitat and landscape scales (Tables 3.9. and 3.10).

Failure rates across the city were higher during the chick-rearing (post-hatch) period compared with the incubation (pre-hatch period), with 55.55% of total breeding failures linked to brood mortality events. Most partial and total failures that occurred during the chick-rearing period were related to starvation rather than predation, with nestlings found dead but unharmed in the nest. Evidence of predation events of eggs and chicks was rare (n = 31 nests), and restricted to only a few sites, which were subsequently dropped from analyses. Predation, where it occurred was due to small mammals, most notably Grey Squirrels (*Sciurus carolinensis*) but also some bird species such as Woodpeckers (*Dendrocopos* spp.).

Observed variation in rates of pre- and post-hatch breeding failure across the urban gradient were strongly supported by the built models (Table 3.9), with both habitat and landscape-scale variables found to be correlated with all three binary success measures investigated. In contrast ULC models only found a significant correlation between binary success outcomes and tree diversity, with no effect of the categorical urban metric detected (Table 3.10).

At the habitat level, mean broadleaved tree diversity had the most significant correlational effect on binary breeding success/failure (Tables 3.9-3.10). A highly significant quadratic effect of broadleaved tree diversity on the probability of fledging success was established from both built and ULC models, with significant knock-on impacts to overall rates of binary breeding success (z = -2.622, res. d.f. 738, *P* = 0.0087; built model, Table 3.9). However, compared with other models in which this relationship was detected, the non-linear response curve was less pronounced and the probability of success in sites with the highest tree diversity remained higher, compared to those sites with the lowest tree diversity.

In contrast to the negative impact observed on pre-hatching response variables, increasing distance of nestboxes to the edge of connected tree cover was predicted to increase the probability of at least one egg surviving to hatching and one egg surviving to fledging in the built model (Table 3.9). Concomitantly, the probability of at least one hatchling surviving to fledging was predicted to decrease with increasing (log) site area.

The wider urban landscape also exerted a strong influence on the probability of breeding success or failure, with A highly significant non-linear effect of the quantitative urban gradient (% built landcover) was also observed across all three probabilistic metrics analysed (Table 3.9). Model predictions suggest that there was a high probability of success when the percentage of built landcover was below 40-50%. However, once the density of built landcover in the urban matrix surrounding greenspace exceeded this threshold, the probability of breeding attempts hatching and/or fledging at least one chick rapidly declined (Table 3.9; Fig. 3.16).

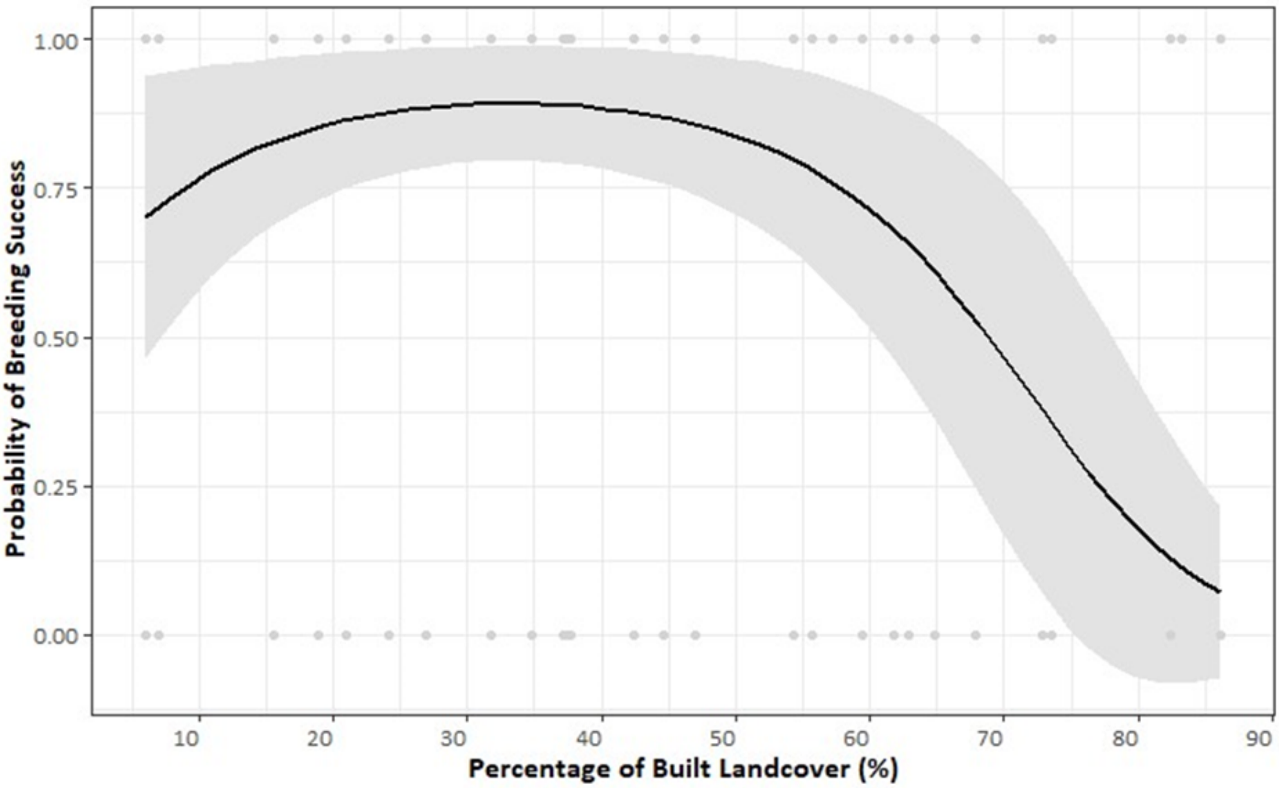


Figure 3.16. The non-linear relationship of the quantitative urban gradient (%BLC) and the probability of breeding success for Blue Tits breeding along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). The raw data (binary probability) of at least one egg surviving to fledge is represented by grey dots. The solid line is the prediction curve (and grey ribbons the 95% CIs). All other fixed covariates were kept at their mean. (n = 752 observations).

Finally, models revealed a consistent and highly significant negative correlation between the percentage of garden landcover and the probability of hatching and fledging success, implying that as the availability of gardens in the matrix surrounding sites increased, the risk of complete breeding failure also rose. This increased risk appeared to impact both reproductive phases equally, with significant knock-on effects to overall breeding success (z = -4.546, res. d.f. 738, *P* = <0.0001).

3.4. DISCUSSION

Overall, results revealed variation in both the strength and direction over which different breeding traits respond to specific features of the nesting habitat and the wider urban matrix. Measures of pre-hatch and hatching success appeared more strongly linked with the seasonal timing of breeding and changes in the structure and composition of vegetation (i.e. habitat quality) immediately surrounding nestboxes, with little quantifiable effects of landscape-scale variables associated with the urban matrix. In comparison, post-hatching success outcomes, overall breeding success and the risk of breeding failure whilst phenologically driven, were also significantly correlated with environmental factors at both landscape and habitat scales.

3.4.1. Effects of landscape scale variables on breeding performance

3.4.1.1. The urban gradient

This study supports existing research modelling the direct ecological impacts of urbanisation on avian life-history strategies using more robust quantifiable measures of the urban gradient when compared with the traditional dichotomous urban-rural comparative approach and considering potential effects across different spatial scales and gradient lengths (e.g. Corsini *et al.* 2017; Sprau *et al.* 2017; Satgé *et al.* 2019; Muller *et al.* 2020; Szulkin *et al.* 2020). Aligning with these studies, a subtle but quantifiable pervasive negative effect of urbanisation on breeding success across both pre-hatching and post-hatching periods was observed. However, the direct impacts of increasing urbanisation on reproductive performance in the Birmingham Blue Tit population were more nuanced and less consistent across different response variables and phases of the breeding season than expected.

As hypothesised, the continuous, quantitative urban metric proved a marginally better predictor of the effects of increasing urbanisation across the short, high-resolution intra-city urban gradient compared with the categorical factor more commonly used in larger-scale urban-rural comparative studies (e.g. Wawrzyniak *et al.* 2015; Bailly *et al.* 2016; Biard *et al.* 2017; Glądalski *et al.* 2017).

Built models revealed that increasing urbanisation had the strongest and most consistent impact on breeding failure with the risk of failure during both incubation and brood-rearing rising significantly once built landcover within the matrix surrounding greenspace exceeded 40% (e.g. Fig. 3.16). Furthermore, despite high levels of observed intra-site variability in breeding response data (e.g. Fig. 3.11), built models also predicted higher rates of nestling loss with increasing urbanisation (Table 3.6), resulting in fewer fledged young (Table 3.8), and a decline in overall breeding success (Table 3.7).

In contrast, there was less evidence of an effect of increasing urbanisation on pre-hatching breeding responses measures. However, clutch sizes across the 28 sites were generally lower compared to the average of 11 to 12 eggs laid by birds in rural deciduous woodland (Perrins, 1979; Dhondt 1989; Kempenaers *et al*. 1998). This suggests that clutch size is potentially linked to urbanisation effects operating at wider (i.e. city or regional) scales (Satgé *et al.* 2019). This concurs with the findings of other urban Blue and Great Tit studies, which have shown that broader landscape-scale impacts and processes are linked with reduced clutch sizes (by 10-20%) in urban compared with woodland nests (Solonen 2001; Marciniak *et al.* 2007; Wawrzyniak *et al.* 2015; Bailly *et al.* 2016 except see Vaugoyeau *et al.*

2016). As a short-lived species Blue Tits are more likely to optimise clutch size due to the fitness benefits conferred (e.g. Perrins and Moss 1975; Monaghan and Nager 1997). A potential hypothesis therefore is that smaller clutch sizes in urban areas are an adaptive response by females to compensate for the reduced availability of natural food resources for provisioning nestlings (Chamberlain *et al.* 2009). However, an alternative theory is that reduced clutch size in urban areas are the result of high gene flow across different habitats (i.e. across greenspace patches or between the city and a nearby source woodland population) (Dhondt *et al.* 1990; Hõrak 1993). However, as with many breeding studies, it remains unclear if reduced clutch size in the Birmingham Blue Tit population was genetically driven or due to phenotypic plasticity.

Whilst ULC models predicted reduced hatchling numbers (Table 3.5) and lower rates of hatching success (Table 3.4) in more urbanised sites (ULC2-4) compared with the greenest sites (ULC1), the strength and significance of the differences detected were inconsistent across different urban categories. Notably, any differences in brood size and hatching success between the two extreme urban land classes were found not to be statistically significant. Whilst these results suggest these aspects of breeding success may also be similarly constrained at the city-wide scale, they could equally be explained by the variance in the dataset and/or the high rates of hatching success relative to the very few breeding attempts that were observed in the most urbanised sites.

Despite laying smaller than average clutches, and the capacity of females to adjust clutch size to compensate for delayed laying (Fig. 3.5), rates of brood reduction were high and increased significantly with the urban gradient resulting in decreased fledging numbers and reduced breeding success, suggesting that females were potentially laying larger than optimal clutches (Dhondt *et al.* 1990; Chamberlain *et al.* 2009; Shutt *et al.* 2018). Whilst larger than optimal clutches have been hypothesised to have a genetic basis (Dhondt *et al*. 1990; Chamberlain *et al.* 2009) researchers have alternatively suggested that disparities between earlier breeding decisions and later breeding outcomes may arise because pairs are unable to accurately assess the future quality of breeding habitat (i.e. during chick rearing; e.g. Harrison *et al.* 2010; Seress *et al.* 2018; Shutt *et al.* 2018). Consequently, therefore, such disparities in the effects of urbanisation across pre- and post hatching breeding phases might suggest that breeding in the city is maladaptive (Sumasgutner *et al.* 2014; Demeyrier *et al.* 2017).

However, another alternative hypothesis that deserves further consideration is that females breeding in poor quality habitats with low or unpredictable food resources such as cities may strategically lay more eggs and then selectively starve nestlings post-hatch to optimise brood size according to the availability of key food resources such as caterpillars (Gottlander 1987; Slagsvold and Amundsen 1992). Although correlative, the results from this study suggest that females may have adopted this brood reduction strategy.

Although beyond the scope of this current research, it is likely that the effects of increasing urbanisation, particularly on post-hatching breeding success within the city are linked to several different environmental axes (e.g. see Sprau *et al.* 2017) that have been found to covary with the urban gradient including: temperature (Deviche and Davies 2014; Arct *et al.* 2022), light (Hale *et al.* 2015; Dominoni 2015; Gaston *et al.* 2015), noise (Halfwerk *et al.* 2011; Injaian *et al.* 2018b), pollution (Eeva *et al.* 1997, 2005, 2008) and human disturbance (e.g. Glądalski *et al.* 2016; Corsini *et al.* 2017). Fine-scale variations in these environmental parameters can impact directly on the growth, development and survival of nestlings, or indirectly by altering parental physiology and foraging behaviour, and reducing the availability of natural high quality food (Corsini *et al.* 2017, 2021; Szulkin *et al*. 2020).

3.4.1.2. Garden landcover

In Britain gardens make up approximately 25% of all urban landcover and it is estimated that nearly 50% of all households feed birds on a regular basis (Davies *et al.* 2012; Amrhein 2014; Orros and Fellowes 2015). In Birmingham, the average percentage of garden landcover surrounding study sites was 23.15% (range: 0.66-60.17%), cumulatively accounting for 20% of the total area surveyed, and therefore my study was comparable to the national picture. Whilst Blue Tits appeared to benefit initially from the availability of gardens, with significantly higher rates of hatching success associated with increasing garden landcover (ULC Model; Table 3.4), they were also more likely to experience lower rates of fledging success (Built Model; Table 3.6).

Although my research was only correlative in nature and thus it was not possible to establish the mechanisms by which gardens were impacting breeding performance, it is reasonable to suggest that the availability of supplementary food might be playing a fundamental role. I hypothesise that supplemental feeding in gardens potentially buffered the lack of natural food resources within breeding territories enabling females to attain breeding condition and/or provided them with the energy to forage for longer periods to acquire nutrients and proteins required during egg laying and incubation (e.g. see Robb *et al*. 2008; Harrison *et al.* 2010). However, this may have resulted in a mismatch post-hatching due to differences between the perceived and true quality of breeding habitats, ultimately leading to non-adaptive breeding decisions and investments and resulting in a negative influence of gardens on fledging success (Anderies *et al.* 2007; Plummer *et al.* 2013b; Demeyrier *et al.* 2017).

Indeed, recent scientific advances in animal telemetry (RFID technology) and monitoring (Cox *et al.* 2016; Jarrett *et al.* 2020; Shutt *et al*. 2021), stable isotope analysis (Pollock *et al.* 2017) and faecal metabarcoding (Jarrett *et al.* 2020; Shutt *et al*. 2021) have confirmed that birds will travel beyond their own territories, both prior to and during the breeding season, to exploit key resources, including supplemental food at garden feeders.
Interestingly the divergent responses observed pre- and post-hatching in my study appeared to counteract each other, resulting in little to no observed effect of garden landcover on overall breeding success. This disparity in findings is consistent with the growing scientific consensus that there are both benefits and costs of supplemental feeding on avian reproduction (Jones and Reynolds 2008; Robb *et al.* 2008a,b; Plummer *et al.* 2013a,b; Ruffino *et al.* 2014; Crates *et al.* 2016; Demeyrier *et al.* 2017; Seress *et al.* 2018; Shutt *et al.* 2021).

Comparable to this study, Hedblom and Söderström (2012) linked observed disparities between early and late breeding traits in Great Tits nesting in residential areas in Uppsala, Sweden to potential downstream effects of winter provisioning of supplemental food in residential gardens. They hypothesised that whilst winter provisioning by residents helped females to attain a nutritional threshold for breeding (likely resulting in earlier laying), the widespread cessation of feeding which was known to coincide with spring leaf-out, created a sudden shortage of food resulting in mistimed breeding and lower nestling body condition. A similar hypothesis therefore may (at least partially) explain the offset between the earlier benefits of gardens and later negative impacts post-hatching in my study.

Similar to the effects of built landcover, a strong and pervasive negative effect of gardens was observed on the probability of hatching and fledging success with significant knock-on effects to the probability of overall breeding success.

The different pattern of results observed for the impacts of built and garden landcover on proportional versus binary measures of success suggest that the potential causal factor(s) of total breeding failure may differ from those driving partial loss (i.e. brood reduction) in successful breeding attempts. A potential hypothesis to explain this is that increases in built and garden landcover are associated with higher costs to adults, for example due to increased foraging distances (Hinsley *et al.* 1999), and/or longer foraging periods (Stauss *et al.* 2005) to compensate for a lack of preferred natural food within their own breeding territories. Under such circumstances, adults might be at a higher risk of mortality from human-mediated threats including predation by cats (Seress *et al.* 2011; Evans *et al.* 2015; Pavisse *et al.* 2019), disease transmission at garden feeders (Chace and Walsh 2006; Robb *et al*. 2008) and vehicle/building collisions (Hager *et al.* 2013; Hager and Craig 2014; Loss *et al.* 2014a,b).

3.4.2. Effects of habitat scale variables on breeding performance

3.4.2.1. Tree density and diversity

Compared with preferred oak-rich deciduous and mixed forest habitats (Perrins *et al.* 1965), urban greenspaces are typically characterised by smaller and highly fragmented habitat patches and plant communities with a very different vegetation structure and composition (Mackenzie *et al.* 2014; New 2015; Seress and Liker 2015). Consequently, urban habitats may support a lower abundance and diversity of the high quality prey items including caterpillars (*Lepidoptera* spp.) that form the primary source of food during the energy intensive chick-rearing period (Blondel *et al.* 1991; Perrins 1991; van Noordwijk *et al.* 1995; Naef-Daenzer *et al.* 2000; Tremblay *et al.* 2005). Supporting this, urban-rural comparative studies have linked reduced food resources with changes in parental foraging behaviour (Mackenzie *et al.* 2014; Jarrett *et al*. 2020), reduced chick provisioning (Pollock *et al.* 2017), lower nestling condition (Hinsley *et al.* 2008; Biard *et al.* 2017) and significantly lower breeding success (Glądalski *et al.* 2017; Seress *et al.* 2018; Wawrzyniak *et al.* 2020). Furthermore, the increased planting of non-native and ornamental species, particularly in residential gardens and urban parklands, is also thought to exaggerate natural food shortages with knock-on effects to nestling development and survival (Narango *et al*. 2017, 2018; Corsini *et al.* 2021).

While the availability of natural food was not explicitly evaluated in my study, the quality of the habitat surrounding nests, measured as the availability of native broadleaved deciduous trees and broadleaved (native and non-native) tree species diversity is considered a reliable index of prey availability for tits (Isaksson and Andersson 2007; Glądalski *et al.* 2015; Bueno-Enciso *et al.* 2016b; Dekeukeleire *et al.* 2019). As hypothesised, the average density and diversity of broadleaved trees surrounding nestboxes was positively correlated with pre-hatching breeding outcomes. Crucially, however, and in contrast to predictions, findings suggested that higher numbers of native trees and greater broadleaved species diversity do not necessarily confer benefits on nestling survival, fledging and breeding success.

An offset between the initial benefits of increasing tree density (Tables 3.4 - 3.5) on early breeding traits and subsequent detrimental impacts on downstream fledging success (Table 3.6) resulted in similar numbers of fledglings (Table 3.8) and overall rates of breeding success (Table 3.7) across sites. In contrast, the post-hatching effects of tree diversity were associated with strong, polynomial relationships across all reproductive traits including breeding success and the probability of total breeding failure (Tables 3.7-3.10). This non-linear effect was consistent across all breeding responses in which it was identified, with models predicting a threshold InvSI value (~ 5.5-6.5 species) beyond which further increases in tree diversity adversely impacted reproductive performance (Figs. 3.11 and 3.13).

Although it was not possible to establish the factors linking fine-scale changes in breeding habitat and increased nestling mortality, it is hypothesised that many broods likely suffered from starvation as a result of reduced caterpillar availability (Solonen 2001; Harrison *et al.* 2010; Charmantier *et al.* 2017; Seress *et al.* 2018). Of interest, habitat surveys indicated that the relationship between mean tree diversity and the density of native deciduous trees across breeding sites closely paralleled the non-linear effect of tree diversity on post-hatching breeding responses. Initially, as average territory tree diversity values increased, there was a concurrent increase in native deciduous tree density. Once site diversity scores exceeded ≥ 5.0 species the density of preferred native deciduous trees declined, implying an increased planting of non-native and/or ornamental species. Furthermore, sites in the most heavily urbanised areas of the city were found to have the highest tree diversity (e.g. Fig. 3.13) and the lowest number of native trees (e.g. Fig. 3.9), suggesting that inner-city greenspaces in Birmingham in particular, are dominated by non-native and ornamental species. Other studies conducted in different major European cities (e.g. Mackenzie *et al.* 2014; Pollock *et al.* 2017; Jarrett *et al*. 2020) have similarly shown the importance of native food-rich tree species such as oaks (*Quercus* spp.) and birches (*Betula* spp.) rather than overall plant diversity for successful breeding in Blue and Great Tits.

Although the urban tree assemblage in Birmingham is dominated by Blue Tits preferred species including Common Ash (*Fraxinus excelsior*), Pedunculate Oak (*Quercus robur*), Silver Birch (*Betula pendula*) and sycamores (*Acer* spp.), the density of trees surrounding nestboxes at most sites is low and dominated by small/young trees with little shrub cover (Chapter 2 and pers. obs.). The age, canopy height and maturity of individual trees are known to be important determinants of habitat quality and the availability of food resources for tits, with more mature and larger trees associated with more efficient foraging behaviour and increased breeding performance (Hinsley *et al.* 2008; Mackenzie *et al.* 2014).

It is therefore likely that a number of inter-related factors linked to the small size, low density and quality of preferred tree species contributed to the high levels of brood reduction and loss observed across the urban gradient in my study. Targeted research incorporating arthropod sampling, video-recording at nestboxes and remote sensing (e.g. PIT tags fitted to adult tarsi and use of RFID readers) however, is needed to quantify food availability, and more accurately assess nestling diet. This will help to identify the roles that both natural and supplemental food sources play in driving breeding success in this population (Cox *et al.* 2016; Narango *et al.* 2017; Pollock *et al.* 2017; Seress *et al.* 2018).

3.4.2.2. Greenspace size and edge effects

I hypothesised that breeding success outcomes would be negatively correlated with the total area of each site, however this proved a poor predictor of breeding success in my study. This might be due to the subjective delineation of site boundaries and the fact that this metric did not capture the type (e.g. parkland or woodland) and quality (composition and complexity) of greenspace.

As expected, the impacts of edge effects on pre- and post- hatching breeding success outcomes were complex and difficult to disentangle. Overall, however, results surprisingly indicated that pairs nesting nearer to the edges of connected tree cover experienced lower rates of hatching failure, leading to larger brood sizes and higher fledgling numbers compared with their conspecifics nesting within patches of connected tree cover. However, the same pairs appeared to be at a significantly greater risk of suffering total hatching failure. Few studies have previously investigated edge effects in urban avian breeding ecology (but see Fernández-Juricic 2001; Hedblom and Söderström 2012) and therefore disentangling the potential mechanisms underlying these observations is difficult. Whilst Hedblom and Söderström (2012) found no discernible effect of distance along urban woodland transects on reproductive performance in Great Tits, Fernández-Juricic (2001) reported disparate responses (breeding density) to edge effects among birds breeding in large urban woodland parks in Madrid, Spain.

In my study variation in the strength and direction of edge effects provide tentative evidence that different factors might be causing complete breeding failure compared with partial losses in successful nesting attempts. In natural but highly fragmented forests edge effects are commonly associated with reduced reproductive performance due to the low quality of the habitat (e.g. Hinsley *et al.* 1999; Batáry and Báldi 2004). Therefore the higher risk of hatching failure for tits nesting closer to patch edges could be due to a number of related factors including differences in the micro-climate, reduced food supplies, higher air pollution and predation levels and increased human disturbance (Hinsley *et al.* 1999; Fernández-Juricic 2001; Batáry and Báldi 2004; Buxton and Benson 2015).

The contrasting observed positive edge effects are comparable to the study of Saarikivi and Herczeg (2014) who found higher rates of breeding success in passerines including Blue and Great Tits and Pied Flycatchers (*Ficedula hypoleuca*) nesting in sub(urban) patch edges compared with adjacent forest. These were attributed to changes in habitat quality (including warmer nesting conditions and more suitable foraging areas) as well as potential phenotypic differences in the breeding quality of adults.

Nonetheless, potential edge- and patch-size effects on breeding success are likely complicated by the unique characteristics (size, shape and the ratio of patch interior to edge) of urban greenspaces when compared with natural forested areas (e.g. see Hinsley *et al.* 1999; Lahti 2001). For example, Hedblom and Söderström (2012) highlighted that the type of habitat matrix (i.e. residential, industrial or grasslands) surrounding remnant urban woodland was important in determining how urbanisation impacted on both quantitative and qualitative measures of breeding success in breeding density, hatching date and nestling condition in Great Tits.

3.5. CONCLUSIONS

While the results presented here corroborate the findings of previous studies, they also provide a novel contribution to urban avian breeding research by demonstrating that even across short highly-urbanised gradients, breeding is impacted by a number of interlinked processes and effects operating at different spatial scales. Furthermore, they clearly reflect the emerging wider view that the impacts of urbanisation are both complex and unlikely to be consistent across the breeding cycle or indeed across different breeding populations and species occupying the world’s cities (Charmantier *et al.* 2017; Batáry *et al.* 2018; Plummer *et al.* 2020). Therefore, my results support the need for urban studies that take a comprehensive multi-spatial scale modelling approach, which considers the analysis of multiple response variables across different phases of the breeding cycle (Moll *et al.* 2019; Satgé *et al.* 2019; Strubbe *et al.* 2020).

Overall, my study suggests that reduced breeding success across the urban gradient is primarily driven by increased rates of brood reduction and complete reproductive failure. This supports the hypothesis that the energy-intensive chick-rearing period is the most sensitive phase of the breeding attempt to urban-driven environmental change including increases in built landcover. Failure and loss during chick rearing have been widely proposed as a key factor driving reduced breeding performance of passerines in urban areas (Schroeder *et al.* 2012; Sepp *et al.* 2018; Jarrett *et al.* 2020; Seress *et al.* 2020) with evidence from both observational (e.g. Pollock *et al.* 2017; Seress *et al.* 2018) and experimental studies (e.g. Demeyrier *et al.* 2017; Capilla-Lasheras *et al.* 2017). In particular low nestling survival and high rates of brood reduction have been implicated in the widespread and rapid decline of House Sparrows (*Passer domesticus*) across Europe (Peach *et al.* 2008, 2015; Shaw *et al*. 2008; Meillère *et al.* 2015). In the next chapter I investigate in more detail how variation in the different environmental characteristics of the habitat and wider landscape influence nestling phenotype (size and body condition), and how this impacts on survival rates of nestlings along the urban gradient. In particular I investigate if there is potential correlational evidence for a brood reduction strategy among nesting females.

Chapter Four

Brood-rearing in the city: the impacts of urban-driven environmental change at the habitat and landscape scale on nestling phenotypes and survival

4.1. INTRODUCTION

4.1.1. Breeding timing and the tri-trophic system

For many European insectivorous bird species including most passerines, the energy intensive brood-rearing period (i.e. the period between hatching and fledging) is considered the most demanding and critical phase of the avian reproductive cycle (Ricklefs 1969; Sepp *et al.* 2018; Schöll and Hille 2020). Research conducted in optimal breeding habitats, such as oak-dominant broadleaf woodland have widely demonstrated that divergence in traits used to measure reproductive success during this period in species such as Great Tit (*Parus major*) and Blue Tit (*Cyanistes caeruleus*) are primarily influenced by local variation in environmental conditions and ecological differences in the 'tri-trophic system': more specifically the timing of budburst of trees and the associated phenology and abundance of key and preferred protein-rich food resources such as caterpillars (Southwood *et al.* 2004; Marciniak *et al.* 2007; Kaliński *et al.* 2009). As such, even in optimal habitats, nestlings are under conflicting pressure to grow and fledge as early as possible due to seasonal constraints in high quality protein-rich food resources. Indeed, aligned with these findings, studies have established that there is strong selection for earlier hatching and rapid nestling growth in these species (Hochachka and Smith 1991; Ardia 2005).

For Blue and Great Tits, nestling growth is weakly sigmoidal, with the maximum growth rate usually occurring approximately 9-11 days post-hatching (Van Balen 1973; Perrins 1991). Therefore, tits time their breeding so that this period of maximal food demand is synchronised with the local peak in caterpillar abundance (Gibb 1950; Blondel *et al*. 1990; Tremblay *et al.* 2003), both to reduce the energetic costs of breeding and maximise nestling development and fledging success (Thomas *et al.* 2001). Of further, significance young nestlings (≤ 10-11 days old) are born altricial and poikilothermic, and are unable to thermoregulate, therefore making them particularly vulnerable to changes in abiotic conditions during the early developmental phase (Mertens 1977; Ardia 2005).

4.1.2. Impacts of urbanisation on nestling growth, development and survival

In comparison to natural woodland habitats, urban parklands and other greenspaces typically support a lower abundance of caterpillars (Seress *et al.* 2020), therefore breeding pairs are less likely to be able to meet the nutritional demands of their offspring, resulting in restricted growth, lower body mass and reduced survival rates (Nur 1988; Naef-Daenzer and Keller 1999; Stauss *et al.* 2005). Indeed, there is increasing evidence from comparative urban-rural studies (e.g. Demeyrier *et al.* 2017; Seress *et al.* 2018; Satgé *et al.* 2019) to suggest that urban nestlings exhibit several phenotypic differences and a lower probability of fledging compared with broods raised in more natural woodland environments, linked to anthropogenic-driven environmental changes in breeding habitat and in particular limitations in the availability of natural invertebrate food. For example in a long-term comparative study conducted in Lódz, central Poland, Glądalski *et al.* (2015, 2017) and Wawrzyniak *et al.* (2020) reported reduced fledgling numbers and fledging success of Blue and Great Tits in urban parklands compared to birds breeding in a nearby forest which were attributed to differences in the trophic ecology between the two habitats (Marciniak *et al.* 2007; Kaliński *et al.* 2009). The quality of breeding habitat was found to be lower and the associated abundance of caterpillars reduced in urban parklands due to the highly fragmented tree cover, increased disturbance including light pollution, low density of preferred oak trees, and intensive greenspace management. Bailly *et al.* (2016) reported reduced growth during both embryonic and nestling developmental stages, lower body mass and condition and lower survival in Blue and Great Tits, reared in both a smaller and larger city in France compared with their conspecifics raised in nearby forests. These differences were correlated with the comparatively lower density and smaller size of deciduous trees and subsequent limited availability of natural foods in the two cities. Similarly, Biard *et al.* (2017) reported that 14 day old Great Tit nestlings reared in urban parks within a large (Paris) and medium sized city (Niort), France were structurally smaller and less colourful (suggesting a lower carotenoid-based diet) compared with their conspecifics raised in a rural site within the same region.

While the quality of the environment immediately surrounding nesting sites (largely determined by the structure and composition of vegetation) may drive anthropogenic-mediated effects at the habitat level, variation in abiotic conditions including the environmental structuring of cities at larger landscape spatial-scales likely also shape the impacts of urbanisation on breeding success during chick rearing. Compared with natural woodland habitats, cities are characterised by increased temperatures (the urban heat island effect), elevated light and noise, pollution levels, and disturbance which also likely impact detrimentally on the growth, development and survival of nestlings via a number of different mechanistic pathways: either directly, through changes in the tri-trophic system, or indirectly by altering parental physiology and behaviour (Biard *et al.*, 2017; Corsini *et al.* 2017, 2021; Szulkin et al. 2020).

Despite the recent intensification in research to understand the effects of increasing urbanisation on early avian development (as reviewed by Sepp *et al.* 2018), the specific habitat and landscape-scale factors and the associated underlying casual mechanisms driving variation in nestling phenotypes and survival remain relatively poorly studied and understood (Biard *et al.* 2017; Sprau *et al.* 2017; Corsini *et al.* 2021). Yet, research conducted in optimal breeding habitats has widely demonstrated that early developmental conditions are crucial. In the short-term they influence morphological markers such as nestling body size and condition and the probability of successful fledging (Perrins *et al.* 1965; Nur, 1984, 1987; Thompson *et al*. 1999; Stauss *et al.* 2005). In turn, the condition of chicks when they leave the nest (the end product of nestling development) determines their long-term survival and recruitment into the breeding population and their own future reproductive success as breeding adults (Visser and Verboven 1999; Metcalfe and Monaghan 2001; Monaghan, 2008). Consequently, nestling phenotypic traits and associated brood survival outcomes are widely considered critical components of avian reproductive success and thus reliable measures that reflect the suitability of habitat for breeding (Bailly *et al.* 2016).

In the few studies that have incorporated a quantitative approach and/or included a hierarchical modelling framework, the negative impacts of increasing urbanisation on nestling growth, body condition and survival have been confirmed. For example, Corsini *et* *al.* (2021) found that with increasing levels of impervious surface landcover, the age of peak nestling growth in Blue Tits in Warsaw, Poland was increasingly delayed, the weight of both Blue and Great Tit nestlings declined across different phases of chick rearing, and mortality increased between five and 10 days post-hatch. In contrast, Sprau *et al.* (2017) found that whilst Great Tits breeding in the city of Munich, Germany bred less successfully than conspecifics in forest sites, variation in nestling body mass and fledgling body condition across urban sites was not explained by quantitative measures of urbanisation using four different environmental axes (i.e. temperature, humidity, light and noise). Therefore, variation in breeding traits were likely either driven by other factors not investigated within the study such as the availability of food or more complex interactions between the different metrics tested. Sprau *et al*. (2017) highlighted the importance of incorporating different quantitative measures of urbanisation in determining how urban-driven environmental change impacts breeding of birds, particularly within highly urbanised intra-city sites and emphasised the need for a more holistic approach in considering the quantification of urbanisation effects on brood rearing and nestling development at higher spatial resolutions and using multiple spatial scales (cf. Moll *et al.* 2019; Satgé *et al.* 2019; Szulkin *et al.* 2020). This is crucial if we are to disentangle the habitat and landscape features of urbanised areas that influence avian growth and survival, and more accurately quantify the strength and direction of their individual effects (Sprau *et al.* 2017; Corsini *et al.*, 2021).

4.1.3. Quantifying nestling growth, development and survival

In the first instance, more accurately quantifying variation in nestling growth and development is important to understand in greater detail the consequences of increasing built landcover (i.e. urban densification) on the early development of wild birds (Biard *et al.* 2017). Offspring are commonly assessed using a number of different morphometric markers that are considered reliable measures that reflect the suitability of habitat for breeding (Bailly *et al.* 2016), including body mass, tarsus length, and their combined expression as body condition (Hochachka and Smith, 1991; Stauss *et al.* 2005; Kaliński *et al.* 2009, Sepp *et al.* 2018).

Secondly, the fate (death or survival) of individual nestlings is a frequently used direct measure of reproductive success in avian urban ecology (Biard *et al.* 2017). In low quality habitats with poor or unpredictable food resources, females may strategize egg laying by producing potentially larger than optimal clutches and subsequently selectively starve nestlings to optimise brood size according to the prevailing environmental conditions (Gottlander 1987; Slagsvold and Amundsen 1992).

The results from Chapter Three, although correlative, suggest that clutch sizes across greenspace within the city are sub-optimally large, potentially indicating that breeding performance of Blue Tits in Birmingham is driven by brood reduction in response to the low quality and/or unpredictable conditions (e.g. availability of food resources) of the breeding environment. To test this hypothesis, four response variables derived from the raw data were used to explore how rates of brood survival and loss differed across two distinct stages of nestling development: ‘early’ (day of hatching to 10-12 days post-hatching) and ‘late’ (approx. 12 days post-hatch to fledging).

Aligned with the brood reduction strategy, a rank (nestling weight) hierarchy may be established within broods. Asymmetry in the mass of offspring within a brood (or ‘weight spread’ after Gottlander 1987) may be linked to individual investment by parents and/or competition between nestlings. Such competition and conflict for resources may be particularly acute when food abundance is low or the availability of food resources are unpredictable (Gottlander 1987; Slagsvold and Amundsen, 1992). As a consequence, the lightest nestlings will undergo slower growth, have lower body masses and higher mortality rates than their heavier siblings (Gottlander 1987). Variation in brood mass asymmetry is also considered within this study, as a potential indicator of food limitation as well as evidence of brood reduction.

4.1.4. Aims and hypotheses

In this chapter I am to identify how specific elements of urban environmental change at both the landscape and habitat scale impact on measures of nestling morphometrics (body mass and body condition) and their probability of surviving to fledge. More specifically I investigate if there is evidence for covariation between nestling body mass and survival, and if this varies in response to urbanisation and aspects of breeding territory quality including the composition and structure of vegetation surrounding nestboxes. I also explore how brood mass asymmetry varies across the urban gradient and if rates of chick mortality are higher during early compared with later nestling development, and if this might be suggestive of females using a brood reduction strategy to optimise breeding success post-hatching.

I hypothesise that:

(1) there will be a pervasive negative effect of increasing urbanisation on mean nestling mass, body condition and brood mass asymmetry.

(2) the probability of individual nestling survival will decrease with increasing built landcover, with a concomitant increase in rates of brood reduction across both early and late developmental phases. Rates of brood reduction will be significantly higher during the early developmental compared with the late developmental phase. Furthermore, nestling body mass at ringing will be positively correlated with offspring survival (with smaller, lighter nestlings having a lower probability of fledging), and this effect will be synergistic with the urban gradient.

(3) Aligned with hypothesis 2 the proportion of early deaths (relative to total nestling deaths across both developmental stages) will significantly covary with the percentage of built landcover.

(5) individual nestling and averaged brood traits will be significantly influenced by characteristics of the habitat immediately surrounding nestboxes including the density of preferred native deciduous trees including oak, birch and sycamore; the diversity of deciduous (native and non-native) trees and edge effects.

(6) nestlings in larger broods will be smaller and have lower body condition, broods will exhibit greater body mass asymmetry and survival will be lower due to increased intra-specific competition for food. Concomitantly, sites with higher rates of occupancy will also be negatively correlated with nestling and brood-level response variables due to potentially increased levels of inter-site competition between Blue Tit broods. Broods hatched later in the season are hypothesised to exhibit lower nestling mass and body condition and higher rates of mortality.

4.2. METHODS

4.2.1. Study design

The overall research design, fieldwork and analytical approaches follow those described in Chapter 2 and in section 3.2.

Many studies target the period of maximum nestling growth and food demand (9-11 days post hatch) as a critical phase of development, when assessing the effects of environmental conditions on variation in nestling morphometrics and survival (e.g. Hinsley *et al.* 2008; Wilkin *et al.* 2009; Bailly *et al.* 2016; Dekeukeleire *et al.* 2019). However, due to the logistical challenge associated with visiting numerous sites within a short timeframe, particularly in seasons with highly synchronous breeding, it was not possible to collect nestling data within the preferred 10-12-day ringing window for all individuals at all sites. Consequently, morphometric measurements were taken when nestlings were between eight and 15 days old, therefore capturing the rapid phase of nestling growth (Bailly *et al.* 2016), with a cut off at the asymptote of body mass which is reached at approximately day 15 (Van Balen 1973; Hedblom and Söderström 2012). Nonetheless, the average age of nestlings at ringing was 10.60 ± 1.37 days (mean ± 1 SD), with 77% of all active nestboxes visited when nestlings were 10-12 days old.

4.2.2. Defining response variables

4.2.2.1. Nestling morphometrics and brood mass asymmetry

Four response variables were derived from the raw morphometric data for the assessment of variation in nestling size and body condition across the urban gradient: (1) nestling body mass, (2) nestling tarsus length, (3) body condition, and (4) brood mass asymmetry. To control for potential issues of pseudo-replication of datapoints within broods, for each nest, average brood morphometrics (mean nestling body mass (n= 509 nests) and mean tarsus length (n = 453 nests) were calculated from the raw nestling data. For broods in which body mass and tarsus lengths were not obtained for all nestlings (n = 13 nests), mean values were determined using the total number of chicks measured rather than the brood size at ringing.

A body condition index was calculated for each nestling measured during ringing (n = 3,048). This response variable provides a measurement of body mass which controls for body size and was derived for each nestling as a residual from a regression of body mass on tarsus length using all data (Jakob *et al*. 1996; Brown 1996; Ardia 2005; Labocha and Hayes 2011). Analyses excluded all data from 2013 (364 records) and 44 nestlings from 2016 for which tarsus length was not measured. An average body condition index was then determined for each brood, calculated as the mean body condition of nestlings (n = 453 broods).

Brood mass asymmetry was used to quantify the spread (i.e. variation) in body mass of nestlings and was calculated as the range in body mass between the heaviest and lightest nestling in each brood. All nests with ≥ 2 nestlings alive at ringing (n = 500) were retained for analysis.

4.2.2.2. Individual nestling survival and brood reduction

Variation in the rates of brood reduction and loss were investigated for two distinct stages of the chick-rearing period: (1) between hatching and ringing, and (2) ringing and fledging (hereafter referred to as early and late phase brood success, respectively).

Whilst adults will remove young dead nestlings from the nest, they rarely remove deceased older and larger chicks (Smith *et al.* 1989), providing a reliable means to determine the fate of individuals using ringing records. All nestlings were assumed to have fledged if no remains were recovered during final nest checks and the nest was undisturbed and well-trodden with evidence of feather scales and/or droppings (British Trust for Ornithology 2003). For nests with evidence of partial brood loss, the remains of deceased nestlings as far as possible were identified from their individual BTO ring number and their siblings were assumed to have fledged. Fledglings were categorised as successful (i.e. survived; 1) or failed (i.e. deceased; 0). Of the initial 3,494 nestlings recorded across six breeding seasons, only 44 had to be removed for analysis because survival outcome could not be determined, resulting in 3,450 nestling records from 510 nests.

Early phase brood success was calculated for each nest as the proportion of nestlings surviving to ringing (i.e. at least 8 days post-hatching) relative to the number that initially hatched. All nests with at least one hatchling were retained for analysis, including nests that later suffered total brood failure (n = 662 nests). Late phase brood success was calculated as the proportion of nestlings that survived to fledging relative to the total number alive at ringing (n = 575 nests) and included all nests in which at least one chick remained alive at ringing, as well as total brood failures.

The proportion of nestling deaths that occurred during the early and late brood-rearing phases, (relative to total deaths across both periods combined) were also calculated for each nest. These data were then used in the analysis of proportional brood reduction to determine how the ratio of early to late stage nestling loss varied across the urban gradient. All nests that experienced the death of at least one nestling were included in analyses (n= 415 nests). Nests which suffered complete brood-loss, either gradually over the entire nestling period or in one mass loss event were also retained.

4.2.3. Abiotic and biotic covariates

Habitat and landscape covariates were included for analyses to investigate the effects of the urban environment on breeding outcomes as described in Chapter 2 and section 3.2.3 in Chapter 3.

Biological covariates were included in each model to account for the reproductive investment of pairs during previous stages of the breeding cycle relative to the response variable under investigation. Studies have widely demonstrated seasonal declines in brood size, nestling body condition and survival, linked to temporal variation in the availability of food (Verhulst and Tinbergen 1991; Norris 1993; Barba *et al.* 1995). Therefore, a phenological term, (April laying or hatching date) was included as a fixed covariate in models for survival and body mass/body condition response variables, respectively. Brood size was *a priori* included as a covariate in models of mean nestling mass, body condition, individual nestling survival and brood asymmetry to control for increased competition between siblings in larger broods (Nur 1988; Dijkstra *et al.* 1990; Naef-Daenzer and Keller 1999; Neuenschwander *et al.* 2003). Proportional occupancy was included as a proxy measure of potential density-dependent effects including intra-specific competition for resources between nests (Dhondt *et al.* 1992; Both 1998; Wilkin *et al.* 2006; Shutt *et al.* 2018). Finally, ringing age was included as a fixed covariate in models to account for the different ages at which nestlings were ringed.

4.2.4. Statistical analysis

4.2.4.1. Analytical framework and models

The analytical framework and construction of models followed the same approach described in sections 2.5.2, 2.5.3 and 3.2.4.

An interaction term between the percentage of built landcover and April laying (or hatching) date was initially included in all models to investigate potential variation in phenological effects on brood rearing across the urban gradient.

The final (global) model parameterisation used in the analysis of each breeding response variable is illustrated in Fig. 4.1, whilst details of the fixed and random effects structures for each model are provided in the accompanying Appendix 4. Analyses were conducted on each metric using the appropriate dataset.

Figure 4.1. Schematic diagram of the analyses used to investigate variation in nestling morphology, survival and rates of brood reduction across two stages of brood rearing in a population of Blue Tits breeding across the intra-city urban gradient in the city of Birmingham, UK. Model parameterisation for nestling (mean) morphometric variable analyses are highlighted in blue, proportional survival for each stage of development (i.e. early and late brood reduction models) in pink, and nestling survival outcome (analysed for individual nestlings) and the proportion of nestling deaths occurring during early development in dark red. Breeding Information for each response includes the type of data and the distribution of data/family used in model parameterisation. Response variables with a Gaussian distribution were modelled using lmer models and those with a binomial or betabinomial distribution as glmers.

4.2.4.2. Nestling morphometric & brood asymmetry model parameterisation

The analysis of mean tarsus length was abandoned due to the heavy negative skew of the data which, despite several modelling attempts using different family and link specifications resulted in continued heteroscedasticity of residuals. The mean body condition response variable demonstrated a heavily right-skewed distribution which required the log-transformation of data. All response variables were analysed using linear mixed models (Gaussian distribution).

The nested random effect variable Nestbox ID was removed from both mean nestling mass (MNM; built and ULC) models and the brood asymmetry (ASYM) built model, whilst Site ID was dropped from both mean body condition (meanRBC; built and ULC) models due to model convergence issues associated with variance estimates collapsing to zero.

Only the second order polynomial term for broadleaved tree diversity was retained in built MNM and meanRBC models. All other squared terms and interactions that were *a priori* included in global models, including an interaction term between laying date and the urban gradient (to investigate potential phenological effects on brood rearing across the urban gradient) were dropped as no significant effects were detected. Finally, the fixed term occupancy was dropped from the ULC MNM model to aid model validation.

4.2.4.3. Nestling survival and brood reduction model parameterisation

The model analysing (the probability of) individual nestling survival (PNS; binary response variable) was fitted with a binomial distribution. Due to issues with model validation and in particular spatial autocorrelation, data from 2013 (n = 364 records) had to be removed from analyses resulting in a reduced dataset (n = 3,086 individual nestling outcomes).

The potential for non-independence of nestlings within each brood was initially controlled for by including Brood ID as a random factor, with year specified as a fixed factor. However, with the exception of the built LBS model, all final models retained the default nested random effects structure. An interaction term between nestling body mass and the urban gradient was also *a priori* included in models.

The two brood reduction response variables (the proportion of nestlings surviving early and late brood-rearing phases; EBS and LBS models respectively) were specified as a binomial response (number of nestlings survived, number of nestlings died). The EBS model was fitted using a betabinomial error distribution and the LBS model with a binomial error distribution to account for overdispersion in the data (Zuur *et al.* 2009; Zuur *et al.* 2013; Bolker 2017). Zero-inflation models (Brooks *et al.* 2017, 2019) were included in all final EBS and LBS models to account for the high number of structural zeros, related to the lack of total brood losses in the data. The occurrence of zeros was found not to be dependent on Site ID, and thus the zi-formula in each model was set to ~*1*.

The nested random effect term Nestbox ID was removed from all but the built LBS model. All models included April laying date and with the exception of the built EBS model, occupancy, which was dropped due to collinearity issues associated with the urban gradient term. Fixed effects also included exponential terms for both broadleaved tree diversity and the percentage of garden landcover. Brood size at hatching and brood size at ringing age were not included in the analyses of early brood survival and late brood survival respectively, as direct measures of overall productivity of nests, these terms were captured within the response variables.

The proportion of all nestling deaths occurring during early development was also analysed using a binomial response and parameterised using a betabinomial distribution to correct for significant issues with overdispersion. April laying date was included as a fixed effect and all second order polynomial terms for environmental and biotic covariates that were *a priori* included, were ultimately dropped from the final model. Random effects included Site ID and Year. All binomial and beta binomial models were run with the default *logit-link* function.

4.3. RESULTS

4.3.1. Results: overview

Although models were initially run with both the linear built (%BLC) and categorical (ULC) urban metric, the quantitative gradient was consistently found to be a much more reliable and better predictor of urbanisation effects on breeding outcomes. Therefore, only the results from built models are considered in this chapter.

Of the 662 nests across the six breeding seasons that successfully hatched at least one nestling, 583 (88.1%) were still active (≥ 1 chick alive in the nest) ≥ 7 days post-hatching. Brood rearing data were collected from 514 nests equating to 87.1% of the total active nests. Across all years, only 69 broods (11.8% of nest records) were not ringed. Broods were missed due to logistical constraints, site access issues and poor weather conditions. A further five nests (total 38 nestlings) were subsequently excluded from analyses because nestlings were ringed outside of the 8-15 day post-hatching period. In 13 nests (2.55% of all nests), a small percentage of nestlings in the brood were too small to be ringed or weighed. However, these nests were retained and the data from measured chicks included in analyses. A total 3,456 individual nestlings (n = 509 nests) were weighed and 3,048 tarsus (n

= 453 nests) measurements were taken. Morphometrics of nestlings by year, site and measure are presented in Table 4.1 and Figure 4.2.

Table 4.1. The morphometrics (i.e. body mass and tarsus length) retained for analyses by year of all Blue Tit nestlings reared across 28 sites in Birmingham, UK over six consecutive breeding seasons (2013-2018). The total number of breeding records for each year are provided together with the total number of nestlings processed in brackets.

Year	Number of Records for Body Mass	Number of Records for Tarsus Length
2013*	49 (357)	0 (0)
2014	99 (727)	99 (727)
2015	105 (700)	105 (700)
2016*	51 (307)	44 (256)
2017	94 (596)	94 (596)
2018	111 (769)	111 (769)
Total	**509** (3456)	**453** (3048)

* Tarsus measurements were not recorded in 2013 & for a subset of broods in 2016 tarsus measurements were also not taken.

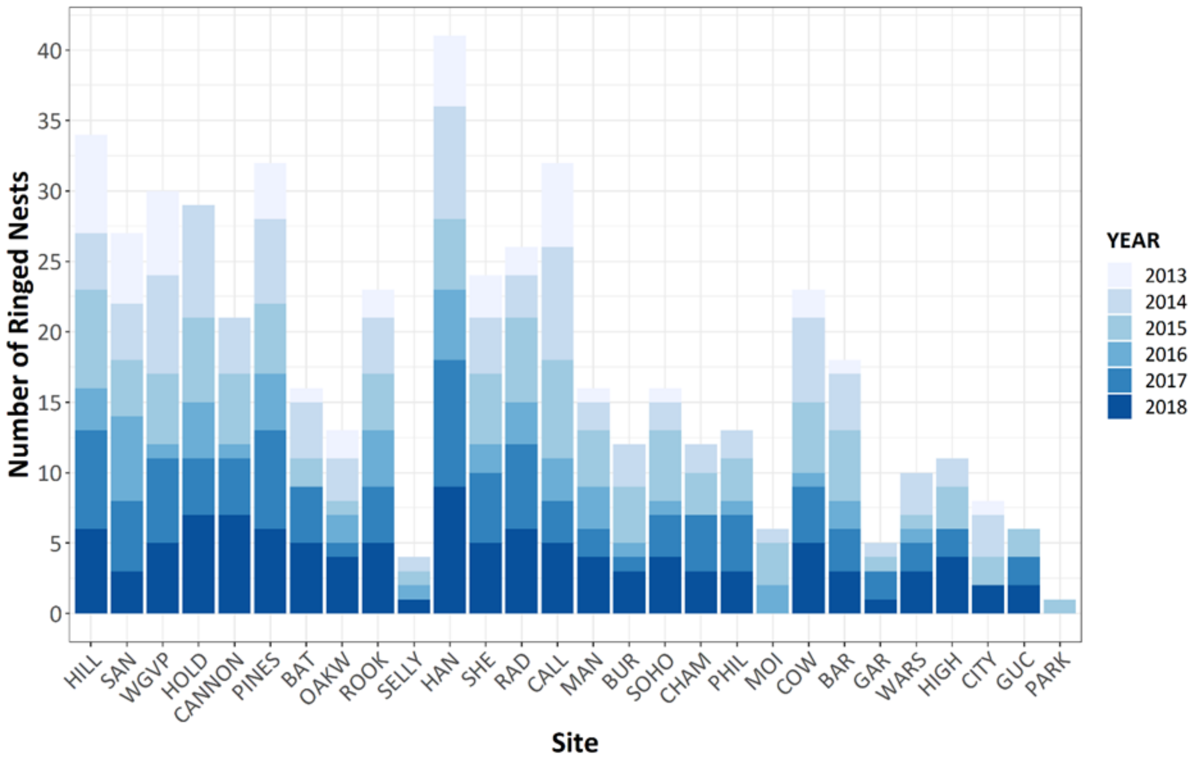


Figure 4.2. Bar plot of the maximum number of Blue Tit nest ringing records collected from 28 study sites in Birmingham, UK between 2013 and 2018 (inclusive). Sites are in order of increasing urbanisation. Descriptions of site acronyms (Table 2.2) and locations (Fig. 2.8) are provided in section 2.2.3.).

4.3.2. Urban-driven environmental effects on nestling morphometrics and brood mass asymmetry

From the global model the mean nestling body mass (± 1 SD) at ringing age across all breeding seasons was 9.4 ± 1.3 g (range: 5.7-12.4 g, n = 509 nests). Mean body mass differed between years (Fig. 4.3), with nestlings on average heaviest in 2018 (10.2 ± 1.1 g, range: 7.0-12.4 g, n = 111 nests) and lightest in 2015 (8.5 ± 1.2 g, range: 5.9-10.9 g, n = 105 nests).

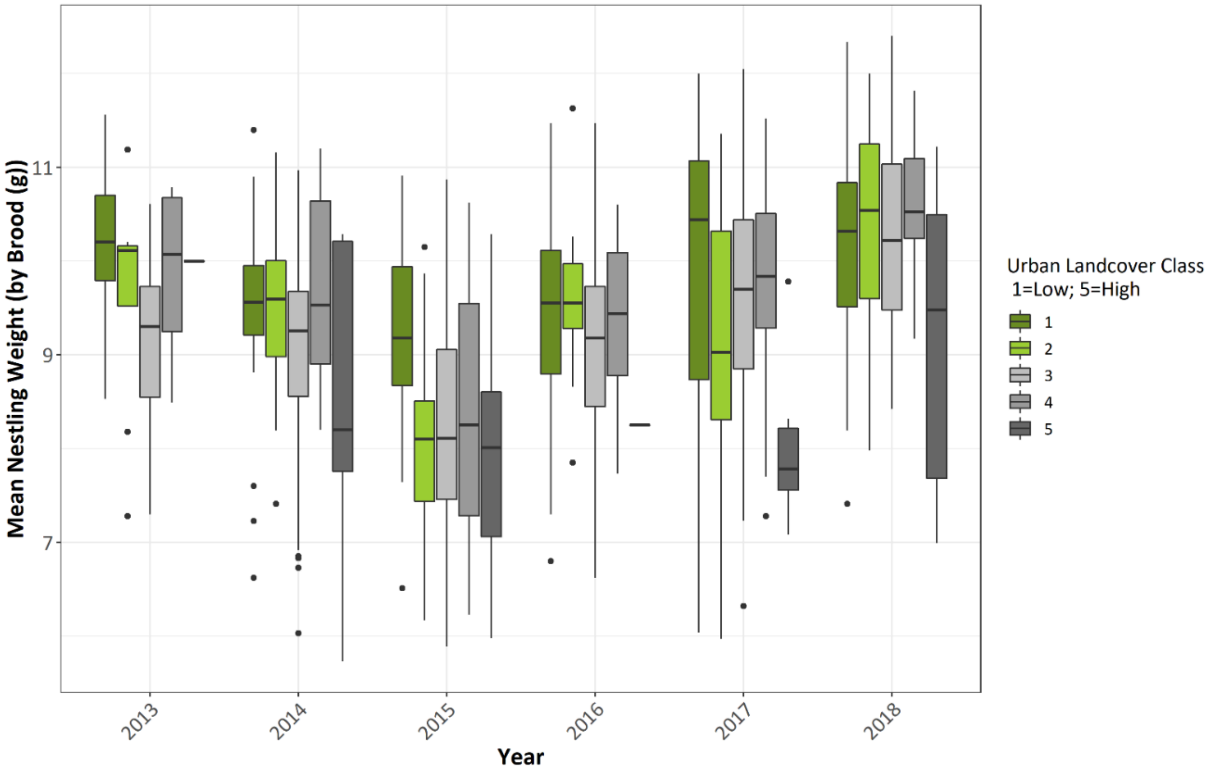


Figure 4.3. Box-and-whisker plots of mean nestling body mass of Blue Tit chicks reared in nestboxes across 28 sites along an urban gradient in Birmingham, UK for each breeding season *(*2013 - 2018 inclusive). Annual plots are further subdivided by urban land classes from ULC1 (suburban sites = dark green), to ULC5 (the most densely built-up sites = dark grey). For full description of urban land class categories see Section 2.2. Midlines in boxes are the medians, box limits are the 75th and 25th percentiles, and the whiskers are the ranges of data. Points represent the outliers. Site acronyms (Table 2.2) and locations (Fig. 2.8) are provided in section 2.2.3.

There was considerable intra- as well as inter-site variance in the average body mass of nestlings, resulting in a lack of a clear pattern of body mass variation between the five urban land classes (Fig.4.4). However, the lightest nestlings recorded (7.9 ± 1.6 g, range = 5.7-10.0g, n = 8 nests) were reared in City Centre Gardens, a densely urbanised site, with one of the lowest occupancies and breeding success rates. In contrast, nestlings raised in nestboxes in the greenest site (i.e. Hilltop), were on average over 2 g heavier (10.2 ± 1.1 g, range = 7.4-12.0 g, n = 34 nests).

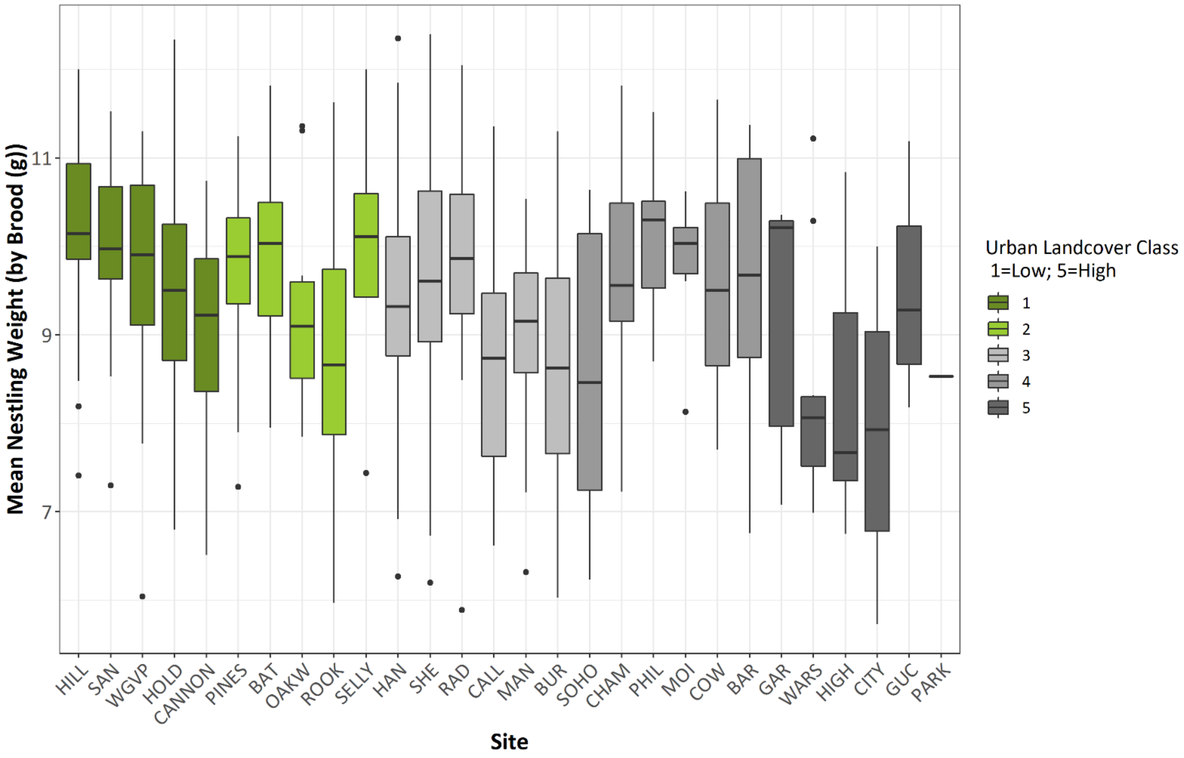


Figure 4.4. Box-and-whisker plots of mean nestling body mass of Blue Tit chicks reared in nestboxes across 28 sites along an urban gradient in Birmingham, UK between 2013 and 2018 (inclusive). Sites are colour coded depending on their urban land class from ULC1 (suburban sites = dark green), to ULC5 (the most densely built-up sites = dark grey). For full description of urban land class categories see Section 2.2. Midlines in boxes are the medians, box limits are the 75th and 25th percentiles, and the whiskers are the ranges of data. Points represent the outliers. Site acronyms (Table 2.2) and locations (Fig. 2.8) are provided in section 2.2.3.

The quantitative built model demonstrated a significant decline in mean nestling body mass at ringing age (8-15 days post hatching) with increasing built landcover within the urban matrix surrounding sites (Table 4.2). At the habitat level, only a significant correlation between mean nestling body mass and the diversity of broadleaved trees in the territory immediately surrounding nestboxes was found.

Table 4.2. Model summary of the results from the global built model (lmer analysis) of mean nestling mass (MNM; g) of Blue Tit broods raised along an urban gradient within Birmingham, UK over six breeding seasons (2013-2018). MNM was regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*).

Mean Nestling Weight (g) (MNM) **n = 509 nests (3456 chicks)**					
Fixed Term	**Coefficient**	**±SE**	**t value**	**Confidence Intervals** **(2.5%)**	**(97.5%)**
Intercept	10.039	0.232			
Year: 2014	-0.578	0.257	-2.245*	-1.073	-0.047
2015	-1.259	0.234	-5.387***	-1.729	-0.830
2016	-0.521	0.237	-2.201*	-0.999	-0.045
2017	-0.908	0.270	-3.359***	-1.420	-0.339
2018	0.463	0.229	2.020*	-0.009	0.936
Me BOS Trees	-0.077	0.143	-0.540	-0.365	0.218
Me NDB Trees	0.021	0.120	0.178	-0.229	0.283
Inverse Simpson's Index	-0.028	0.108	-0.264	-0.251	0.198
Inverse Simpson's Index^2	-0.142	0.057	-2.495*	-0.253	-0.039
Me Edge Distance (m^2)	-0.145	0.126	-1.153	-0.379	0.103
Site Occupancy	-0.123	0.092	-1.333	-0.296	0.075
(Log) Site Area (m^2)	-0.030	0.129	-0.235	-0.310	0.221
Built Landcover (%)	-0.348	0.143	-2.423*	-0.655	-0.044
Garden Landcover (%)	-0.151	0.103	-1.469	-0.356	0.043
April Hatching Date	-0.318	0.071	-4.461***	-0.456	-0.164
Brood Size	-0.214	0.054	-3.977***	-0.333	-0.109
Ringing Age	0.303	0.05106	5.938***	0.205	0.403
Random Terms	Variance	±SD			
Site ID	0.149	0.385			
Residual	1.090	1.044			

A non-linear effect of broadleaved tree diversity was predicted from the built model, with heavier nestlings associated with sites with greater tree diversity, up until a threshold value of ~5.0-5.5 was reached. Sites with higher tree diversity than this threshold were associated with nestlings of lower body mass. Indeed, model predictions revealed that, when holding all other environmental and biotic covariates constant at their mean, nestlings reared at sites with the highest tree diversity were approximately 1.0-1.5 g lighter than those raised in greenspaces with (relatively) fewer different tree species (Fig. 4.5).

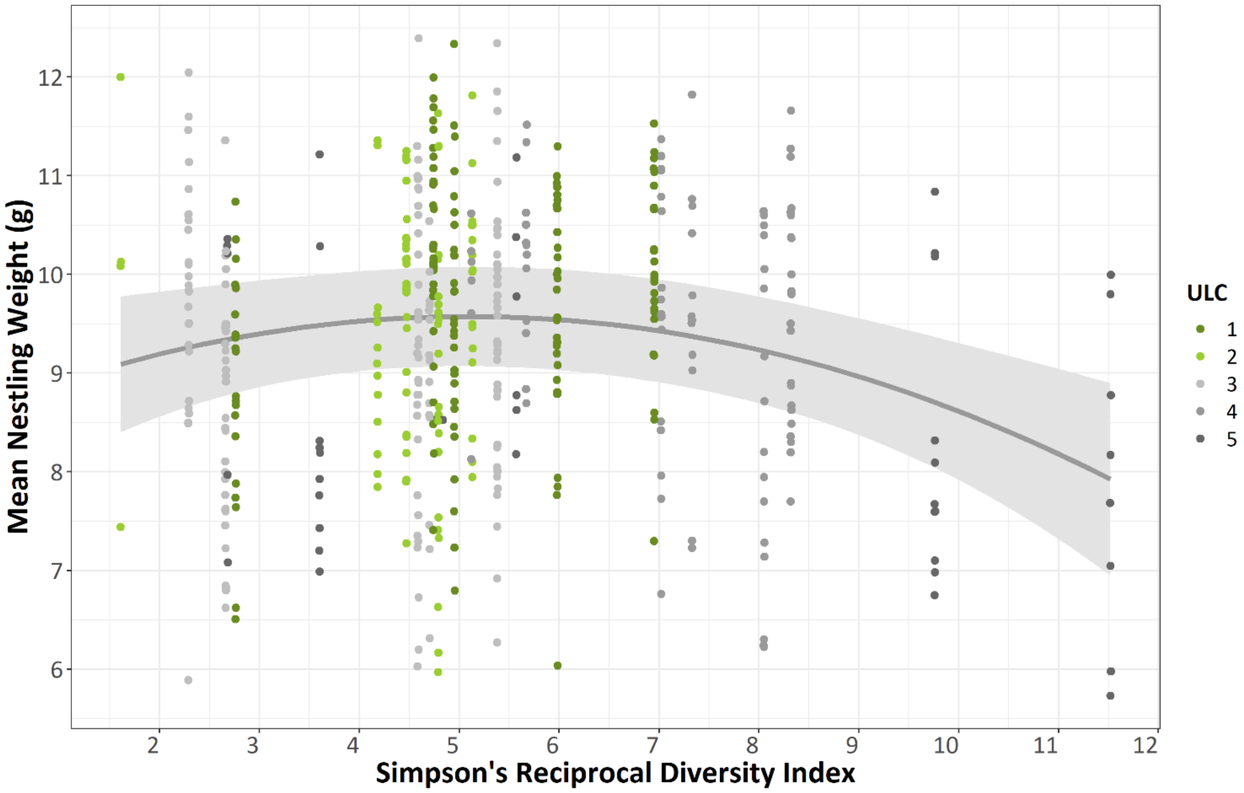


Figure 4.5. The non-linear relationship between (mean) diversity of broadleaved (native and non-native) trees in the habitat surrounding nestboxes and mean nestling mass in Blue Tit broods raised across an urban gradient in Birmingham, UK between 2013 and 2018. Raw data are represented by coloured points categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a linear mixed model (lmer, family = gaussian) in glmmTMB and using the *predicts* function in R. The urban gradient was specified using %BLC (n = 509 observations).

Both the built and ULC models confirmed a consistent and strong effect of all three biotic covariates on mean nestling body mass (Table 4.2). Nestling body mass was negatively correlated with both brood size and hatching date, with nestlings in larger broods and hatched later in the season on average significantly lighter compared with their conspecifics hatched earlier and raised in smaller broods. Although, nestlings ringed at older ages were heavier as would be expected, the significant effect of ringing age did not mask the potential effects of other biotic, habitat or landscape covariates.

Whilst variation in (mean) nestling body condition was not significantly influenced by the urban gradient (built model: β ± SE = -0.068 ± 0.063, *P* = >0.05) it was however, correlated with the percentage of garden landcover in the urban matrix surrounding greenspace (Table 4.3).

Table 4.3. Model summary of the results from the global built model (lmer analysis) of mean (brood) body condition (mean RBC) of Blue Tit broods raised along an urban gradient within Birmingham, UK over five breeding seasons (2014-2018). Mean RBC was regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*). '-' values denote covariates initially included in models but subsequently removed.

Average Nestling Body Condition (RBC) **n = 452 nests (3048 chicks)**					
Fixed Term	**Coefficient**	**±SE**	**t value**	**Confidence Intervals (2.5%)**	**(97.5%)**
Intercept	-0.039	0.088			
Year: 2015	-0.022	0.109	-0.207	-0.230	0.194
2016	0.871	0.159	5.480***	0.572	1.172
2017	-0.097	0.112	-0.870	-0.320	0.133
2018	0.535	0.118	4.533***	0.319	0.764
Me BOS Trees	-0.044	0.066	-0.672	-0.173	0.090
Me NDB Trees	-0.048	0.054	-0.893	-0.156	0.067
Inverse Simpson's Index	0.105	0.050	2.079*	0.006	0.210
Inverse Simpson's Index ^{2}	-0.087	0.030	-2.938**	-0.147	-0.026
Me Edge Distance (m^2)	0.040	0.057	0.706	-0.073	0.154
Site Occupancy	-0.024	0.059	-0.410	-0.135	0.094
(Log) Site Area (m^2)	-0.015	0.056	-0.259	-0.124	0.094
Built Landcover (%)	-0.068	0.063	-1.067	-0.190	0.061
GLC (%)	-0.117	0.047	-2.519*	-0.207	-0.021
April Hatching Date	-0.355	0.049	-7.169***	-0.450	-0.260
Brood Size	-0.284	0.039	-7.307***	-0.366	-0.207
Ringing Age	0.011	0.039	0.271	-0.072	0.090
Random Terms	Variance	±SD			
Site ID	-	-			
Box Number	0.070	0.264			
Residual	0.491	0.701			

Specifically, the global built model predicted that on average nestlings with relatively lower body condition were more likely to be associated with sites with higher garden landcover (> 30% %GLC) in the surrounding urban matrix (Fig. 4.6), suggesting a tipping point beyond which the presence of gardens has a negative impact on early nestling development.

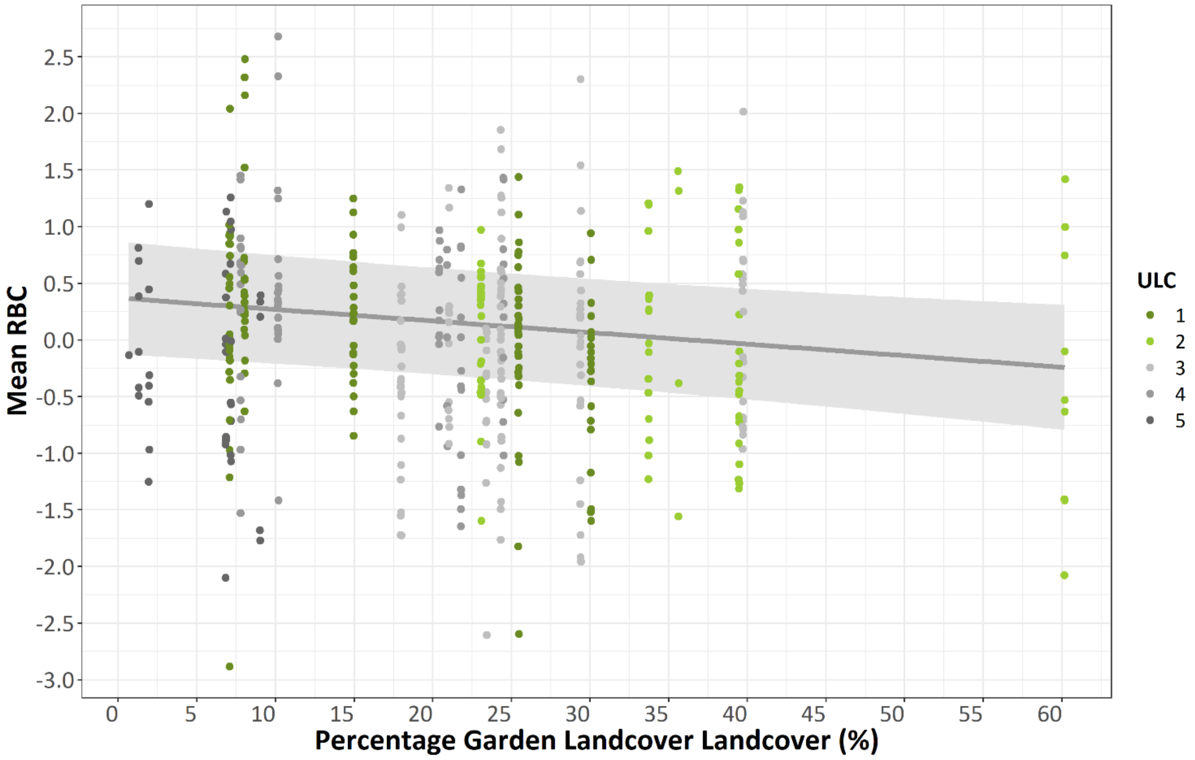


Figure 4.6. The negative correlational relationship between the percentage of garden landcover (%GLC) within a 500m radius of the centre of each site and mean (brood-level) body condition for nestlings raised along an urban gradient in Birmingham, UK over five breeding seasons (2014-2018). Positive mean RBC values indicate broods had higher than average body condition and negative values lower than average body condition (compared with the global average calculated from five years of nestling data: 2014-2018). Raw data are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a linear mixed model (lmer, family = gaussian) in glmmTMB and using the *predicts* function in R. The urban gradient was specified using %BLC. All other fixed covariates were kept at their mean (n =452).

There was much more variability in the body condition of nestlings raised at sites classified as moderately urbanised and with a concomitant high percentage garden landcover, compared with those at more urbanised sites in which the percentage of garden landcover was lower.

The built model of nestling body condition also predicted a strong polynomial effect of broadleaved tree diversity (Fig. 4.7).

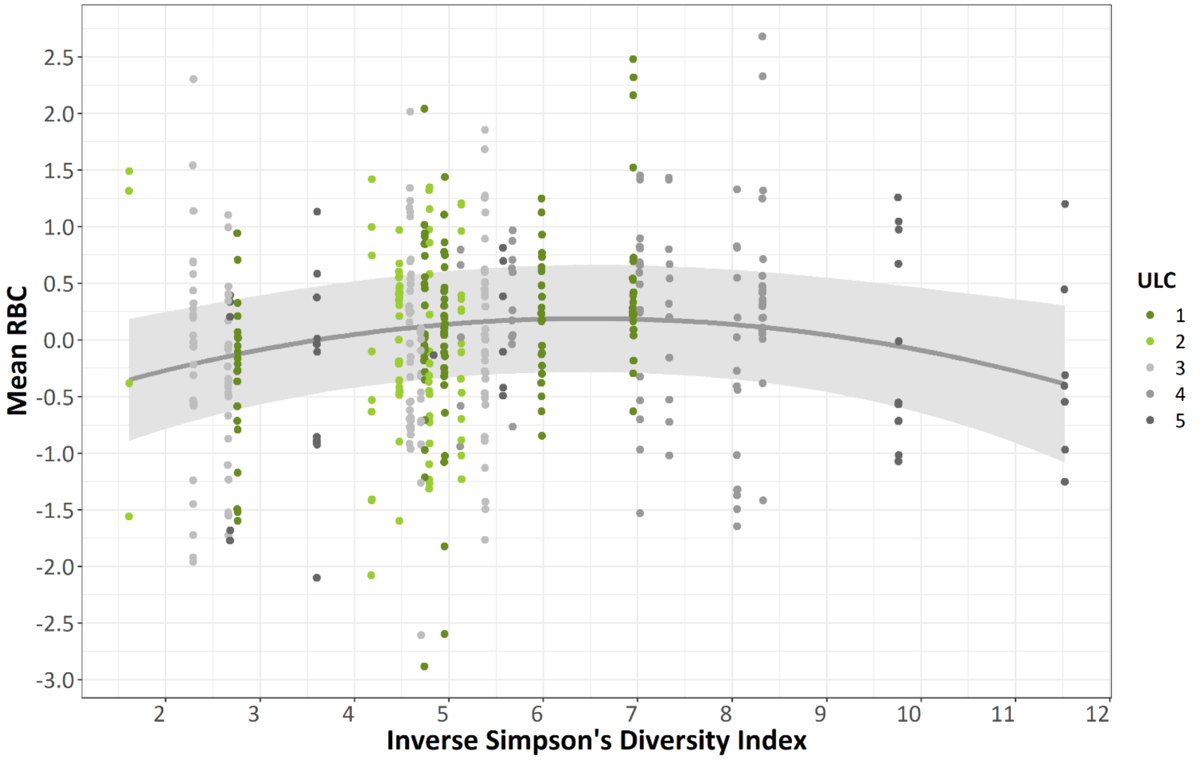


Figure 4.7. The nonlinear relationship between the (mean) diversity of broadleaved (native and non-native) trees (InvSI) in the habitat surrounding nestboxes on mean (brood) body condition (mean RBC) in nestlings raised across an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). The raw data is represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a linear mixed model (lmer, family = gaussian) in glmmTMB and using the *predicts* function in R. The urban gradient was specified using %BLC and all other fixed covariates were kept at their mean (n =452).

Again, although there was high variance in nestling body condition data, model predictions suggest that nestlings reared in sites with either low (InvSI values ≤ 4.0) or high (InvSI values ≥ 9.0) broadleaved tree diversity were in significantly lower body condition than those reared in greenspaces with moderate levels of tree diversity (InvSI values of approximately 4-6).

Nestling body condition was estimated to be lower in larger broods and declined with delayed hatching date. Although nestling weight, as expected, increased with the age at which nestlings were ringed, this did not significantly influence variation in body condition, (P = ≥0.05). Therefore, variation in ringing age was unlikely to mask the effects of other biotic or environmental variables on nestling body condition.

Overall, the analysis of brood mass asymmetry determined very little correlative effect of habitat or landscape variables (Table 4.4). The global built model only detected a significant but weak positive correlational relationship between percentage garden landcover and brood mass asymmetry. This weak effect was likely due to the high variability in the range of nestling weight differences recorded both among and within sites. Although a weak effect, this results implies that gardens had a negative influence on broods with the disparity in size between the smallest (i.e. lightest) and largest (heaviest) nestling increasing with increasing garden landcover in the matrix surrounding greenspace.

Table 4.4. Model summary of the results from the global built model (lmer analysis) of brood weight asymmetry (ASYM; g) of Blue Tit broods raised along an urban gradient within Birmingham, UK across six breeding seasons (2013-2018). Response values were log-transformed and regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*). '-' values denote covariates initially included in models but subsequently removed.

(log)Brood Weight Asymmetry (g) (ASYM) **n = 500**					
Fixed Term	**Coefficient**	**±SE**	**t value**	**Confidence Intervals** **(2.5%)**	**(97.5%)**
Intercept	1.007	0.063			
Year: 2014	**0.247**	**0.076**	**3.241****	**0.111**	0.396
2015	**0.208**	**0.069**	**3.031****	**0.076**	0.346
2016	0.032	0.070	0.458	-0.109	0.170
2017	**0.232**	**0.080**	**2.894****	**0.091**	0.390
2018	-0.026	0.067	-0.391	-0.150	0.111
Me BOS Trees	0.025	0.033	0.756	-0.038	0.087
Me NDB Trees	-0.037	0.027	-1.329	-0.094	0.016
Inverse Simpson's Index	0.029	0.023	1.257	-0.016	0.075
Inverse Simpson's Index^2	-	-	-	-	-
Me Edge Distance (m^2)	0.012	0.028	0.430	-0.043	0.069
(Log) Site Area (m^2)	-0.020	0.029	-0.706	-0.078	0.034
Site Occupancy	0.017	0.026	0.643	-0.037	0.069
Built Landcover (%)	0.036	0.033	1.112	-0.033	0.097
Garden Landcover (%)	**0.055**	**0.023**	**2.348***	**0.008**	**0.103**
April Hatching Date	**0.107**	**0.021**	**5.031*****	**0.063**	**0.150**
Brood Size	**0.152**	**0.016**	**9.601*****	**0.122**	**0.184**
Ringing Age	-0.015	0.015	-0.978	-0.044	0.013
Random Terms	**Variance**	**±SD**			
Site ID	0.005	0.073			
Box Number	-	-			
Residual	0.095	0.308			

With respect to breeding timing and biotic influences, whilst no correlational effect of ringing age on brood mass asymmetry was detected (Table 4.4), a consistent and highly significant negative effect of brood size and hatching date (Fig. 4.8) was observed.

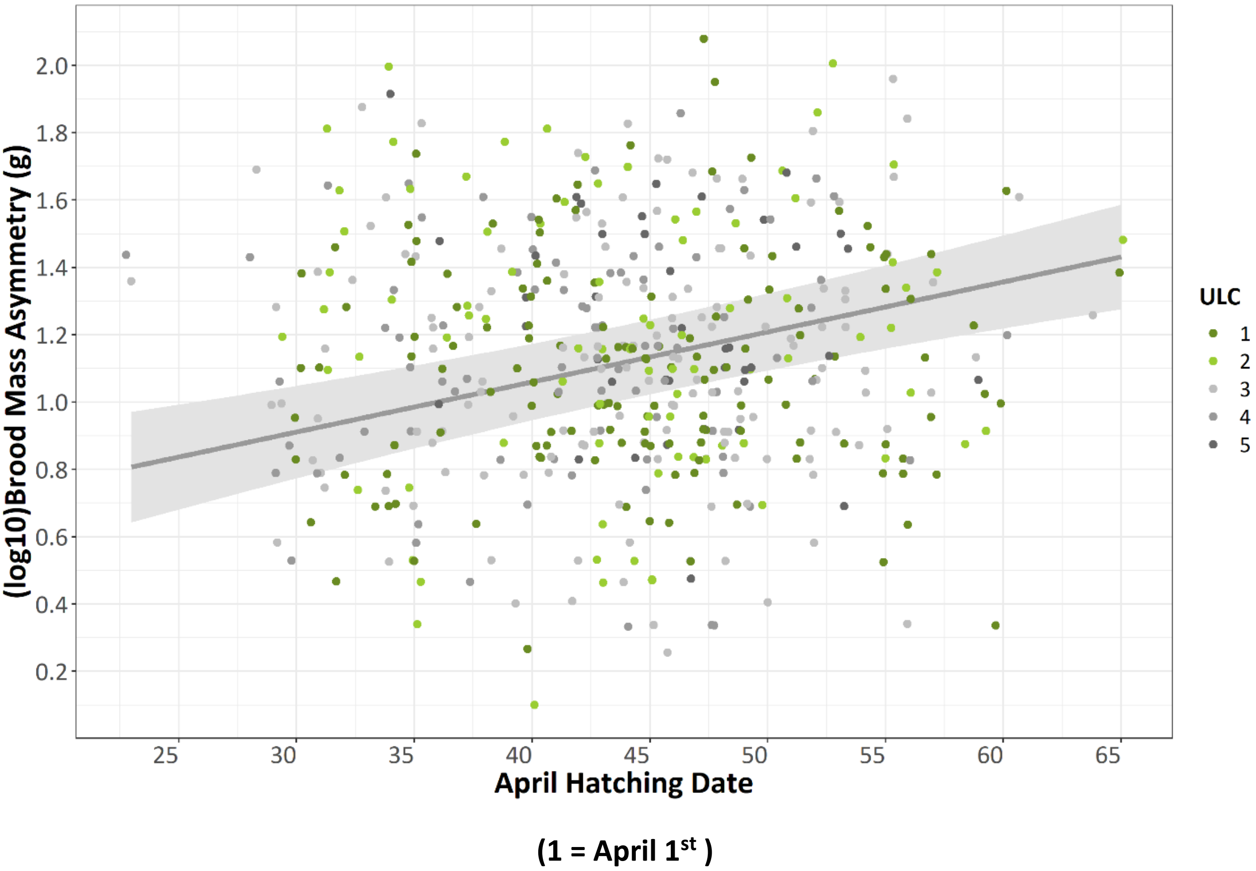


Figure 4.8. The positive correlational relationship between brood mass asymmetry and hatching date of chicks raised in nestboxes along an urban gradient within Birmingham, UK across six breeding seasons (2013-2018). Raw data (log10-scaled) are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a linear mixed model (lmer, family = gaussian) in glmmTMB and using the *predicts* function in R. The urban gradient was specified using %BLC and all other fixed covariates were kept at their mean. (n =500).

4.3.3. Urban-driven environmental effects on nestling survival

In total 3,200 nestlings survived to fledging over the six breeding seasons. With the exception of Park St Gardens (one of the most densely urbanised sites: see Table 2.2 and

Fig. 2.8 in sections 2.2.3) all sites successfully fledged at least one chick from one brood. Once broods reached ringing age (i.e. 8-15 days post-hatch) the probability of individual nestlings fledging, although variable between years and among sites, remained high (Table 4.5 and Fig. 4.9).

Table 4.5. Comparison of annual total fledging and mortality numbers for Blue Tit nestlings reared in nestboxes along an urban gradient in Birmingham, UK over six breeding seasons (2013 and 2018). The percentage fledged is calculated from the total number of nestlings that hatched in each year.

Year	Fledged	Died	% fledged
2013	364	0	100
2014	674	35	95.1
2015	605	93	86.7
2016	269	20	93.1
2017	558	58	90.6
2018	730	44	94.3
Total	**3200**	**250**	**92.8**

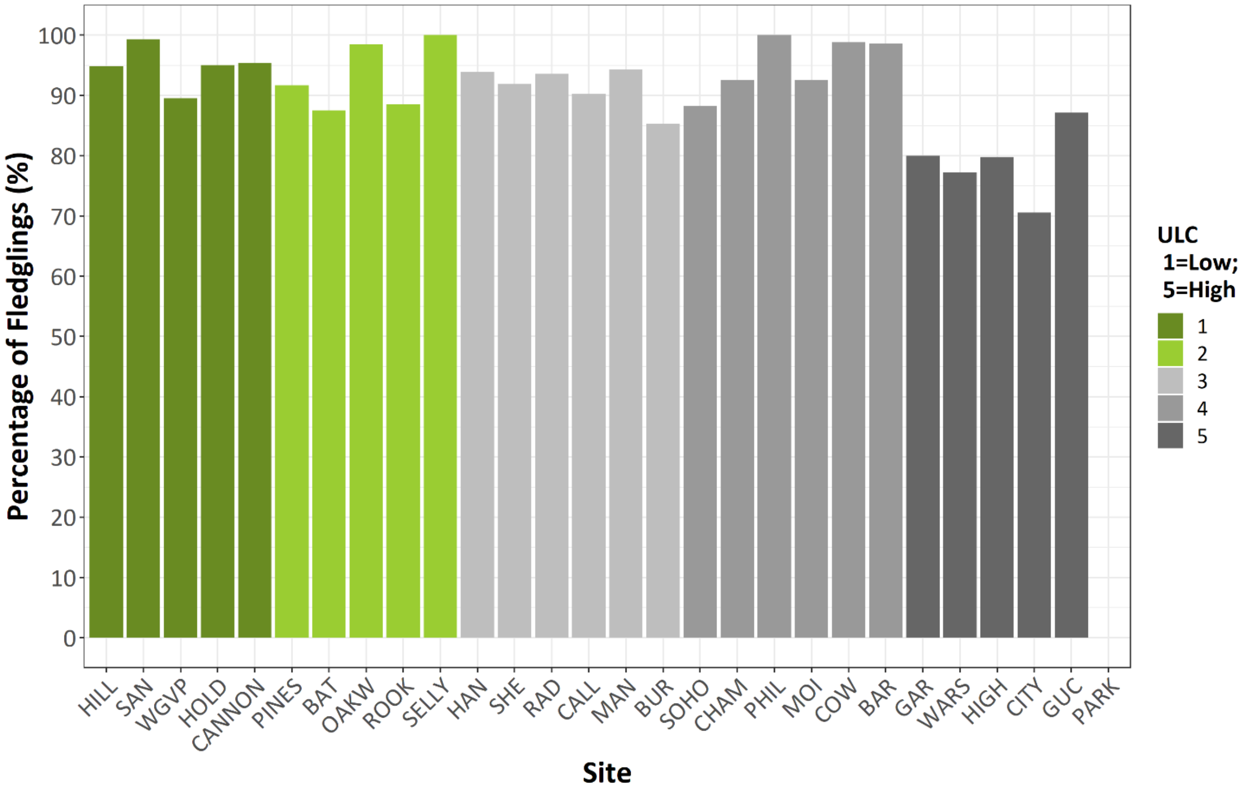


Figure 4.9. The percentage of nestlings surviving to fledging by site (based on the total number of nestlings that were alive at ringing and therefore individually identifiable) from nestboxes across 28 sites stratified along an urban gradient in Birmingham, UK over six breeding seasons (2013 – 2018). Sites are listed in order of increasing built landcover and categorized into one of five urban landcover classes (ULC1=least urbanised (suburban) sites and ULC5 = dense urban). Site acronyms (Table 2.2) and locations (Figs. 2.8) are provided in section 2.2.3.

The percentage of nestlings fledging in the most densely urbanised sites (ULC5), although variable, was lower (65.8 ± 32.7%, range: 0-87.1%) in comparison to the other sites across the rest of the urban gradient (ULC1-4: 93.7 ± 4.3%, range: 85.3-100.0%) (Fig. 4.9).

The original final global built model used to analyse the probability of an individual surviving to fledge, initially included an interaction term (body mass × %BLC) to establish if nestling survival covaried with the body mass of individual chicks, and if this was influenced by the urban gradient. Whilst a highly significant effect was detected, on inspection of the prediction plots for the relationship between survival and the two terms, the predictive power of models was low particularly for the survival/death of lighter nestlings. Consequently, the body mass covariate was dropped from this model. The final model analysed that excluded the nestling body mass term, established that the probability of individual nestlings successfully fledging was influenced by variables at both the habitat and landscape scale (Table 4.6).

Table 4.6. Model summary of the results from the global built model (glmmTMB analysis, family =binomial) of the probability of individual nestling survival to fledging for Blue Tit broods reared across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2014 -2018). The binary response (1=fledged, 0=died) was regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*).

Nestling Survival **n = 3086 chicks**					
Fixed Terms	**Coefficient**	**±SE**	**z value**	**Confidence Intervals** **(2.5%)**	**(97.5%)**
Intercept	3.858	0.426			
Me BOS Trees	-0.296	0.254	-1.163	-0.838	0.233
Me NDB Trees	-0.076	0.210	-0.360	-0.514	0.372
Inverse Simpson's Index	0.271	0.184	1.472	-0.113	0.657
Inverse Simpson's Index^2	**-0.209**	**0.094**	**-2.222***	**-0.396**	**-0.006**
Me Edge Distance (m^2)	0.308	0.237	1.300	-0.211	0.775
(Log) Site Area (m^2)	**-0.587**	**0.235**	**-2.498***	**-1.069**	**-0.084**
Site Occupancy	-0.081	0.191	-0.424	-0.461	0.290
Built Landcover (%)	**-0.743**	**0.268**	**-2.766****	**-1.344**	**-0.236**
Garden Landcover (%)	-0.122	0.193	-0.631	-0.500	0.301
April Hatching Date	**-1.157**	**0.147**	**-7.857*****	**-1.452**	**-0.874**
Brood Size	**-0.496**	**0.123**	**-4.026*****	**-0.743**	**-0.260**
Random Terms	**Variance**	**±SD**			
Box: Site ID	2.1883	1.4793			
Site ID	0.0478	0.2186			
Year	0.6234	0.7896			

The probability of fledging once nestlings had reached ≥ 8 days post-hatch was significantly negatively correlated with the percentage of built landcover surrounding sites. Furthermore, a significant negative effect of site area was also confirmed (Figure 4.10), together with a non-linear effect of broadleaved tree diversity. The correlation between broadleaved tree diversity and nestling survival was consistent with the relationship observed across other breeding response variables.

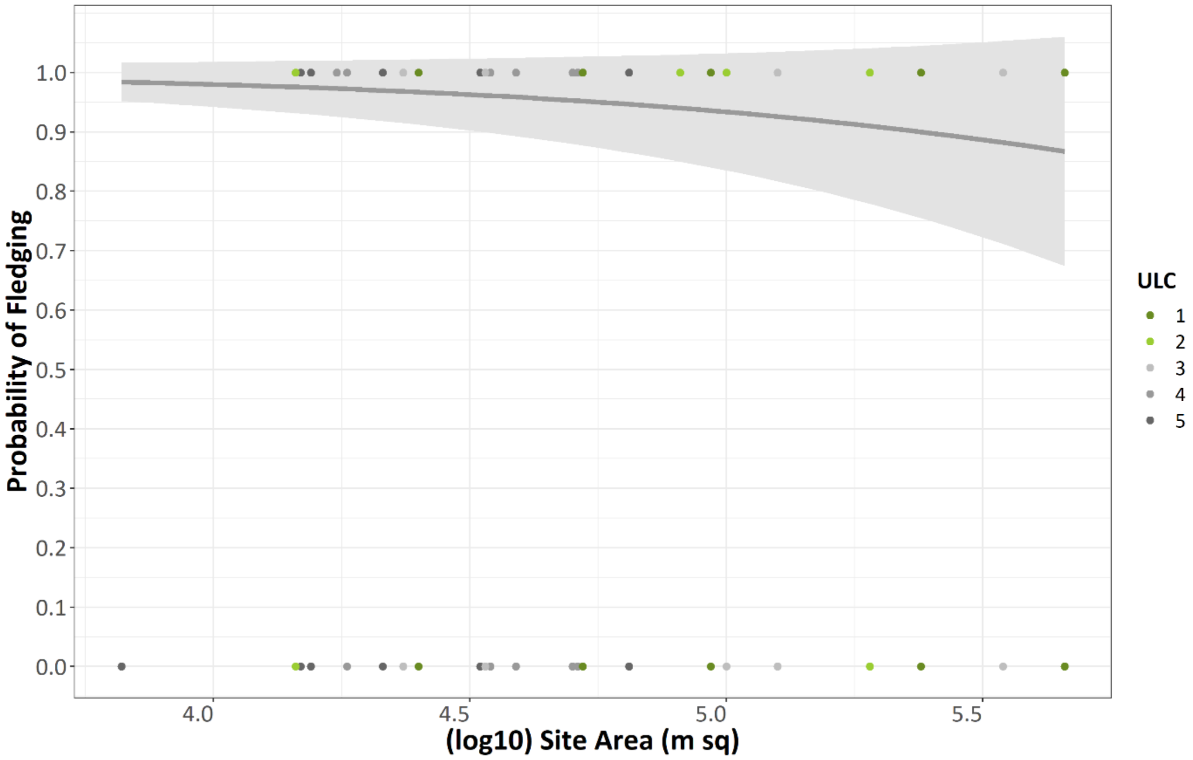


Figure 4.10. The relationship between (log10) total site area (m^2) of greenspace and the probability of individual nestlings surviving to fledging. Analyses were based on data collected from broods of ringed nestlings (≥ 8-15 days post-hatching) across 28 sites along an urban gradient in Birmingham, UK between 2014 and 2018 (inclusive). Probability of survival to fledging was fitted for each nestling as a binary response (1=fledged, 0 = died). The raw data (unscaled) are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = binomial) in glmmTMB and using the *predicts* function in R. The urban gradient was specified using %BLC: all fixed covariates were kept at their mean (n = 3,086 nestlings).

4.3.4. Comparison of urban-driven environmental effects on proportional survival rates of nestlings during early and late of brood-rearing stages

The proportion of nestlings within a brood surviving the early developmental stage (i.e. brood-rearing period between hatching and ringing = EBS) were consistently lower (global mean = 0.73 ± 0.35, n = 662 nests), compared with the later post-ringing developmental phase (or late brood rearing stage = LBS) (global mean = 0.89 ± 0.25, n = 575 nests) across all years of the study (Table 4.9) and along the urban gradient (Figs. 4.11a and b).

Table 4.7. The breakdown of the mean ± 1 SD proportion of Blue Tit nestlings within a brood surviving the early brood-rearing stage (i.e. from hatching to ringing age (≥8 days)) and late brood-rearing stage (i.e. post-ringing to fledging) across 28 sites along an urban gradient in Birmingham, UK for each breeding season (2013-2018). Early developmental (brood-rearing) survival (EBS) was specified as the proportion of nestlings within a brood surviving to ringing age relative to the total number initially hatched and late brood-rearing survival (LBS) as the proportion of nestlings that survived to fledge relative to the total number alive at ringing (≥8 days old). The global average is derived from all breeding records across all years.

Year	EBS: average proportion of nestlings surviving early brood-rearing stage (number of nestboxes)	LBS: average proportion of nestlings surviving late brood-rearing stage (number of nestboxes)
2013	0.74 ± 0.37 (62)	0.98 ± 0.11 (53)
2014	0.78 ± 0.32 (110)	0.93 ± 0.17 (100)
2015	0.71 ± 0.36 (122)	0.84 ± 0.29 (106)
2016	0.69 ± 0.37 (126)	0.87 ± 0.28 (100)
2017	0.72 ± 0.35 (115)	0.84 ± 0.32 (102)
2018	0.74 ± 0.32 (127)	0.94 ± 0.19 (114)
Global average	**0.73 ± 0.35 (662)**	**0.89 ± 0.25 (575)**

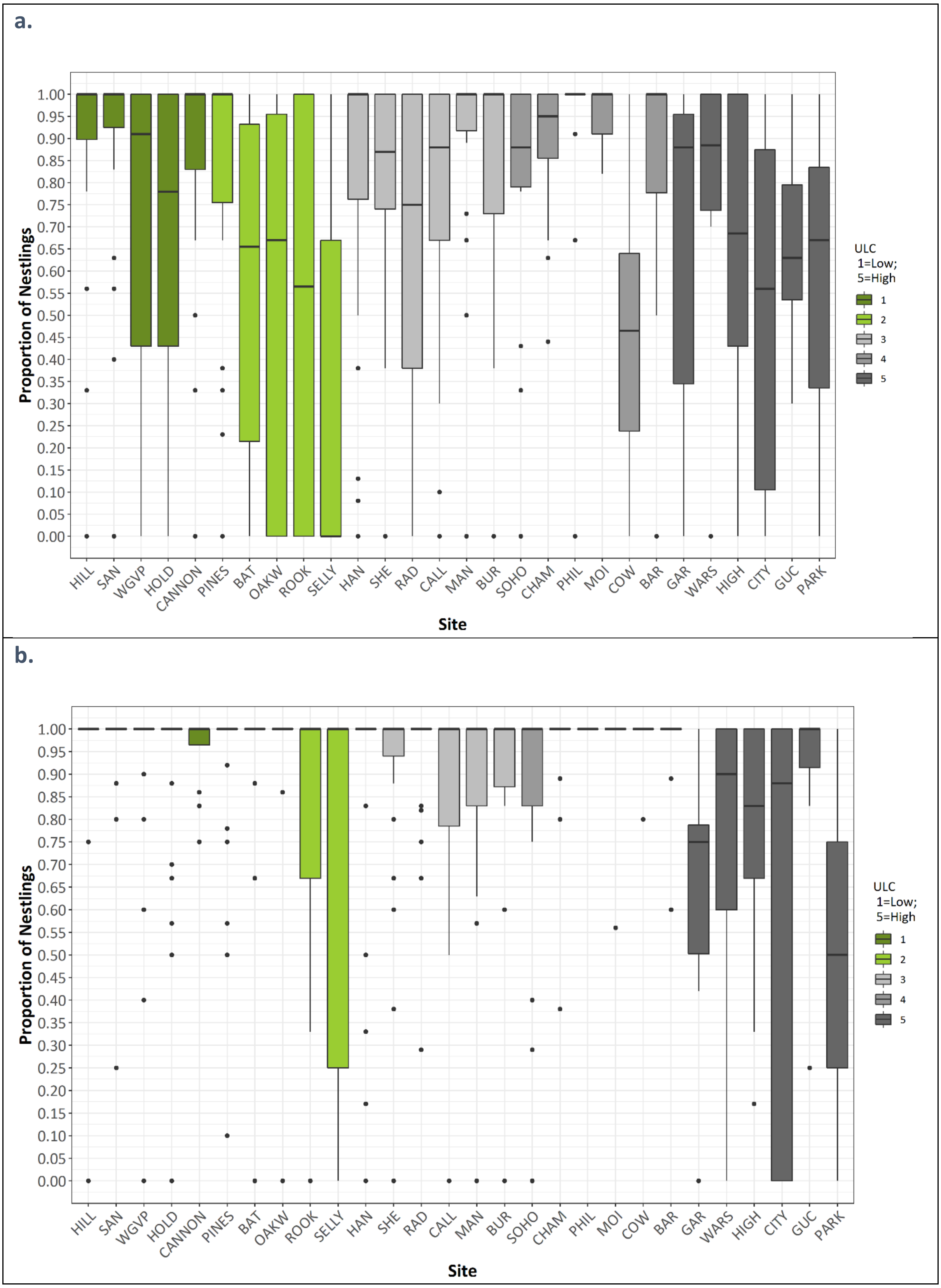


Figure 4.11. Box-and-whisker plot summaries of proportional **(a)** early brood-rearing (EBS) and **(b)** late brood-rearing (LBS) survival based on the number of nestlings in individual broods surviving each stage of development for all breeding attempts recorded for each site across six consecutive years (2013-2018). Summary data are calculated for all breeding attempts in which at least one nestling hatched for EBS (n = 662 nests) and one nestling was observed alive at ringing for LBS (n = 575 nests).

Box midlines are the median proportion of nestlings surviving, box extents are the 75th and 25th percentiles, whiskers are the ranges of minimum and maximum survival and points are outliers. Sites are listed in order of increasing built landcover and categorized into one of five urban landcover classes (ULC1=least urbanised (suburban) sites and ULC5 = dense urban).

Global built models determined that proportional survival rates (and therefore rates of brood reduction) during the two separate stages of brood-rearing considered were significantly influenced by environmental factors at both the habitat- and landscape-scale (Tables 4.8-4.9). Whilst, there was a highly significant negative effect of laying date on the proportion of nestlings surviving the later brood-rearing phase (post-ringing to fledging period: Table 4.9), a similar negative correlation of breeding phenology on proportional survival during the early developmental phase (hatching to ringing age) was not found to be significant (Table 4.8).

Table 4.8. Model summary of the results from the global built model (glmmTMB analysis, family =betabinomial) of the proportion of nestlings in a brood surviving to ringing age (8-15 days post-hatch) for Blue Tits breeding in nestboxes across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013 – 2018). The brood-level response variable (number of nestlings surviving to ringing age, number of nestling deaths pre-ringing) was regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*). (n=3,086 individual nestlings). (662 observations).

Early Phase Brood Survival (Proportional) **n = 662 nests**					
Conditional Model Fixed Terms	**Coefficient**	**±SE**	**z value**	**Confidence Intervals (2.5%)**	**(97.5%)**
Intercept	1.967	0.190			
Me NDB Trees	**-0.387**	**0.141**	**-2.750****	**-0.675**	**-0.095**
Inverse Simpson's Index	0.198	0.149	1.325	-0.084	0.508
Inverse Simpson's Index^2	**-0.252**	**0.075**	**-3.345*****	**-0.405**	**-0.107**
Me Edge Distance (m^2)	0.182	0.147	1.235	-0.106	0.490
(Log) Site Area (m^2)	-0.249	0.1623	-1.529	-0.596	0.070
Built Landcover (%)	**-0.323**	**0.160**	**-2.016***	**-0.650**	**0.006**
Garden Landcover (%)	-0.166	0.141	-1.172	-0.454	0.121
Garden Landcover^2 (%)	**-0.191**	**0.088**	**-2.164***	**-0.375**	**-0.017**
April Laying Date	-0.112	0.082	-1.375	-0.277	0.046
Random Terms	**Variance**	**±SD**			
Box Number : Site ID	-	-			
Site ID	0.155	0.394			
Year	0.037	0.194			
Zero-inflation Model	**Coefficient**	**±SE**	**z value**	**Confidence Intervals (2.5%)**	**(97.5%)**
Intercept	**-2.262**	**0.169**	**-13.41*****	**-2.639**	**-1.961**

Table 4.9. Model summary of the results from the global built model (glmmTMB analysis, family =binomial) of the proportion of nestlings in a brood surviving to fledging for Blue Tits breeding in nestboxes across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013 – 2018). The response variable (number of nestlings surviving to fledge, number of nestling deaths post-ringing) was regressed against fixed covariates from two environmental (habitat and landscape) and one biotic predictor block. All significant slopes are indicated in bold (significance codes: ≤0.001***, ≤0.01**, ≤0.05*). (n=3,086 individual nestlings) (575 observations).

Late Phase Brood Survival Post Ringing (Proportional) n = 575 nests					
Conditional Model Fixed Terms	**Coefficient**	**±SE**	**z value**	**Confidence Intervals (2.5%)**	**(97.5%)**
Intercept	4.101	0.461			
Me BOS Trees	-0.288	0.237	-1.212	-0.753	0.178
Me NDB Trees	-0.055	0.202	-0.273	-0.451	0.340
Inverse Simpson's Index	**0.390**	**0.174**	**2.246***	**0.050**	**0.731**
Inverse Simpson's Index^2	**-0.296**	**0.101**	**-2.916****	**-0.494**	**-0.097**
Me Edge Distance (m^2)	0.336	0.216	1.554	-0.088	0.760
(Log) Site Area (m^2)	**-0.543**	**0.228**	**-2.383***	**-0.990**	**-0.096**
Site Occupancy	-0.151	0.180	-0.840	-0.505	0.202
Built Landcover (%)	**-0.675**	**0.250**	**-2.695****	**-1.165**	**-0.184**
Garden Landcover (%)	-0.107	0.187	-0.570	-0.474	0.260
April Laying Date	**-0.694**	**0.129**	**-5.373*****	**-0.947**	**-0.441**
Random Terms	Variance	±SD			
Box Number : Site ID	1.564	1.251			
Site ID	0.106	0.325			
Year	0.920	0.959			
Zero-inflation Model	Coefficient	±SE	z value	Confidence Intervals (2.5%)	(97.5%)
Intercept	-3.202	0.224	-14.28***	-3.641	-2.763

Both brood survival models detected a significant negative impact of increasing built landcover on the proportion of nestlings within a brood surviving each developmental stage. The EBS model (Table 4.8) predicted that the average proportion of nestlings surviving to ringing age declined from a high of ~0.85 in the least built-up (suburban) sites to a low of 0.70 in the most densely built up sites (Figure 4.12).

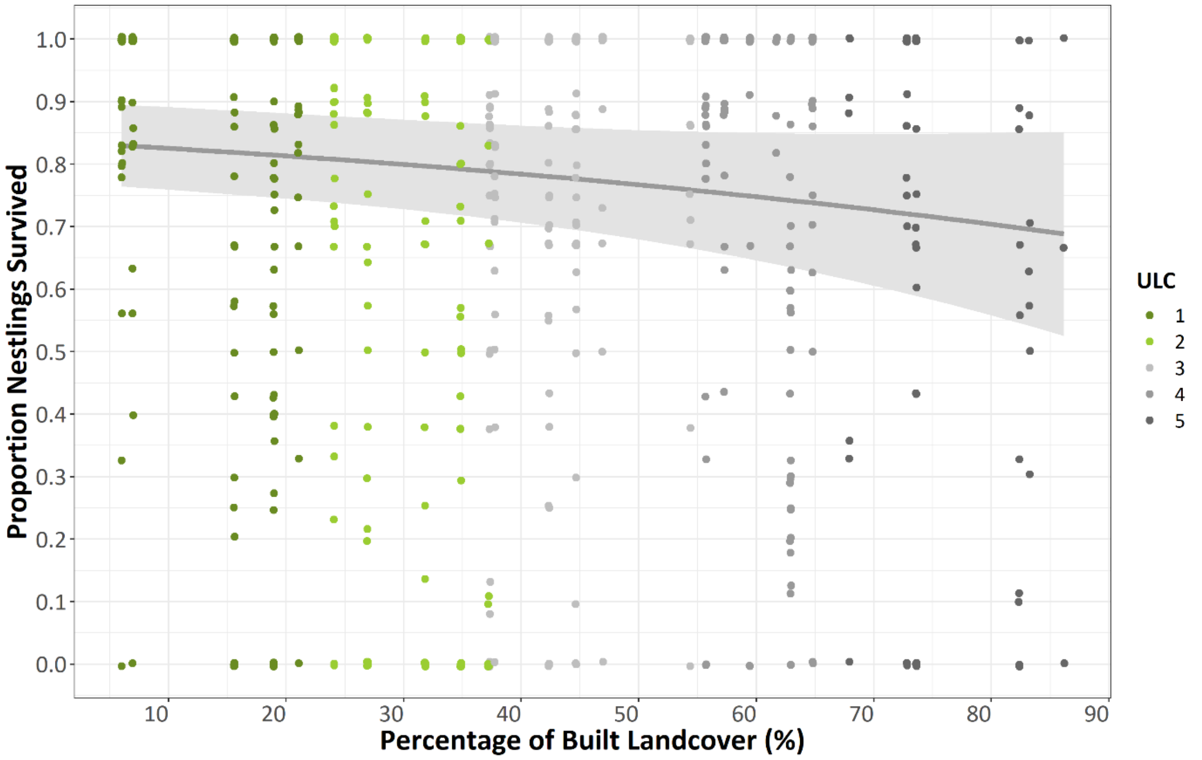


Figure 4.12. The negative correlational relationship between early brood survival (the proportion of nestlings in a brood surviving to ringing age (≥8 days) relative to the number initially hatched) and the degree of built landcover (%BLC) for Blue Tit broods reared across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013 and 2018 inclusive). Survival was fitted as a binomial response (number of nestlings surviving to ringing age, number of deaths pre-ringing). Raw survival data are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = betabinomial) in glmmTMB and using the *predicts* function in R. All fixed covariates were kept at their mean. (n = 662 nests).

The LBS model showed a similar negative correlation, with the proportion of nestlings within a brood surviving the late developmental stage declining with increasing built landcover. However rates of survival to fledging once nestlings reached ringing age, remained consistently high across the urban gradient, with model predictions suggesting rates declined from a high of 0.90 in the least built up sites to 0.80 in the most densely urbanised sites.

The proportion of nestlings in a brood surviving the early developmental stage also significantly varied with the percentage of garden landcover in the urban matrix surrounding sites. Model predictions indicated a non-linear effect, with the proportional survival of nestlings remaining relatively high and stable (~0.7-0.8) until the percentage of garden landcover reached ~30%. Beyond this threshold, however, increasing garden landcover was associated with higher rates of brood reduction, resulting in only 40% of nestlings per brood surviving to ≥ 8 days in sites associated with the greatest percentage area of garden landcover (i.e. ~60%).

Similarly, the EBS model predicted a non-linear effect of broadleaved tree diversity on the proportion of nestlings in a brood that survived the early development phase. Broods nesting in sites with lower broadleaved tree diversity (InvSI = ~2) also had lower rates of nestling survival, with 0.6 nestlings per brood surviving to ringing age. Early brood-rearing success increased with initial increases in tree diversity to a peak of 0.8 (i.e. 80% of nestlings within a brood surviving to ringing age) at moderate (Inverse) Simpson Diversity Index scores of 5-7. However, sites with even higher tree diversity suffered higher rates of brood reduction with the proportion of nestlings within a brood surviving to ringing age declining to 0.4 in sites with the highest tree diversity scores (11-12). Whilst similar correlational relationships were detected in the later brood-rearing phase, when plotted the prediction curve indicated that the effect was relatively weaker, with brood survival remaining consistently high (ranging between 0.8 -0.9) across sites, regardless of tree diversity.

The proportion of nestlings surviving the early brood-rearing period was also significantly negatively correlated with the density of native deciduous trees (Table 4.8 and Fig. 4.13). Model predictions suggest that brood-rearing success during this period declined from 0.85 at sites supporting the lowest number of native deciduous trees, (also associated with the most densely urbanised sites; ULC1), to 0.6 - 0.7 at sites with the highest tree density (associated with the least urbanised (suburban) sites: ULC1-2). In comparison, the proportion of nestlings in a brood successfully surviving the period post-ringing to fledge was significantly negatively impacted by the total area of the site with pairs breeding in larger greenspaces fledging proportionally fewer young than birds breeding in smaller sites (Table 4.9).

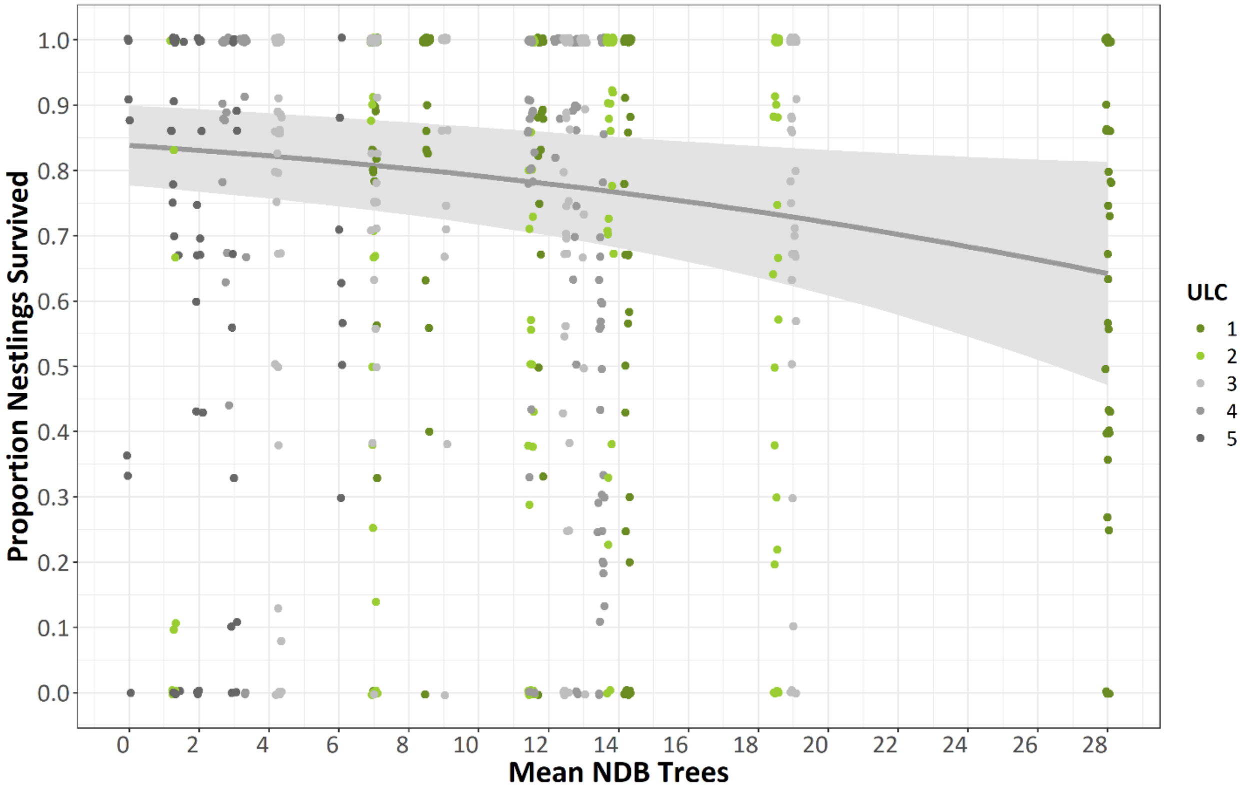


Figure 4.13. The negative correlational relationship between the mean number of native deciduous broadleaved trees and the probability of individual nestlings surviving to ringing (EBS), for Blue Tits breeding across 28 sites, along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). EBS was fitted as a binomial response (number of nestlings surviving to ringing age, number of nestling deaths pre-ringing). Raw data are represented by coloured points (categorised by urban land class (ULC): ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = beta binomial) in glmmTMB and using the *predicts* function in R. All fixed covariates were kept at their mean (n =662).

4.3.5. Comparison of brood reduction rates across two brood-rearing phases

The proportion of nestling deaths occurring during the early compared with the late brood-rearing phase (relative to the total number of deaths recorded across the breeding season for each brood) were overall higher (Figure 4.14). Although variable, and with the exception of one site (i.e. Castle Vale (code MAN), this finding was, largely consistent both across the urban gradient and among years.

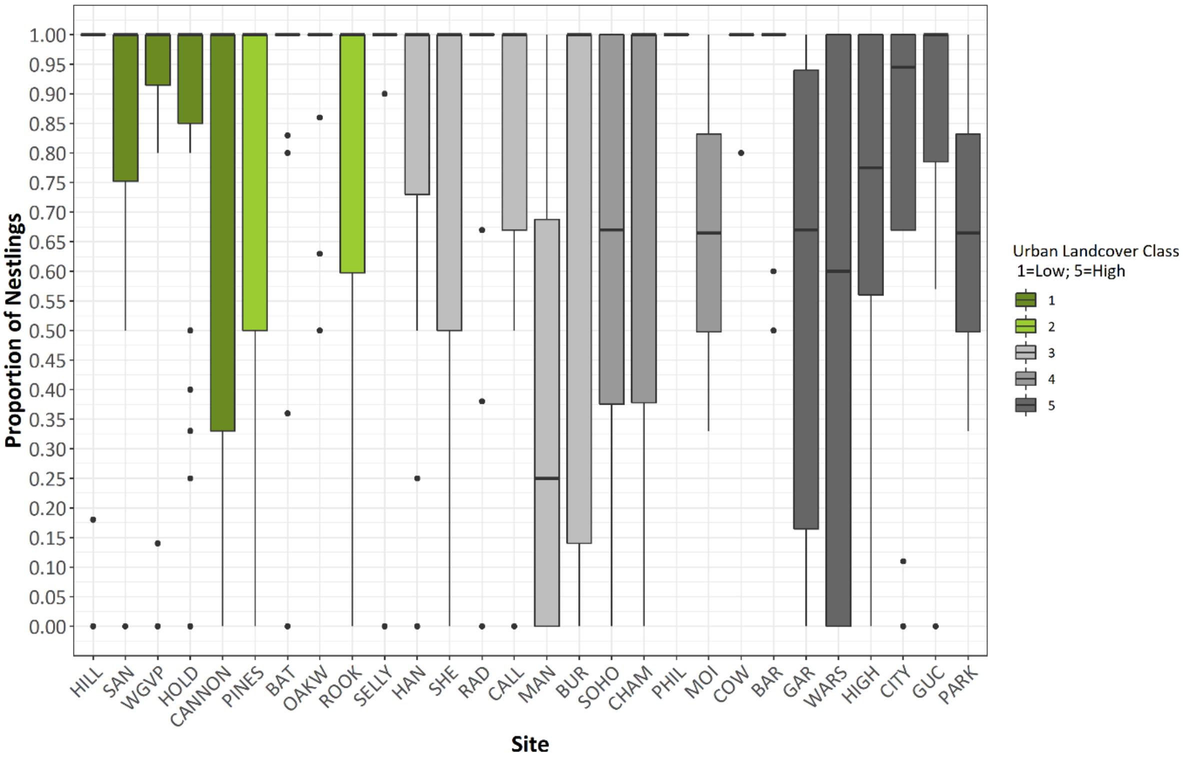


Figure 4.14. Boxplot summary of the proportion of nestling deaths occurring during early development (between hatching and approximately 8-12 days of age), relative to the total number of

deaths recorded across both brood-rearing periods (EBS+LBS) for broods reared across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Summary statistics include all breeding efforts in which at least one nestling death was recorded (n=575 nests). Black lines within boxes indicate the median proportion of nestling deaths occurring during early development, upper hinges the 75th percentile and lower hinges the 25th percentile of the data. The vertical lines ('whiskers') indicate the minimum and maximum proportion of deaths. Outliers are represented by points. Sites are in order of increasing %BLC and categorized into one of five urban landcover classes (ULC1=least urbanised (suburban) sites and ULC5 = dense urban). Site acronyms (Table 2.2) and locations (Fig. 2.8) are provided in sections 2.2.3).

Due to the low rates of breeding failure observed during late stage nestling development (and consequently the high number of zeros in the associated mortality term specified in LBS models), and the random effects structure of the data, it was not possible to conduct robust analyses using the required binary logistic framework; a problem that is not uncommon in demographic studies of birds (e.g. Seress *et al.* 2018). Consequently, a final global built model is not presented here for this response variable.

Similarly, relatively few nests suffered total brood failures irrespective of whether it was early or late in breeding season (Table 4.10), therefore preventing any further formal comparative analyses of failure rates across the urban gradient and/or the different stages of brood-rearing. However, the average number of total failures occurring during the early brood rearing phase was higher (13.2 ± 3.4, range: 9-18, n = 79 nests) compared with failures during late phase brood rearing (4.7 ± 4.2, range: 0-11, n = 28 nests).

Table 4.10. Brood failures and successes recorded by breeding season and broken down by developmental stage for broods reared across an urban gradient in Birmingham, UK over six years. The first three columns provide the raw data for the early brood-rearing period: 0 = no nestlings survived to ringing (column 1), 1 = at least one nestling survived to ringing age (column 2). The total annual % early brood failures (column 3) are specified relative to the total number of breeding attempts in which at least one nestling hatched. Columns 4 through 6 provide analogous data for the late brood-rearing period (post-ringing through fledging).

Year	Early Brood Failure (Binary Response 0)	≥1 Nestling Survived (Binary Response 1)	% Early Brood Failures	Late Brood Failure (Binary Response 0)	≥1 Nestlings Fledged (Binary Response 1)	% Late Brood Failures
2013	9	53	14.52	0	53	0.00
2014	10	100	9.09	1	99	1.00
2015	16	106	13.11	4	102	3.77
2016	18	108	14.29	8	92	8.00
2017	13	102	11.30	11	91	10.78
2018	13	114	10.24	4	110	3.51
Total	**79**	**583**	**11.93**	**28**	**28**	**4.87**

4.4. DISCUSSION

The results presented here confirm a pervasive negative effect of the urban environment on the growth and survival of nestlings in this population of Blue Tits. Variation in reproductive parameters across sites were strongly associated with elements of the urban environment at both the habitat and landscape scales, as well as with biotic variables including breeding timing and brood size.

As is typical for altricial passerine species in seasonal environments, nestling body mass and condition, and survival declined as the breeding season progressed, whilst brood mass asymmetry increased with later hatching (Kaliński *et al.* 2009, 2019). Such patterns are primarily linked to temporal changes in ecological conditions, including predation (Verhulst and Tinbergen 1991; Naef-Daenzer *et al.* 1999, 2001), intra- and inter-specific competition

(Verhulst *et al.* 1995; Verboven and Visser 1998) and, in particular, the high availability of insect prey (Kaliński *et al.* 2009, 2019). Seasonal declines in breeding success are also thought to reflect variation in the quality of early compared with later breeders (Barba *et al.* 1995; Rodríguez *et al.* 2016).

Concomitantly, the demands and time constraints on provisioning parents increase with nestling growth and increasing brood size, resulting in slower development, lower nestling mass and reduced survival (Nur 1984; Gottlander 1987; Slagsvold and Amundsen 1992; Harrison *et al.* 2011). The results from this research, are therefore consistent with my hypothesis and with the findings from other studies (investigating Blue Tit broods reared in more natural woodland), with larger broods exhibiting lower average body mass, body condition and survival, and greater brood mass asymmetry. Contrary to predictions, however, there was no significant effect of nestbox occupancy on any of the response variables analysed and very little evidence of an impact of site area.

4.4.1. Effects of increasing urbanisation on brood-rearing outcomes

Globally, a strong and significant negative effect of increasing built landcover was observed on both nestling body mass (Table 4.2) and survival (Table 4.6). A clear negative effect of the linear urban gradient was also detected on both early (Table 4.8, Fig. 4.12) and late (Table 4.9) brood survival outcomes, providing a direct parallel to the adverse impacts of increasing urbanisation observed on fledgling numbers, fledging and overall breeding success in Chapter 3. However, contrary to predictions, variation in nestling body condition and brood mass asymmetry were not explained by the quantitative urban gradient. This may be due in part to the high degree of variance in the mean body condition data among nests within greenspaces. The lack of a more discernible effect of the urban gradient may also be attributable to the low number of breeding attempts recorded in sites at the higher end of the urban gradient.

Such heterogeneity in findings has been reported across other species and populations including Great Tits (Hedblom and Söderström, 2010; Biard *et al.* 2017), House Sparrows (Peach *et al.* 2008; Meillère *et al*. 2015, 2017) and Eurasian Kestrels (*Falco tinnunculus;* Sumasgutner *et al*. 2014). Meillère *et al.* (2015), for example, found inconsistent effects of urbanisation on the morphology and body condition indices in a dichotomous urban-rural comparison of adult and juvenile House Sparrows. They hypothesised this may be driven by variation in sample sizes across sites, as well as the localised effects of specific characteristics of each site investigated. It is possible that the failure to detect an effect of urbanisation on nestling body condition and brood mass asymmetry in my study, may also be due to variation in sample sizes across the urban gradient. Furthermore, high variance in the mean body condition values among nests within sites, suggests that body condition may be influenced by other nestbox-level biotic factors such as genetic and phenotypic variation in parental quality (Ardia 2005; Isaksson *et al*. 2006; Berthouly *et al.* 2008; Guibert *et al*. 2012), which were not considered in my study, thus limiting the model's ability to predict an urbanisation effect.

Although the availability of natural prey was not directly quantified for the purposes of this study, the overall clear and consistent negative relationship between urbanisation and brood metrics supports the hypothesis that developmental conditions within the city are constrained. Therefore, lower survival rates associated with the urban gradient are likely mediated by a lack of readily available preferred natural food, resulting in higher incidents of food limitation and consequently reduced nestling body mass (Bailly *et al.* 2016;

Demeyrier *et al.* 2017; Glądalski *et al.* 2017; Seress *et al.* 2018; Satgé *et al.* 2019; Wawrzyniak *et al.* 2020). However, considering the fine-scale quantitative nature of my study, other environmental axes that may covary with the urban gradient could also potentially constrain nestling quality and survival either directly or indirectly through parent-mediated effects including pollution, temperature, light, noise, and disturbance (Biard *et al.* 2017; Corsini *et al.* 2017; Sprau *et al.* 2017).

Corsini *et al.* (2021) reported similar parallel effects of increasing urbanisation on nestling body mass and survival in Blue and Great Tit nestlings in Warsaw, Poland, which they also concluded were related to declining natural food availability. Similar to my study, they also found that urbanisation negatively impacted on Blue Tit nestlings during the same developmental phase (i.e. between 10 and 15 days post-hatch). Furthermore, they found that whilst survival of both tit species in their study declined with increasing urbanisation in both the mid- (5-10 days) and late- (10-15 days) nestling period, no such urban effect was detected after 15 days post-hatch. Similarly, Biard *et al.* (2017) also found reduced development, growth and body condition of Great Tit chicks reared in a large urban centre (i.e. Paris) and a moderate town (i.e. Niort) compared with birds in a rural woodland, suggesting that this was due to reduced natural food availability. They also found inconsistency in the pattern of impact of urbanisation on nestling structural size, body mass, plumage characteristics and telomere length.

4.4.2. The effects of increasing garden availability on brood-rearing outcomes and potential for implications of supplemental feeding

Mean nestling body condition (Table 4.3) and brood mass asymmetry (Table 4.4) were associated with the availability of gardens in the urban matrix surrounding sites (e.g. Fig. 4.6) and a significant negative correlation was also found between the percentage of garden landcover and early brood success. Although more frequent nestling measurements will be required to elucidate the relative importance of gardens at different stages of chick rearing, these results tentatively suggest that the increased availability of gardens in the urban matrix surrounding greenspaces might impact nestling body condition, particularly during early development. Other studies have indirectly linked reduced breeding success in (sub)urban areas with the negative impacts of garden bird feeding (e.g. Hedblom and Söderström 2012; Meillère *et al.* 2015; Seress and Liker 2015). Meillère *et al.* (2015) proposed that the smaller structural size and lower fat scores of city-reared juvenile Song Sparrows, compared to their rural conspecifics, provided evidence that urban parents compensated for a lack of natural arthropod prey by changing nestling diet to include food from garden bird feeders. Similarly, Hedblom and Söderström (2012) suggested that low nestling condition in residential areas might have resulted from carry over effects of winter garden bird feeding that improved the pre-breeding body condition of adults and triggered their earlier laying, ultimately resulting in a phenological mismatch between timing of brood rearing and the peak in availability of natural food. More recent evidence from both observational and experimental field studies has further demonstrated potential links between winter supplemental feeding of birds and downstream negative effects on the growth, development and survival of chicks in a number of different passerine species

(Cuervo *et al.* 2011; Plummer *et al*. 2013b, 2018; Demeyrier *et al.* 2017 except see Robb *et al.* 2008b; Ruffino *et al.* 2014).

The patterns found in this chapter are correlative and the causal mechanisms linking features of the wider urban gradient, including gardens with variation in nestling growth, body condition and survival within this population need to be investigated directly, for example using site or garden-based supplementary feeding experiments (e.g. following Hanmer *et al.* 2016; Demeyrier *et al.* 2017; Plummer *et al.* 2013a,b, 2018), and/or through the quantification of nestling diet using observational and experimental techniques (e.g. Narango *et al.* 2017, 2018; Pollock *et al.* 2017; Jarrett *et al.* 2020; Seress *et al.* 2020).

4.4.3. Habitat-level effects on nestling growth, condition and survival

With the exception of brood mass asymmetry, a consistent, highly significant non-linear effect of broadleaved tree diversity was observed across all brood-rearing measures (e.g. Figs. 4.5 and 4.7). In contrast, the effects of other habitat variables were less consistent. The density of native deciduous trees, for example, was only found to be significantly negatively correlated with early brood survival (Table 4.8, Fig. 4.13), whilst greenspace area was weakly negatively associated with the probability of individual nestling survival (Table 4.6) and the proportion of nestlings surviving from ringing to fledging (Table 4.9).

As such, my results indicate that in Birmingham the growth, body condition and survival of nestlings reared in urban greenspaces are significantly constrained by human-mediated environmental change operating at the habitat, as well as at the wider landscape scale. Whilst the causal mechanisms linking reduced reproductive success with variation in the diversity and density of trees need to be investigated directly, I hypothesise that my findings reflect the reduced quality of breeding habitat including the patchy and fragmented nature of greenspace, together with more nuanced changes in the biotic interactions of the tri-trophic (i.e. tree-caterpillar-tit) food chain, as reported in other studies (e.g. Hinsley *et al.* 2008; Glądalski *et al.* 2017; Seress *et al.* 2018; Wawrzyniak *et al.* 2020; Corsini *et al.* 2021). Sites with higher native tree density may be associated with a lower availability of broadleaved tree species such as oaks and birches that support a greater base of preferred arthropod prey of Blue Tits (e.g. Pollock *et al.* 2017; Narango *et al.* 2017; Seress *et al.* 2018; Tallamy and Shriver 2021). The low quality of urban greenspace in providing foraging substrate for birds may further be exacerbated by fine-scale variation in the characteristics of individual trees, including their size and total canopy cover which can further increase the functional, as well as the structural, patchiness of breeding habitat (Arriero *et al.* 2006; Hinsley *et al.* 2008; Mackenzie *et al.* 2014 Amininasab *et al.* 2016). Finally, reduced avian reproductive success at sites with high levels of broadleaved tree diversity could be related to greater temporal variance in peak availability of caterpillar biomass between different species and individual trees, resulting in reduced synchrony in the timing of peak caterpillar availability and the maximum period of food demand in nestlings (Marciniak *et al.* 2007; Hinsley *et al.* 2008; Seress *et al.* 2018).

4.4.4. Differences in the effects of urban-driven brood reduction during early and late nestling development

One of the most valuable results from my research was the finding that brood reduction was significantly higher during the early developmental phase (i.e. during the post-hatching to ringing brood-rearing period) compared with the later developmental phase post-ringing. Indeed, although there was a strong negative effect of increasing built landcover on early brood survival (Fig. 4.12), once nestlings had reached ≥ 8 days post-hatch, their probability of fledging remained relatively high across the urban gradient. My results suggest that human-driven selective mortality in tits is more likely to occur before or around the age of maximum food demand (i.e. ~10 days: Stauss *et al*. 2005), a pattern that has also recently been shown by Corsini *et al*. (2021). This result could potentially also explain why no clear correlations between the urban gradient and brood mass asymmetry or mean body condition were found. Whilst very few studies have investigated the relationship between the degree of urbanisation and brood mass asymmetry (but see Hedblom and Söderström 2012), it is assumed that body mass hierarchies among offspring in a brood are caused by selective starvation, resulting in higher rates of mortality of the lightest young, thus optimising the provisioning and survival of the remaining larger chicks (Gottlander 1987; Slagsvold and Amundsen 1992). Since nestlings were weighed around or after the point of their maximal food demand, this suggests that the weakest offspring had already died (or been selectively eliminated from nests) and, therefore, were not represented in the datasets analysed (e.g. see also Biard *et al*. 2017).

Overall, therefore, my results suggest that the early brood-rearing period is associated with the highest risk of nestling mortality and, thus, likely represents the most precarious point during nestling development. Further supporting this assumption, the output of the built global model for early brood survival (the proportion of nestlings surviving to ≥8 days) closely paralleled the model of fledging success described in Chapter 3, with highly comparable predictor-response relationships of a similar strength and direction. Consequently, and as hypothesised, the increased mortality of nestlings during the early brood-rearing period is likely one of the main contributing factors of overall reduced breeding success of Blue Tits in Birmingham.

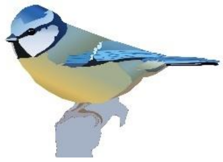
4.5. CONCLUSIONS

My results support the hypothesis that nestling growth and development in urban passerine species such as Blue Tits are constrained by the breeding environment. The associated decrease in average nestling body mass and their lower body condition as sites become increasingly urbanised is likely a direct effect of poor environmental breeding conditions both within greenspaces and the wider surrounding urban matrix. Although not directly assessed, I hypothesise that this is potentially linked to the low quantity and quality of natural food including caterpillars, available during the critical and energy intensive brood-rearing period, or to fine-scale changes in abiotic conditions associated with other environmental factors (e.g. pollution, light or temperature). In this population, the early (pre-ringing) developmental phase was significantly related to the survival of nestlings to fledging, with knock-on effects on overall breeding success. Therefore, my findings are consistent with similar research, indicating that urban-adapted species may not derive benefits from city-living and associated human-provided resources, at least in terms of their breeding success (Sumasgutner *et al.* 2014).

Environmental conditions during development shape the life histories of individuals, including their survival post-fledging, breeding recruitment and subsequent breeding success in future years (Meillère *et al.* 2015; Seress *et al.* 2018). As a result, the lower body mass and condition of nestlings that do survive to fledging may have significant consequences for their future survival and fitness and thus the population dynamics of the Birmingham Blue Tit population. Furthermore, this also implies that urban parents are less able to compensate for poor breeding decisions and/or additional environmental stress (e.g.

extreme weather) that may be experienced earlier in the season: an issue that was highlighted by Satgé *et al.* (2019), and a theme that will now be explored in Chapter 5.

Chapter Five



The interactive effects of urbanisation and weather conditions on nestling body mass, hatching success and fledging success in Blue Tits (*Cyanistes caeruleus*): an exploratory analysis using sliding windows.

5.1. INTRODUCTION

The impacts of both long- and short-term variation in weather conditions on avian reproduction are complex: their effects vary across different phases of the breeding cycle, and influence breeding outcomes both directly and indirectly via a multitude of different pathways (Pipoly *et al.* 2013; Marrot *et al*. 2017; Marques-Santos and Dingemanse 2020). Warmer spring temperatures, for example result in the earlier onset of egg laying (Crick *et al*. 1997; Cresswell and McCleery 2003; Visser *et al*. 2003), as well as decreased nestling development time and advanced fledging dates (e.g. see Matthysen *et al*. 2011). Contrastingly, cold, wet springs reduce the availability of food and increase energetic demands leading to delayed egg laying (e.g. Bailly *et al*. 2016; Glądalski *et al.* 2014, 2018), a lag in incubation and hatching (Whitehouse *et al*. 2013; Coe *et al.* 2015) and reduced hatching success (Nord and Nilsson 2011; Martin *et al*. 2017; Higgot *et al*. 2020). Heavy and persistent rainfall during brood rearing may cause rapid heat loss (chilling) in nestlings due to soaking, resulting in hypothermia and increased nestling mortality (Siikamäki 1996), and even cause complete brood failure (Wesolowski et *al*. 2002; Bordjan and Tome 2014; Schöll and Hille 2020). Extreme rainfall or strong winds may also indirectly affect nestling growth and development (Keller and van Noordwijk 1994) by reducing the availability of caterpillars (Schöll *et al*. 2016; Morganti *et al*. 2017) and negatively impacting parental foraging behaviour and feeding rates (Öberg et *al*. 2015; Mainwaring and Hartley 2016) resulting in starvation and in some cases abandonment of the nest (Bordjan and Tome 2014). On the other hand, higher ambient temperatures can cause heat stress in nestlings, which can decrease nestling mass, cause hyperthermia and reduce breeding success and post-fledging survival (Greño *et al.* 2008; Rodriguez *et al*. 2016; Marques-Santos *et al*. 2021).

Given climate change scenarios are forecasting changes in daily mean temperatures and precipitation, as well as the frequency and magnitude of extreme weather events in temperate regions (IPCC 2018, 2021), there is growing interest for studies that provide detailed assessments regarding the impacts of weather on key life-history events such as reproduction to help predict the future downstream consequences on wildlife population demographics (Marques-Santos and Dingemanse 2020 Schöll and Hille 2020; Sauve *et al*. 2021).

However, although the effects of weather have been intensively studied in birds, research has primarily focused on the long-term impacts of climate change and has largely been limited to only a few life-history traits including changes in the phenology of recurring spring events including migration arrival and reproduction (Parmesan and Yohe 2003; Root *et al*. 2003; Charmantier and Gienapp 2014; Thackeray *et al*. 2016). Indeed, one of the most widely accepted and recognised impacts of climate change is the advancement of breeding phenology, with mounting evidence demonstrating that earlier laying in birds is likely a response to warming spring temperatures, which results in widening trophic mismatches and altered species interactions (Yang and Rudolf 2010; Schaper *et al.* 2012; Visser *et al.*

2008; 2012; Reed *et al.* 2013; Pipoly *et al.* 2013). More specifically, a number of studies have shown that an increase of 1°C in temperature equates to an approximate 2 – 5 day advancement in clutch initiation in tits and other passerine species (e.g. Visser *et al*. 1998; Vedder *et al.* 2013; Chevin *et al*. 2015; Phillimore *et al*. 2016).

However, the more immediate and sudden effects of unpredictable or extreme weather events (e.g. severe changes in temperature or precipitation) have been less well studied (Martin *et al.* 2017; Marques-Santos and Dingemanse, 2020). With respect to reproduction, most studies have focused on weather conditions prior to clutch initiation and their effect on the plasticity of early breeding responses such as clutch size and laying date (Marques-Santos and Dingemanse 2020). Consequently, how yearly variation and sudden changes in weather conditions post-hatch (i.e. that occur after initial reproductive decisions have been made) influence life-history traits such as nestling condition and survival are less well documented, even in well-studied biological systems such as tits (Öberg *et al.* 2015; Marques-Santos and Dingemanse 2020). Yet birds are likely less able to respond to sudden changes in local weather conditions during this period, and may have to invest extra energy on behavioural or physiological responses or abandon the breeding attempt altogether (Greño *et al*. 2008; Mainwaring and Hartley 2016). Finally, in comparison to temperature, relatively little research has been conducted on the impacts of rainfall, multiple weather variables or the potential for interactive effects between different weather signals on biological systems (Li *et al*. 2021).

Incubation and brood rearing are particularly physiologically and energetically demanding phases of the reproductive cycle (Perrins 1965; Ricklefs 1969; Nur 1984). Changes in temperature and precipitation can influence female incubation behaviour and the optimal thermal environment, therefore influencing embryonic development and nestling phenotype (Coe *et al*. 2015). For example, the exceptionally cold wet spring of 2012 was observed to significantly disrupt egg laying and incubation in a population of Blue and Great Tits breeding in both natural and urban sites in Cambridge, UK (Whitehouse *et al.* 2013), causing a lag in hatching, and resulting in significantly reduced brood productivity and delayed fledging. In another more recently documented extreme weather event, a sudden, significant drop in temperature early in the breeding season of 2017 was widely reported to cause significant hatching delays across multiple Blue and Great Tit populations in northern Europe with knock on effects to breeding productivity (as reported by Glądalski *et al.* 2018)

Blue and Great Tit chicks are particularly vulnerable to changes in environmental conditions during the early nestling phase as they lack feathers which provide insulation and waterproofing and are unable to thermoregulate (Perrins 1979; Stenning 2018). Therefore, short-term temporal variability in weather conditions and unpredictable weather extremes during this period are likely to have a major impact on nestling development and survival, with downstream effects to breeding success and long-term demographic processes (Öberg *et al.* 2015; Morganti *et al.* 2017).

It is imperative, therefore, if we are to gain a better and more complete understanding of the impacts of variation in weather conditions and in particular extreme events that research takes a more holistic approach that considers the periods both prior to and during the various phases of the breeding season as well as multiple reproductive responses (Charmantier *et al.* 2008; Goodenough *et al.* 2011; Marrot *et al*. 2017; Marques-Santos and Dingemanse, 2020; Sauve *et al.* 2021a). This will help to (i) determine how and when weather signals affect different aspects of breeding season phenology, breeding productivity and the development (growth and condition) of nestlings and (ii) identify the stages of the breeding cycle most sensitive to shifts in weather (Marques-Santos and Dingemanse 2020; Sauve *et al.* 2021a). The need to explore the potential for longer lag effects of weather (i.e. occurring outside of the breeding season) has also been highlighted as a research priority since prenatal conditions may impact resource availability and the condition of adults and therefore indirectly influence nestling development and breeding success (Sauve *et al.* 2021a). Equally important, is improving our knowledge regarding the interactive effects of different weather signals as variation in the timing and/or patterns in one weather variable may exacerbate or reduce the impacts of another (Sauve *et al.* 2021a).

Recent key advances in the statistical analyses of weather effects, particularly those incorporating a sliding window approach (see Appendix 5) have facilitated the exploration of the effects of different weather signals on various aspects of ecology and life-history traits in different taxa and across multiple competing timeframes (van de Pol *et al.* 2016; Marques-Santos and Dingemanse 2020). Millán et al (2020), for example used sliding window analyses to determine that reduced rainfall associated with climate change, resulted in poorer environmental conditions for breeding, leading to phenological delays in the rutting season and decreased intensity in rutting behaviour, but positively impacted sexual selection and polygyny in Iberian Red Deer (*Cervus elaphus hispanicus*) in Doñana Biological Reserve (Southwest Spain). Li (2021), investigated the effects of different rainfall patterns (timing and amount) on phenological asynchrony between plants including rye grasses (*Leymus chinensis*) and Brandts Voles (*Lasiopodomys brandtii*) and to provide evidence for fitness consequences on population size, in a long-term manipulative experiment conducted in semiarid steppe grassland in Inner Mongolia. Ren *et al.* (2022) used sliding window analyses to determine the most important factors regulating autumn leaf senescence (including pre-season temperatures, precipitation, sunshine hours and leaf out date) for 41 species of herbaceous plant species in China, (equating to 10533 ground phenological observations and 201 stations).

As such, the more recent advances in sliding window analyses provide an opportunity to test the sensitivity of breeding responses in avian species to variation in weather conditions within more biologically relevant timeframes (e.g. during incubation or brood-rearing) (e.g. Hidalgo Aranzamendi *et al*. 2018; Samplonius *et al* 2018; de Zwaan *et al*. 2020; Marques-Santos *et al*. 2021; Sauve *et al.* 2021a, b; Visser *et al*. 2021;) and to explore the potential interactive effects of climate with other aspects of the environment, for example urbanisation as recently undertaken by Marques-Santos and Dingemanse (2020).

Here I use ‘critical climatic time window analyses’ (van de Pol and Cockburn 2011; van de Pol *et al*. 2016) to explore the influence of weather variables including temperature and precipitation on measures of breeding success that were previously shown in Chapters 3 and 4 to shape reproductive performance in a population of Blue Tits nesting along a gradient of increasing urbanisation in the city of Birmingham, UK over six consecutive breeding seasons.

5.1.1. Study aims and hypotheses

Using weather variables as a proxy for climate, the overarching aim of this chapter is to identify the key time periods and associated climatic signals that best explain variation in breeding outcomes across the reproductive cycle in a population of urban-breeding Blue Tits. Using the critical time window approach I investigate if and how different temperature and precipitation signals influence breeding phenology, hatching success, nestling mass and survival, and to determine, relative to two reproductive phases, prehatching (egg laying to hatching) and brood rearing (hatching to fledging) respectively, the specific time-frames when breeding birds are most sensitive to variation in weather. I also aim to establish if the degree of urbanisation potentially exacerbates or buffers the effects of the weather signal on breeding outcomes.

I hypothesise that:

1. Increasing temperatures and drier conditions prior to and during the pre-hatching phase will lead to increased hatching success, whilst lower minimum temperatures and longer periods of precipitation and heavier rainfall will be associated with lower hatching success and a higher probability of hatching failure.
2. Compared with the pre-hatching phase, breeding responses associated with the brood rearing phase will appear more sensitive to variations in weather and that effects of temperature and rainfall will be exacerbated for birds nesting in more densely urbanised sites.

Aligned with these hypotheses, I predict: that both nestling mass and survival will be negatively influenced by lower minimum (night-time) and mean (daily) temperatures, increased maximum daily temperatures and increased daily rainfall, and that the probability of a nest successfully fledging any young will decline with these changes in the different weather signals, with nests in the most densely urbanised sites at a higher risk of total reproductive failure.

5.2. METHODS

5.2.1. Study area and breeding data collection

The study design, routine monitoring of breeding attempts and data collection between 2013 and 2018 were the same as described in Chapter 2.

5.2.2. Weather Data

Temperature and precipitation data were collected from three different sources. First, both rainfall data (hourly and daily) and daily mean, minimum and maximum air temperature data (split into daytime (0900 – 2100) and night-time (2100 - 0900) periods) were obtained from the University of Birmingham Winterbourne No. 2 Weather Station (56424) located to the south-west of the city centre (52.456° N, -1.92619° W, 120m a.s.l) and a mean distance 5.95 km, (range = 1.77 – 12.73 km) (Fig. 5.1) from the 28 sites used in the study. All temperature and rainfall data were retrieved from the MET Office Integrated Data Archive System (MIDAS) provided by the U.K. Centre for Environmental Data (CEDA) (Met Office 2019).

Figure 5.1. Map of the core of the Birmingham study area and the location of the Winterbourne Number 2 (56424) Weather Station (turquoise marker) relative to the inner city sites (shown as red

and purple markers). This station was chosen as the closest in distance to the majority of sites (n = 27). (Google Earth Version 7.3.4, (Image date = April 18, 2021). 52°27'40.13" N, 1°47'26.91 W, eye alt 34km. Landsat/Copernicus).

Second, higher temporal and spatial resolution precipitation data were obtained from the U.K.s NIMROD radar system, provided by the U.K. Centre for Environmental Data (CEDA), (Met Office 2019). Radar data, including cumulative rainfall and rainfall intensity were available at 5-minute temporal and 1 km^2 spatial resolutions, with data recorded from the start of each hour. Such a high spatial resolution enabled precipitation data to be captured for each of the individual 28 study sites. There is a degree of uncertainty associated with the range of radar rainfall data, due at least in part to variation in the distance of sites from the radar source, topography and environmental conditions (Villarini and Krajewski 2010; Croghan *et al.* 2019). However, considering the close proximity of the study sites to the nearest radar site (Cleft Hill) which is located less than 50km from Birmingham, as well as to each other, and the relatively small changes in topography across the urban area, any uncertainty in the data is likely to be low.

Finally, during 2017 and 2018, ambient air temperature at the centre and edge of each study site (e.g. Figure 5.2a) were recorded at 5- and 10-minute intervals using Tinytag® dataloggers, (models TGP-4017 and TGP-4020, Gemini Data Loggers, Chichester, UK) (Figure 5.2b) and Thermochron iButton® loggers (model DS1922L, Maxim Integrated Products., Sunnyvale, CA, USA) (Figure 5.2c), respectively.

Figure 5.2a: An example of the typical positioning of temperature dataloggers within a study site (i.e. Gibs Heath (Soho)). iButtons (x2 units per site) are shown as red markers, the TinyTag logger as a yellow marker (x1 units per site) and nestboxes as green circles. (Google Earth Version 7.3.4. (Imagery date =July 3, 2021; Location: 52°29’45.80” N, 1°55’20.09 W, eye alt 387m, Landsat/Copernicus). Photographs illustrate examples of **(b)** the positioning and orientation of a Tinytag® at a height of approximately 2.5m on a tree located in Holders Lane Woods (Photo: A Mason, 2018) and **(c)** a Thermochron iButton® secured to the upper back wall of a nestbox with Velcro® (Photo: Authors own, 2017).

Temperature loggers (hereafter referred to as Tinytag and iButton loggers respectively) were installed in early to mid-March (the beginning of nest laying) and collected after all breeding attempts within each site were confirmed to have finished (all nestlings had fledged and/or nests were abandoned). Both types of dataloggers have a measurement accuracy of approximately ±1-2 C. All dataloggers were calibrated by placing them in a Stevenson screen adjacent to the University of Birmingham Weather Station for a period of at least 48 hours. A small number of dataloggers were found to be defunct and were discarded. Evidence of potential under/over estimation of temperatures for the remaining dataloggers was found to be minimal, and therefore correction factors were not deemed necessary. To monitor air temperature at each site, Tinytag loggers were housed within camouflage coloured plastic shields to minimise vandalism and to prevent radiation directly warming them (Figure 5.2b) before being secured at a height of approximately 2-3m to the main trunk or branch of a tree located as close to the centre of each study site as possible. The loggers were suspended within the shields using heavy duty garden twine to minimise direct contact with the trees. Units were oriented to maximise airflow through the shield and across the logger. iButton loggers were secured on the inside of the lid or backwall of nestboxes with Velcro and away from the top of the nest or brooding female.

Tinytags have a large memory capacity (32 000 readings) and therefore were left in place for the duration of each breeding season. The iButton loggers have a smaller memory capacity (8192 bytes allowing for the collection of data over an approximate 12-13 day period), therefore they were switched out and all data downloaded every ten days. Daily mean, maximum and minimum temperatures were calculated from these data for every site through the two breeding seasons.

5.2.3. Breeding response variables

The critical time window approach was used to explore the potential effects of variation in temperature and rainfall for two key stages of the reproductive cycle (pre-hatching and brood-rearing) using several measures of breeding success, including (a) proportional hatching success, (b) probability of hatching failure, (c) nestling weight, (d) proportional fledging success and (e) the probability of brood failure.

The *Climwin* package cannot currently deal with proportional data and zero inflation, so all failed breeding attempts (i.e. zero data) were filtered out from proportional success datasets to minimise the potential for issues with model convergence and validation. Binary probabilistic measures of success (used to determine rates of failure during pre- and post-hatching phases) were analysed using the relevant full dataset. Due to the narrow climate windows tested for nestling weight (see below) analyses included nestlings ringed and weighed between 8 and 12 days post-hatch (n = 3129 chicks).

5.2.4. Critical time window selection

I used the ‘sliding window’ function from the ‘*climwin’* package for R (van de Pol *et al*. 2016) to search for critical time windows (i.e. weather time periods) during which specified climate variables including temperature, rainfall or dry days, best explained variation in the breeding responses investigated and to evaluate the strength and direction of any significant relationship(s) identified.

Two sets of critical time window analyses were conducted. In the first set of analyses, the potential effects of temperature and rainfall at the city-wide scale were investigated for all five breeding response variables using the climate data obtained from the Winterbourne Weather Station. Secondly I conducted a preliminary exploratory analysis to determine how the spatialisation of weather at the site-level influenced nestling weight using the two years (2017-2018) of daily temperature data collected at each site and daily rainfall data derived from the NIMROD dataset.

The major steps that were used in the *climwin* analysis are detailed below and followed the protocols and procedures as summarised in the accompanying literature (Bailey and van de Pol 2015; van de Pol *et al.* 2016).

5.2.4.1. Step 1: Construction of baseline models

For each response variable, a baseline regression (null model) was constructed (containing no weather effects), against which the performance of competing climate models (below) could be assessed (Table 5.1).

Table 5.1. The key components and structure of the final baseline model for each breeding response variable investigated within the critical climate window analysis using *climwin*. The associated dataset and number of data points is also given.

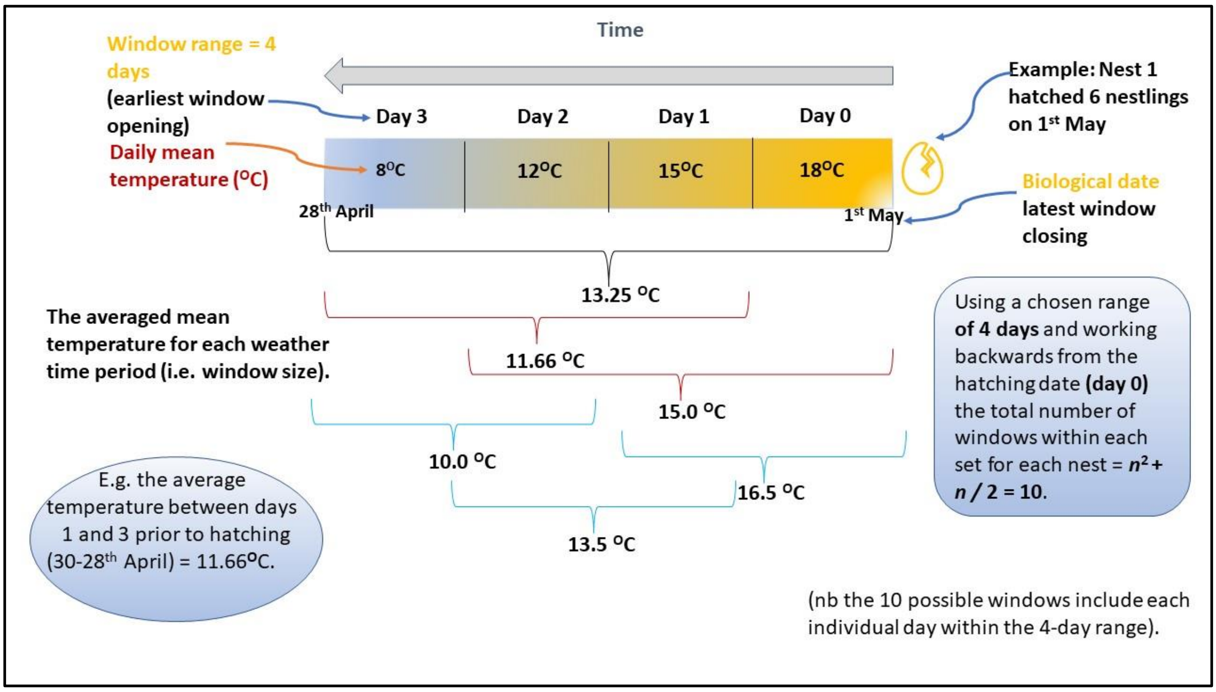
Response variable	Baseline model variables	Baseline random effects	Weight	Model (and family)	Dataset
Proportional Hatching Success	Year	n/a	Clutch Size	glm (binomial)	Hatching-filtered (662)
Binomial Hatching Success	Year	n/a	Clutch Size	glm (binomial)	Clutch-filtered (752)
Proportional Fledging Success	Year	n/a	Brood Size	glm (binomial)	Fledging-filtered (554)
Binomial Fledging Success	Year	n/a	Brood Size	glm (binomial)	Hatching-filtered (662)
Nestling Body Mass (6 years of data: 2013-2018)	Ringing age, Brood size (at hatching)	n/a	Occupancy	lm	Nestlings aged 10-12 (n = 3129)
Nestling Body Mass (2 years of data: 2017-2018)	April hatching date, Occupancy, Brood size (at hatching)	Site ID	n/a	glmer (gaussian)	Nestlings aged 10-12 (n = 1133)

This final model was selected following a comparison of different baseline model structures that included an intercept-only; intercept + year and combinations of potentially confounding phenological and biotic covariates determined to be relevant from previous hierarchical modelling in Chapters 3 and 4. Year was included as a fixed covariate (integer) to control for inter-year environmental variation not explained by the weather signal under consideration. Phenological variables were included to control for potential variation in breeding responses related to seasonal changes and biotic covariates including occupancy, clutch size and brood size were also added to account for variation in intra- and inter-nest competition. All continuous variables included in baseline models were scaled and centred. Due to issues of convergence when running the baseline analyses in *climwin*, (with the exception of spatialised nestling body mass) random effects terms were dropped and generalised linear models (GLMs) used in place of the preferred GLMMs.

5.2.4.2. Step 2: Critical time windows construction and selection

In the next step multiple weather signals were generated and independently added to the respective baseline models, thus creating a suite of potential candidate models for each breeding response. Candidate models comprised all the various different combinations of the main weather variables (temperature, rainfall and dry days), aggregate statistics (mean, minimum, maximum and sum) and functional relationships (e.g. linear or quadratic) that may influence each breeding response.

Within *climwin* the *slidingwin* function initially builds all of the possible set of time windows, each time varying the start date and window length at a daily resolution within a user-specified range (e.g. 20 days). The analysis systematically searches within these windows whilst testing all of the potential weather signal combinations, to determine (1) the most relevant time period (the critical time window) (2) the strongest aggregate statistic and (3) the function of the relationship, that best describes the variation in breeding responses to each climate variable investigated. An example of this process for one weather variable (mean daily temperature) and one response variable (hatching date) is illustrated in Fig. 5.3 below.



The averaged mean temperature for each weather time period (i.e. window size).

E.g. the average temperature between days 1 and 3 prior to hatching (30-28th April) = 11.66°C.

Using a chosen range **of 4 days** and working backwards from the hatching date **(day 0)** the total number of windows within each set for each nest = $n^2 + n / 2 = 10$.

(nb the 10 possible windows include each individual day within the 4-day range).

Figure 5.3. Graphical illustration demonstrating a simplified example of the first stage of the critical climate window analysis using *climwin* for one nest, using hatching date as the breeding response, one weather variable (mean daily temperature) and a window range of 4 days. The *sliding win* function searches for time periods that best predict the breeding trait (hatching date) to a particular weather variable (mean daily temperature). All possible sliding windows are built for an *a priori* specified period of time (e.g. for a range of n = 4 days), working backwards from the biological date (hatching date = Day 0). For each of the time windows identified (total n = 10) the mean daily temperature is set to be averaged as one value. For relative searches this sliding window process is then replicated for each nest in the dataset and for each specified weather variable and its associated aggregate statistics. In this example aggregate statistics including the minimum, maximum and warmth sum for each weather time window would be calculated using the daily mean temperature record.

The maximum size and timing of the window ranges and their associated reference dates were specified according to the breeding response under consideration (Fig. 5.4). All window openings were specified as day 0 (i.e. the date on which the nest event or measurement was recorded).

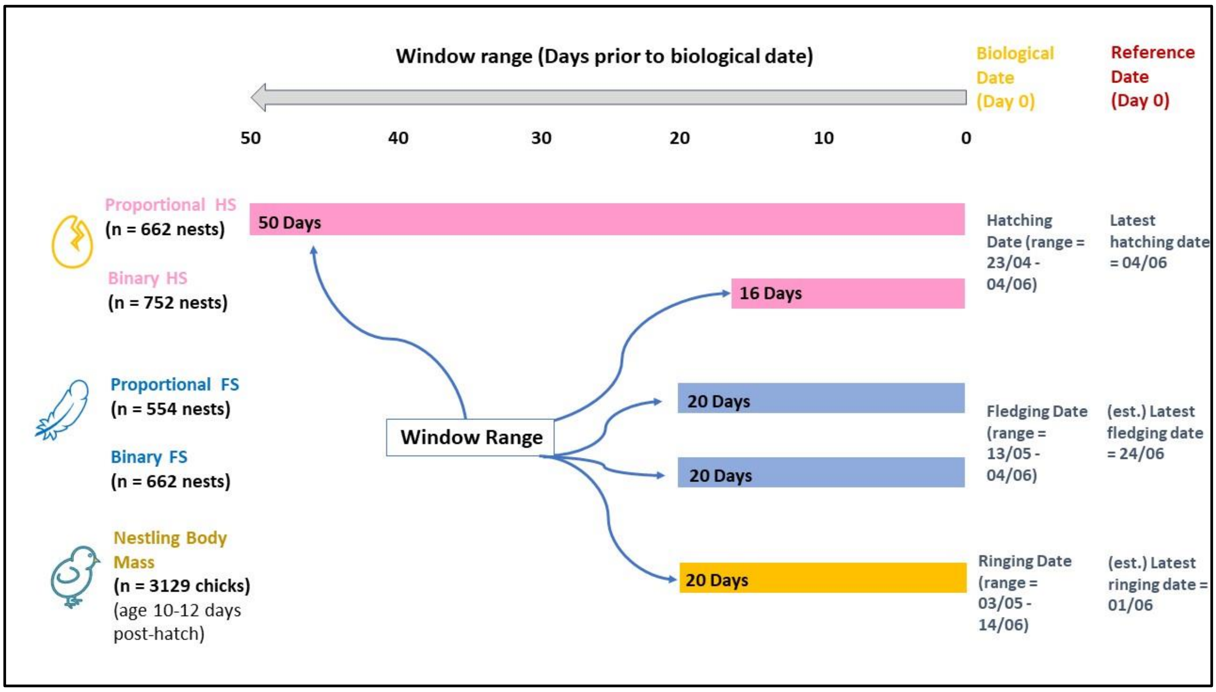


Figure 5.4. A graphical illustration of the window range, biological date, and reference dates specified for searches within *climwin* to identify potential climate signals for each of the five Blue Tit breeding response variables investigated. Dummy hatching and fledging dates were used to specify the biological date for failed nesting attempts in the analysis of binary response variables. Hatching dates were estimated by forward counting 15 days (the mean incubation period of successful nests in this study) from the laying date and fledging dates 20 days from the estimated hatching date.

The focus on narrower window ranges (maximum length = 50 days) in this study takes into consideration the timing and relatively short duration of each reproductive phase in the Blue Tit breeding season (Perrins 1979). Furthermore, shorter time periods reduce the potential for Type I errors (i.e. detecting false positive in a climate signal) due to multiple testing (van de Pol *et al*. 2016; Hidalgo Aranzamendi *et al*. 2019).

The 50 day window range for proportional hatching success takes into consideration variation in weather conditions experienced by breeding pairs in the days leading up to and during nest building, as well as conditions over the average egg laying and incubation period for this population. The shorter 16 day window for binary hatching success reflects the fact that nest failures during incubation are more likely due to a single, sudden event and can only have occurred after clutch completion, since incubation was confirmed for all nests in this dataset. Window ranges for fledging outcomes were set at 20 days to capture the variation in weather nestlings experienced during the brood-rearing period that may directly impact on growth, development and survival (e.g. as reviewed by Sauve *et al*. 2021b).

Analyses of nestling body mass included data on the individual weights (±0.1g) for all chicks that were ringed between 8 – 12 days post-hatch (n = 3129) across all years of the study. The decision was taken to exclude data from older nestlings (ages 13 -15 inclusive) due to the small critical time windows considered in the sliding window analysis. The 20 day window range captures variation in weather during both the early-brood rearing and incubation periods that have previously been shown to affect the behaviour of incubating females and embryonic development (e.g. see Webb 1987; DuRant *et al.* 2013; Pipoly *et al.* 2013; Coe *et al.* 2015).

For the purposes of the nestling body mass subset-analysis (using data from 2017-2018), a new climate dataframe was constructed which combined the daily mean temperature data (March-June) calculated for each site during the 2017 and 2018 field seasons with site-level daily total rainfall data for the same period extracted from the Nimrod dataset. Breeding data were extracted from the six year dataset to create a separate 2 year biological dataframe for use in analysis. Data were analysed using generalised linear mixed models to take into consideration the nested structure of both the climate and biological data.

All searches were set to ‘relative time window’ to take into account variation in the timing of the expression or measurement of breeding traits among individual breeding pairs (e.g. hatching dates for hatching success or ringing dates for the measurement of nestling mass and body condition). Relative time window searches are preferable in studies such as this, where the lag period between the potential weather signal relative to the biological response is relatively short and narrower critical time windows are more likely (Bailey and van de Pol 2016; van de Pol *et al*. 2016). End reference dates (for window ranges used in randomised modelling: see below) were set as the latest recorded nest event or measurement date from the six years of data (appropriate to each breeding response; Fig. 5.4).

For each breeding response, I built and tested candidate models that compared the aggregate statistics crossed with the linear and quadratic relationships between three daily temperature (mean, minimum and maximum) variables and two precipitation (daily rainfall and dry days) variables. The climate variable ‘dry days’, was derived from the rainfall data, with a binary response specified for each day, where 1 = no rainfall and 0 = ≥0.01 mm rainfall. The different combinations of candidate models tested against each climate variable are provided in Table 5.2.

Table 5.2. The three temperature and two precipitation climate variables, together with their associated aggregate statistics and functions that were tested within *ClimWin* to determine the influence of climate on breeding outcomes in a population of Blue Tits breeding in Birmingham between 2013-2018.

Climate Variable	**Aggregate Statistic**				**Function**	
Temperature	Min	Mean	Max	Sum	Linear	Quadratic
Minimum Temperature (°C)	✓	✓		✓	✓	✓
Maximum Temperature (°C)		✓	✓	✓	✓	✓
Mean Temperature (°C)		✓		✓		
Precipitation						
Rainfall (mm)		✓	✓	✓	✓	✓
Dry Days				✓	✓	

Candidate models were compared with the baseline model using the built-in function within *climwin* that automatically compares AICc values. Critical window sets for each climate variable were only considered for further analysis if the top models had a lower AICc value compared with the baseline model (ΔAICc ≥-2) (Burnham and Anderson 2002, 2004).

The AICc values and model outputs for each climate variable – aggregate statistic combination were then compared to determine the strongest potential candidate model, also taking into consideration whether the linear or quadratic function should be retained. Where a temperature variable model clearly performed better, this was retained for further analysis. Where the difference in AICc values across different temperature candidate models were similar, all models were selected and subjected to randomisation analysis.

5.2.4.3. Step 3: Randomisation

Due to the high number of models tested, there is the possibility for Type I errors, (i.e. candidate models performing better than baseline models purely by chance). Therefore, following the identification of potential critical time windows for a breeding response, the built-in randomisation function '*randwin'* from the c*limwin* package was used to quantify the likelihood of obtaining a similar or better AICc value for a climate signal by chance, following van de Pol *et al.* (2016). The weather predictor variable of interest was randomised and the same model building procedure was performed following the initial critical time window analysis, resulting in the generation of 100 randomised best models. The value of the ΔAICc obtained from the real data of the best climate model was then compared with the ΔAICc set of extracted randomised values to determine the likelihood of obtaining the observed AICc value by chance ($P_{\Delta AICc} \leq 0.05$). Results were visually inspected using the '*plotall*' function.

5.2.4.4. Step 4: Exploring more than one candidate climate variable and dealing with correlation between variables

Where a positive signal was detected for a particular temperature, rainfall or dry days variable, only 1-3% of models were included within the top 95% of model weights, therefore the top model (with the lowest AICc value) was selected for further analysis.

Where there was evidence for multiple climate variables (e.g. a signal for both rainfall and temperature) simultaneously influencing a breeding response, as determined by the $P_{\Delta AICc}$ values, the potential for correlation between them was checked prior to their inclusion in final models. Checks for collinearity between weather variables were undertaken using the function '*cross-win*'. When covariance was detected, or where multiple signals for a particular climate variable were identified, (for example due to the detection of potentially different lag effects or a strong influence of more than one aggregate statistic), the best supported signal was added to the baseline model and the analysis was refitted to determine if model support remained. Due to the short time frame of the Blue Tit breeding season this step normally resulted in the loss of weaker climate signals.

5.2.4.5. Step 5: Final Modelling in glmmTMB

In the final step, once climatic windows were identified and validated using *climwin*, they were used to generate the final global models. Climate variables were scaled and centred and fitted as fixed covariates to models, together with all relevant habitat, landscape and biological covariates that were determined as important in Chapters 3 and 4. Analyses were conducted to compare the performance of models including both the quantitative (percentage of built landcover) and five-level categorical (urban land class) urban gradient metrics against an intercept-only and null model following the same procedures described in Chapter Three. The potential for interactive effects were explored, both between different climate variables and also between climate variables and the quantitative urbanisation metric.

5.3. RESULTS

5.3.1. Critical time window selection

5.3.1.1. Identification of critical time windows for hatching success outcomes

Whilst several of the climate models predicting the probability of hatching success had lower AICc values compared with their respective baseline models, randomisation analyses suggested that the majority of the best climate signals likely occurred by chance ($P_{\Delta AICc}$ ≥0.05) (Appendix 6). Although the ΔAICc value for the best minimum temperature model was significantly lower than the randomised climate models ($P_{\Delta AICc}$ 0.04), this climate signal was also not considered further. The critical time window coincided with day 0 (hatching date) and further inspection of model outputs determined that the climate signal was likely weak, suggesting a potentially spurious result.

For proportional hatching success, all of the best models for temperature, daily rainfall and dry days performed better than the baseline models, (all ΔAICc values < -2). With the exception of the minimum temperature signals, comparisons of observed model ΔAICc values with randomised models confirmed that the best climate windows identified were unlikely to have occurred by chance ($P_{\Delta AICc}$ ≤0.05). The best critical climate windows detected for both mean and maximum temperature were very similar (Fig. 5.5), with variation in hatching success best explained by linear or quadratic effects of temperatures in the days immediately preceding hatching (earliest window = day 3, latest window close = day 1). Overall, the mean (and sum) maximum (quadratic) temperature climate model was determined to be the strongest candidate (ΔAICc = -47.96, $P_{\Delta AICc}$ ≤0.01) and was considered for inclusion in the final hierarchical modelling stage.

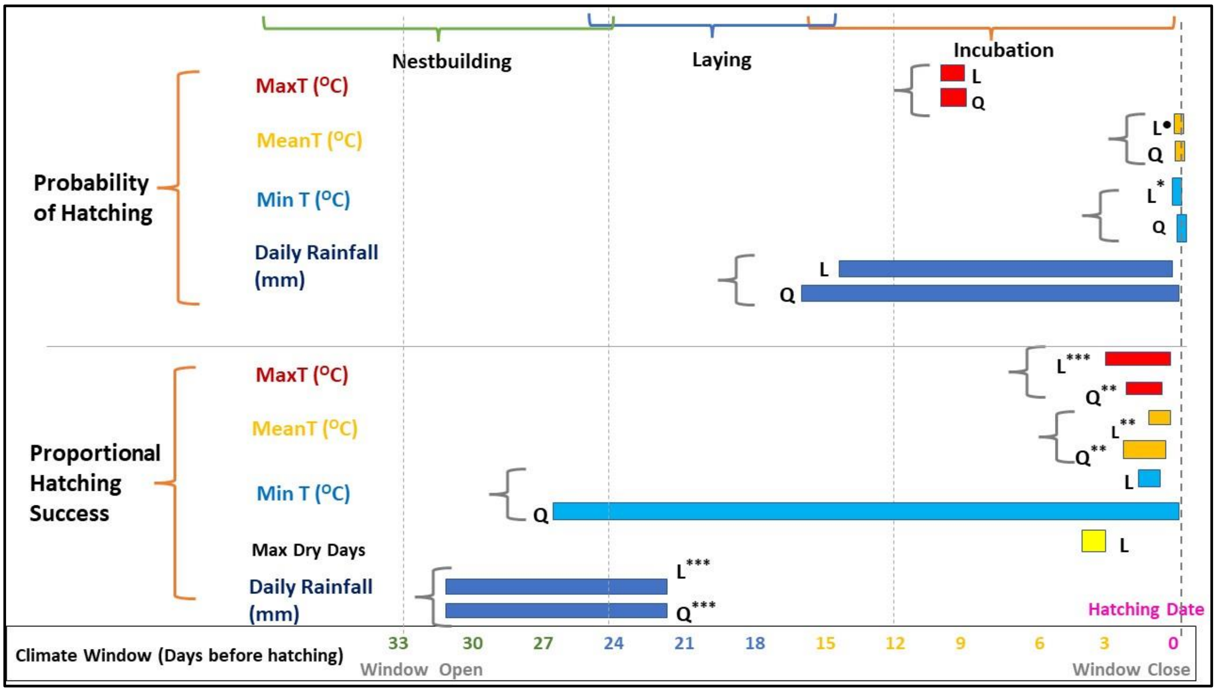


Figure 5.5. Representation of the best critical climate time windows for each weather variable tested for hatching success and probability of hatching success (binary success-failure) for a population of Blue Tits breeding across an urban gradient in Birmingham, UK from 2013 – 2018. Windows are in days relative to hatching date (day 0). For each breeding response variable, the best windows were searched for daily maximum temperature (MaxT), mean temperature (MeanT), minimum temperature (MinT), dry days and daily rainfall. The best critical climate windows are further split into the two functions: linear (L) and quadratic (Q). For each variable-function combination the most probable aggregate statistic is presented. Asterisks and dots show theprobability of a model occurring by chance: significance codes ($P_{\Delta AICc}$) ≤0.001 (***), ≤0.01 (**), ≤0.05 (*), borderline (•). The numerical data derived from climwin analyses on which the figure is based including the window range, ΔAICc value and associated statistical significance values from randomisation analyses (PΔAICc) are provided in Appendix 6, together with examples of the outputs from the plotting tools used to visually inspect and validate the best candidate models.

The critical climate window for rainfall across all best models had a longer lag time (Fig. 5.5), with the window opening 31 days and closing 22 days (i.e. approximately 3-4 weeks) prior to hatching date for each nest. As with the results for temperature, there was no clear best candidate rainfall model, with all ΔAICc values for the four best performing models (linear or quadratic effects of the mean or total rainfall) all within <-2 relative to each other. A comparison of model outputs suggested however, that the strength of the effect of the mean (linear) rainfall signal was likely marginally stronger ($\beta \pm SE = -0.326 \pm 0.047$, $z = -6.962$, $P \leq 0.001$), therefore this variable was retained for further analysis.

Since multiple candidate signals were identified for hatching success, a second set of *climwin* analyses were undertaken, with the temperature variable included in the baseline model to search for potential alternative time windows for rainfall. This confirmed the best candidate critical climate windows and weather signals for rainfall remained similar and therefore the decision was taken to continue analyses using the initial best candidate rainfall signal identified. The visual inspection of the '*crosswin*' function plot (Fig. 5.6) confirmed that there were unlikely to be issues of collinearity between the two weather covariates.

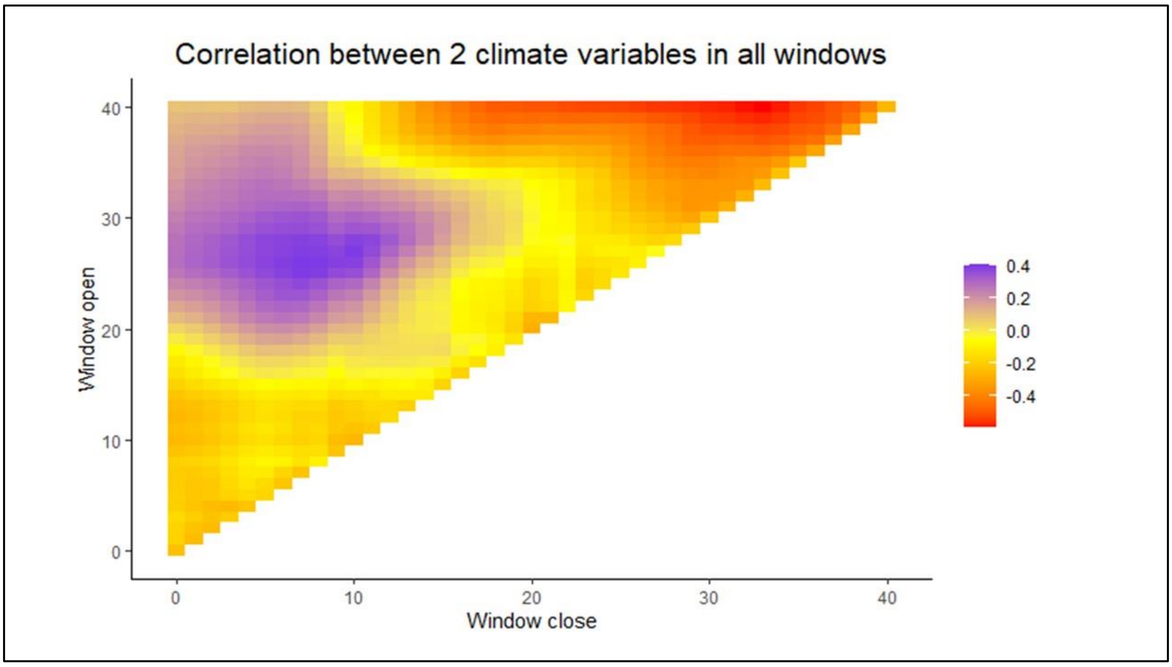


Figure 5.6. Plot of the output from the test of collinearity between the best rainfall (mean, linear) and maximum temperature (mean, quadratic) climate signals using the *crosswin* function from the *climwin* package. The correlation between temperature and rainfall across all of the different time windows searched (range = 40 days, reference day = June 4th) is represented by the different colours. Purple colours show a positive correlation, red a negative correlation and yellow no correlation. The plot therefore visualises periods of time where correlation between climate variables is weak and strong. All correlations identified are between -0.40 – 0.40, and are therefore unlikely to be an issue.

5.3.1.2. Identification of critical time windows for fledging success response variables

Although all of the best candidate models for rainfall, dry days and minimum daily temperature identified to explain variation in proportional fledging success (Fig. 5.7) had AICc values lower than the baseline model (ΔAICc ≤ -2), randomisation analyses determined that they were likely false positives, therefore they could not be considered any further in analyses. In comparison, models testing different mean and maximum temperature signals performed better than the baseline models and these findings were supported by the randomisation analysis ($P_{\Delta AICc}$ ≤0.05). The best performing candidate model suggested that proportional fledging success was explained by the daily maximum temperature specified as a quadratic term (ΔAICc = 40.95) between nestling ages 4 and 13 days old (critical time window = 16 – 7 days prior to fledging date) (Fig. 5.7 and Appendix 6).

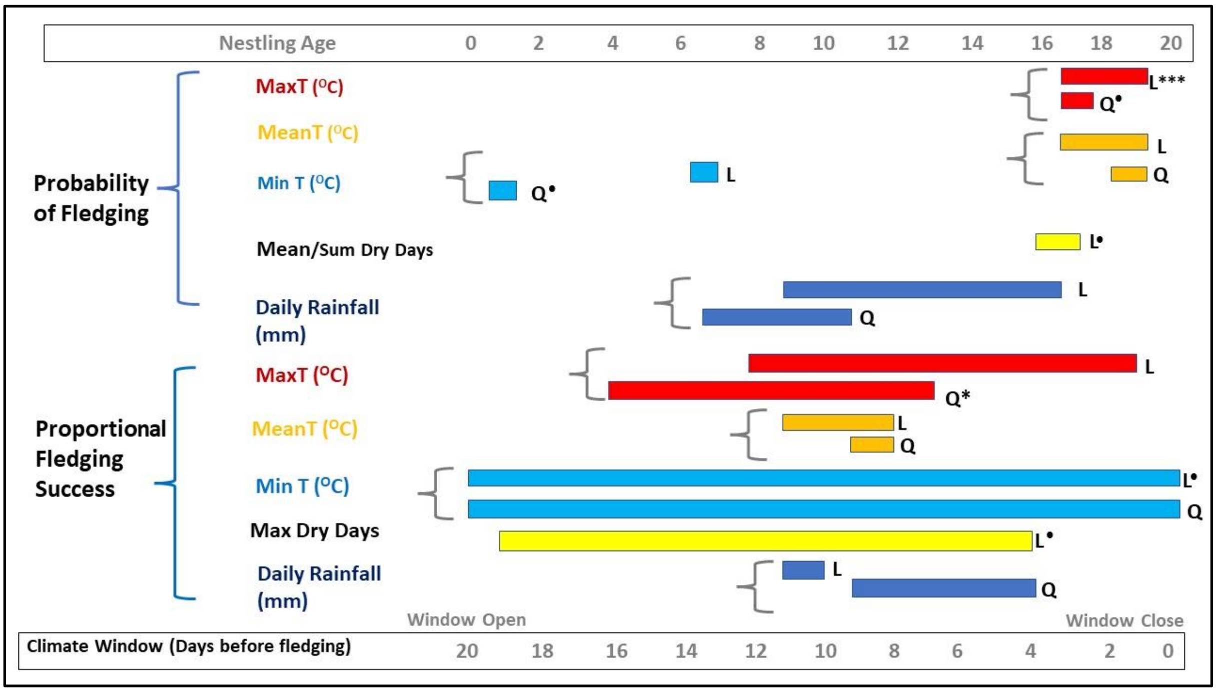


Figure 5.7. Representation of the best critical climate time windows for each weather variable tested for fledging success and probability of fledging success (binary success-failure) in a population of Blue Tits breeding across an urban gradient in Birmingham, UK from 2013 – 2018. Windows are in days relative to fledging date (day 0). For each breeding response variable the best windows were searched

for daily maximum temperature (MaxT), mean temperature (MeanT), minimum temperature (MinT), dry days and daily rainfall. The best critical climate windows are further split into the two functions: linear (L) and quadratic (Q). For each variable-function combination the most probable aggregate statistic is presented. Asterisks and dots show the probability of a model occurring by chance: significance codes ($P_{\Delta AICc}$) ≤0.001 (***), ≤0.01 (**), ≤0.05 (*), borderline (•).

The best model candidates for the probability of fledging success (Fig. 5.7) which included minimum temperature, daily rainfall and dry day weather signals also likely occurred due to chance ($P_{\Delta AICc}$ ≥0.05). Several mean and maximum temperature candidate models were identified from the initial *climwin* analysis, with the majority suggesting a critical time window 3 -1 days prior to fledge date (Fig. 5.7 and Appendix 6). However, randomisation analyses confirmed that only one of the models was unlikely to have occurred by chance ($P_{\Delta AICc}$ ≤0.001). This model, which also had one of the lowest AICc scores (ΔAICc = -106.04) suggested that the daily maximum temperature in the 1-3 days prior to estimated fledging age (20 days post hatch) had the most significant influence on the probability of a nest fledging at least one young. As such only this climate signal was considered for further analysis.

5.3.1.3. Identification of critical time windows for nestling weight

For the analysis of nestling weight using the full (six years) dataset, the best candidate models (Fig. 5.8) identified for mean and maximum daily temperature, daily rainfall, and dry days had lower AICc values than the baseline model (ΔAICc ≤ -2) (Appendix 6).

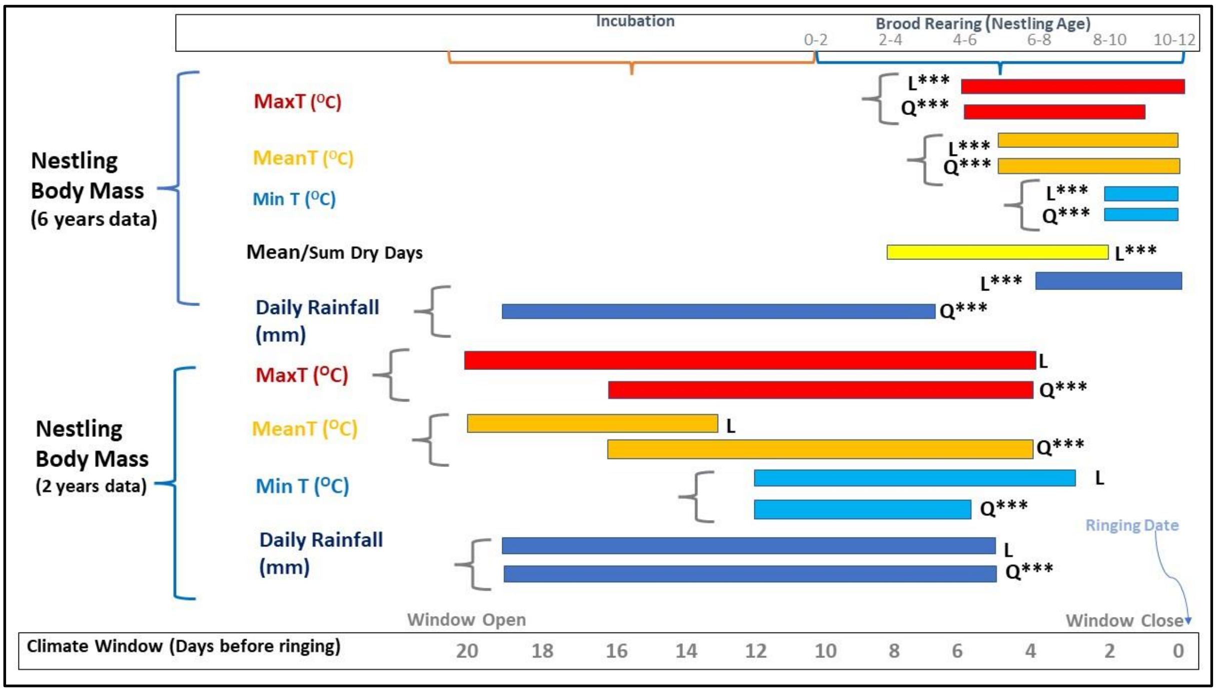
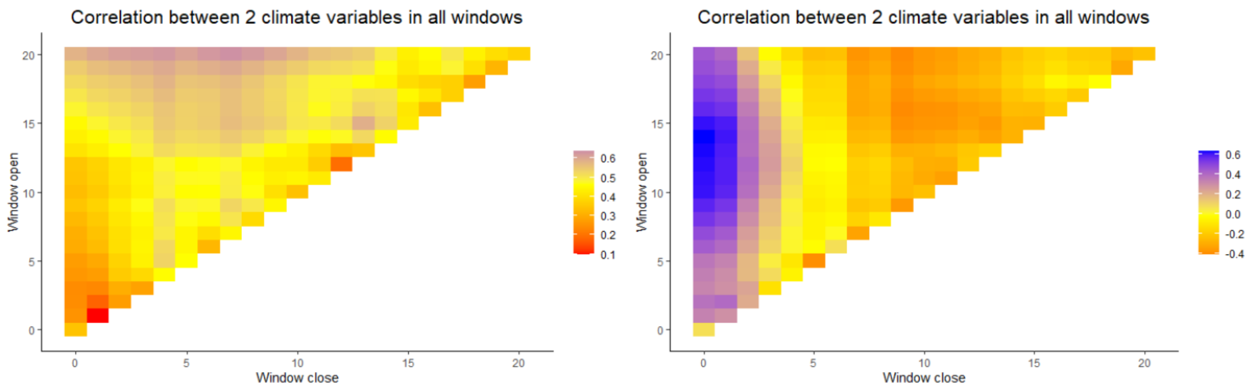


Figure 5.8. Representation of the best critical climate time windows for each weather variable tested for nestling weight in a population of Blue Tits breeding across an urban gradient in Birmingham, UK from 2013 – 2018. Windows are in days relative to ringing date at ages 10-12 (day 0). For each breeding response variable the best windows were searched for daily maximum temperature (MaxT), mean temperature (MeanT), minimum temperature (MinT), dry days and daily rainfall. The best critical climate windows are further split into the two functions: linear (L) and quadratic (Q). For each variable-function combination the most probable aggregate statistic is presented. Asterisks and dots show the probability of a model occurring by chance: significance codes ($P_{\Delta AICc}$) ≤0.001 (***), ≤0.01 (**), ≤0.05 (*), borderline (•).

Comparisons of the different mean and maximum temperature signals revealed a lot of overlap in the critical time windows identified and confirmed that models including a quadratic rather than a linear function overall performed better. Randomisation analyses also confirmed that for the majority of the models which included one of these weather signals, findings likely did not occur by chance ($P_{\Delta AICc}$ ≤0.001). Final model selection was therefore, undertaken by ranking the models on the basis of their AICc values. The best model had an ΔAICc value of -162.74 and included the maximum temperature variable (aggregate statistic = mean or sum, function = quadratic) with a window range of 6 – 1 days (relative to ringing date between nestling ages 10-12 days).

Comparisons of ΔAICc values for the mean, maximum and sum rainfall models identified a clear best candidate model (ΔAICc = -118.82), which was confirmed as being significantly different from the randomised models ($P_{\Delta AICc}$ ≤0.001), and therefore unlikely to have occurred by chance. This model, which also included a quadratic term, suggested that nestling weight was most likely explained by the total (sum) rainfall recorded within a critical time window 19 - 7 days before nestlings reached ringing age. Nestling weight was the only response variable in which a significant critical climate window was identified for the dry days variable. Both the total number and proportion of dry days occurring within the critical time window 8 - 2 days relative to nestling ringing date were identified as potential weather signals. In comparison to the critical window for rainfall, this window is narrower and has a shorter lag time.

Considering the potential for significant correlation between the three climate signals, tests for collinearity between each pair of variables were performed using the *crosswin* function in *climwin.* Visual inspection of the plots determined that the potential for collinearity issues was lower between maximum temperature and dry days compared with rainfall, with the correlation values <0.5 in the critical time windows of interest (Fig. 5.9).



(a) Correlation between the total number of dry days and the (mean) maximum daily temperature (°C)

(b) Correlation between the maximum rainfall and (mean) maximum temperature (°C)

Figure 5.9. Plot of the output from the test of collinearity between the maximum temperature (mean, linear) and **(a)** total dry days (sum,linear) and **(b)** maximum daily rainfall (max, quadratic) climate signals using the *crosswin* function from the *climwin* package. The correlation value (represented by the different colours) between each pair of variables was searched for all potential time windows (range = 40 days, reference day = June 4th).

This was confirmed by further checks for co-correlation issues using a correlation matrix for pairwise comparisons between environment and climate predictor variables to be included in the final global model in the final step of analysis.

The strongest candidate models for explaining variation in nestling weight using the two-year subset analysis, included the mean temperature (aggregate statistic = mean, function = quad), maximum temperature (aggregate statistic = mean, function = quad), and minimum temperature (aggregate statistic = mean, function = quad). All three final candidate models were investigated further and were found not to have occurred by chance ($P_{\Delta AICc}$ ≤0.001). However, visual inspection of the associated distribution of ΔAICc values, model coefficient plots and best model outputs suggested that the signal for maximum temperature was stronger compared with the other two temperature variables. The critical time window identified for maximum temperature was 16 – 4 days before ringing date. A clear best candidate model for rainfall (mean rainfall = ΔAICc -202.16), was also identified which was found to be significantly different from the randomised weather data models. The critical time window for this model was 19 – 5 days relative to ringing date and included a quadratic term.

5.3.2. The effects of temperature and rainfall on hatching success

The initial results from exploratory critical climate window analyses suggest that temperature and rainfall did not significantly affect the probability of hatching success in the Birmingham Blue Tit nestbox population, and therefore weather is potentially not a significant predictor of breeding failure during the incubation phase. In contrast, the average maximum temperature experienced in the days immediately preceding hatching (critical time window days 3 – 1 relative to hatching date) and the longer lag-effect of mean rainfall during the period 31 – 22 days prior to hatching were both found to significantly influence rates of hatching success, with these effects remaining when modelled together with habitat and landscape terms (step 5; Table 5.3).

Table 5.3. Model summary from a GLMM analysis of proportional hatching success for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against habitat, landscape and weather covariates. Weather signals include maximum daily temperature (window open = day 3, window close = day 1) and mean rainfall (window open = day 31, window close = day 22 relative to hatch date). The urban gradient was specified using the categorical metric. ULC gradient intercept = ULC1 (suburban sites). Intercept Year = 2013. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). '-' values denote covariates initially included in models but subsequently removed.

Proportional Hatching Success **n= 662**					
Fixed Term	**Coefficient**	**±SE**	**z value**	**Confidence Intervals** **(2.5%)**	 **(97.5%)**
Intercept	3.272	0.249	13.149		
Me NDB Trees	**0.316**	**0.103**	**3.062****	**0.113**	**0.520**
Inverse Simpson's Index	0.130	0.096	1.352	-0.059	0.319
Me Edge Distance (m^2)	**-0.467**	**0.142**	**-3.273****	**-0.754**	**-0.190**
ULC Model: ULC 2	**-1.093**	**0.439**	**-2.491***	**-1.967**	**-0.234**
ULC3	-0.421	0.277	-1.522	-0.972	0.122
ULC4	**-0.711**	**0.329**	**-2.164***	**-1.360**	**-0.062**
ULC5	-0.228	0.360	-0.633	-0.937	0.485
Garden Landcover (%)	**0.394**	**0.166**	**2.372***	**0.070**	**0.725**
Average MaxT (^{O}C)	**-0.174**	**0.074**	**-2.359***	**-0.319**	**-0.030**
Average Rainfall (mm)	**-0,240**	**0.067**	**-3.580*****	**-0.372**	**-0.109**
Random Terms	**Coefficient**	**±SD**			
Site ID	-	-	-		
Nestbox ID	0.639	0.780			
Year (fixed factor)	0.057	0.239			

The quadratic term for temperature was dropped from the model and replaced with the linear maximum temperature covariate as it was found to be non-significant.

Model predictions revealed a significant reduction in the proportion of eggs successfully hatching as the average maximum temperature increased in the days just before hatching (β ± SE = -0.174 ± 0.074, z = -2.359, *P* ≤0.018). Despite the longer lag-time between the climate signal and biological response, mean rainfall was observed to have a slightly stronger effect on hatching success (β ± SE = -0.240 ± 0.067, z = -3.580, *P* ≤0.001). Higher mean rainfall during this period, which approximately corresponds with the prelaying period, including nest building and early egg laying, was associated with lower hatching rates. Overall, however, hatching rates remained relatively high regardless of the amount of rainfall recorded, with model predictions showing a decline in the proportion of young hatched from 0.95 ± 0.5 under dry conditions (0 – 0.5 mm of rainfall) to 0.8 ± 1.5 for the highest mean rainfall amounts (≥3.5 mm) (Fig. 5.10).

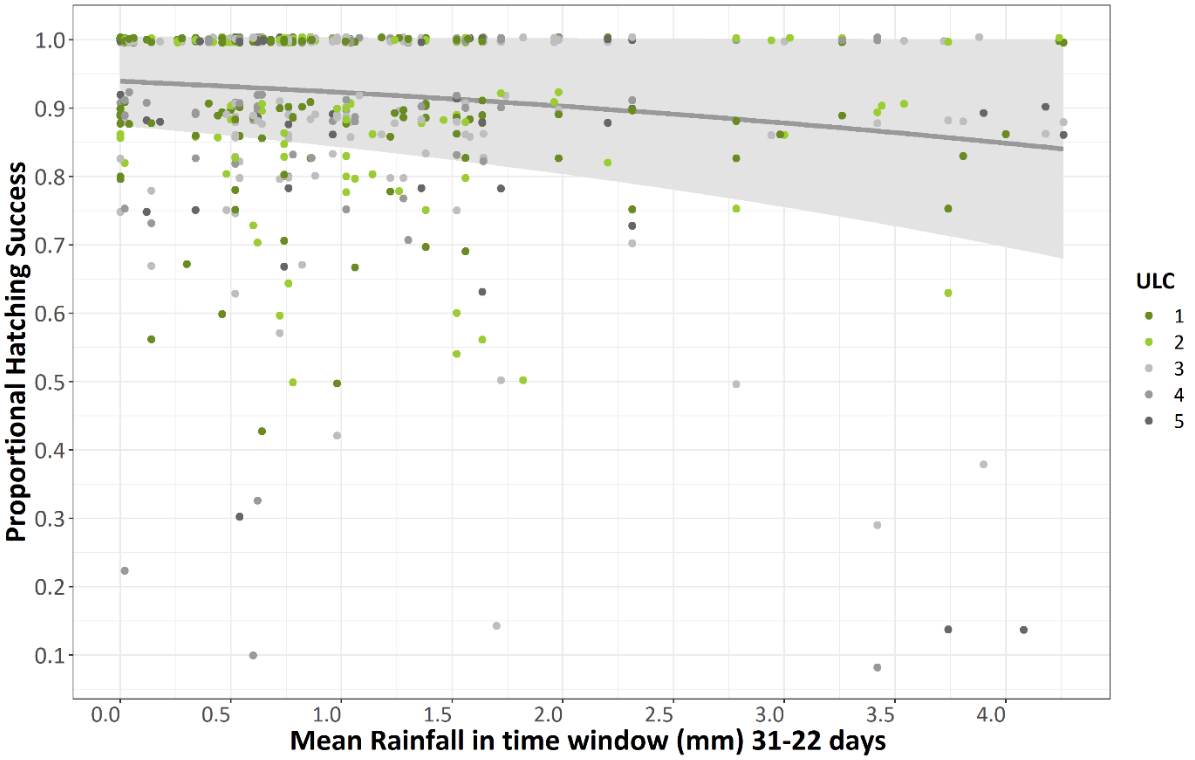


Figure 5.10. The relationship between mean daily rainfall recorded in the period 31 - 22 days prior to hatching date and rates of hatching success for Blue Tits breeding across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points categorised by urban land class (ULC). ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = binomial) in glmmTMB and using the *predicts* function in R. (n = 662).

Although no significant interactive effect between the urban gradient and rainfall was detected, the negative impact of mean rainfall appears to potentially be partially driven by poor hatching success for a small cluster of breeding attempts recorded in highly urbanised sites (ULC4-5), with hatching dates between the 7th – 10th May 2016. The corresponding critical time window (approximately the first two weeks of April) coincides with a period of high rainfall including an intense rainfall event (daily total rainfall = 19mm) on 11/04/2016. The highest mean rainfall (≥3.9 mm) calculated from individual critical time windows for each breeding attempt, was consistently found to coincide with broods hatching between 18th and 21st May 2014. This timeframe also corresponds with a period of consecutive days with moderate to high rainfall (approx. 20/04/2014 – 28/04/2014), including a day of exceptionally high rainfall (daily total precipitation = 23mm) on the 25th April. However out of nine breeding records for this hatching period, only one nest suffered particularly low hatching success (HAN63: hatching rate = 0.38).

5.3.3. The effects of temperature and rainfall on fledging success

The significant non-linear effect of maximum temperature on fledging success detected from the climwin analysis remained when included in the final hierarchical model (Table 5.4). The critical time window for this weather signal opened at 16 days and closed 7 days prior to fledging date for each brood. This finding suggests that the maximum temperature during the brood rearing period equating to nestling ages ~4 – 13 days (post hatch) significantly impacted chick survival and therefore consequently fledging success.

The model revealed a strong non-linear effect of maximum temperature on fledging success (quadratic term: $\beta \pm SE = -0.180 \pm 0.054$, $z = -3.351$, $P \leq 0.001$, Table 5.4 and Fig. 5.9). Model predictions suggest that broods initially benefited from higher temperatures during the chick-rearing phase, with fledging success increasing from ~0.7 ± 0.2 when maximum temperatures were lower (~ 16^{o}C) to a peak of 0.85 ± 0.1 at ~21.5 ^{o}C . However, once maximum temperatures reached this threshold, any further increase in temperature was predicted to result in reduced fledging success. Moreover, a significant interactive effect between the urban gradient and the maximum temperature signal was detected, thus implying that the potentially negative impacts of higher maximum temperatures may be exacerbated in more densely urbanised areas of the city.

Table 5.4. Model summary from a GLMM analysis of proportional fledging success for Blue Tits breeding along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against habitat, landscape and weather covariates. Weather signals include linear and quadratic terms for maximum daily temperature (window open = day 16, window close = day 7 relative to estimated fledging date). The urban gradient was specified using the linear (%BLC) metric. Intercept Year = 2013. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero).

Proportional Fledging Success **n = 554**					
Fixed Term	Coefficient	±SE	z value	Confidence Intervals	
				(2.5%)	(97.5%)
Intercept	2.053	0.221	9.277		
Me NDB Trees	-0.210	0.134	-1.560	-0.485	0.068
Inverse Simpson's Index	0.116	0.131	0.888	-0.141	0.392
Inverse Simpson's Index^2	**-0.216**	**0.070**	**-3.112****	**-0.361**	**-0.079**
Built Landcover (%)	**-0.302**	**0.156**	**-1.931•**	**-0.614**	**0.019**
Garden Landcover (%)	-0.182	0.126	-1.444	-0.436	0.078
MaxT (^{O}C)	0.010	0.065	1.521	-0.028	0.229
MaxT (^{O}C)^2	**-0.180**	**0.054**	**-3.351*****	**-0.286**	**-0.075**
Built * MaxT	**0.128**	**0.047**	**2.716****	**0.036**	**0.221**
April Hatching Date	**-0.459**	**0.087**	**-5.283*****	**-0.630**	**-0.292**
Occupancy	-0.124	0.090	-1.388	-0.299	0.052
Random Terms	**Coefficient**	**±SD**			
Box: Site ID	0.814	0.902			
Site ID	0.208	0.456			
Year (fixed factor)	0.141	0.375			

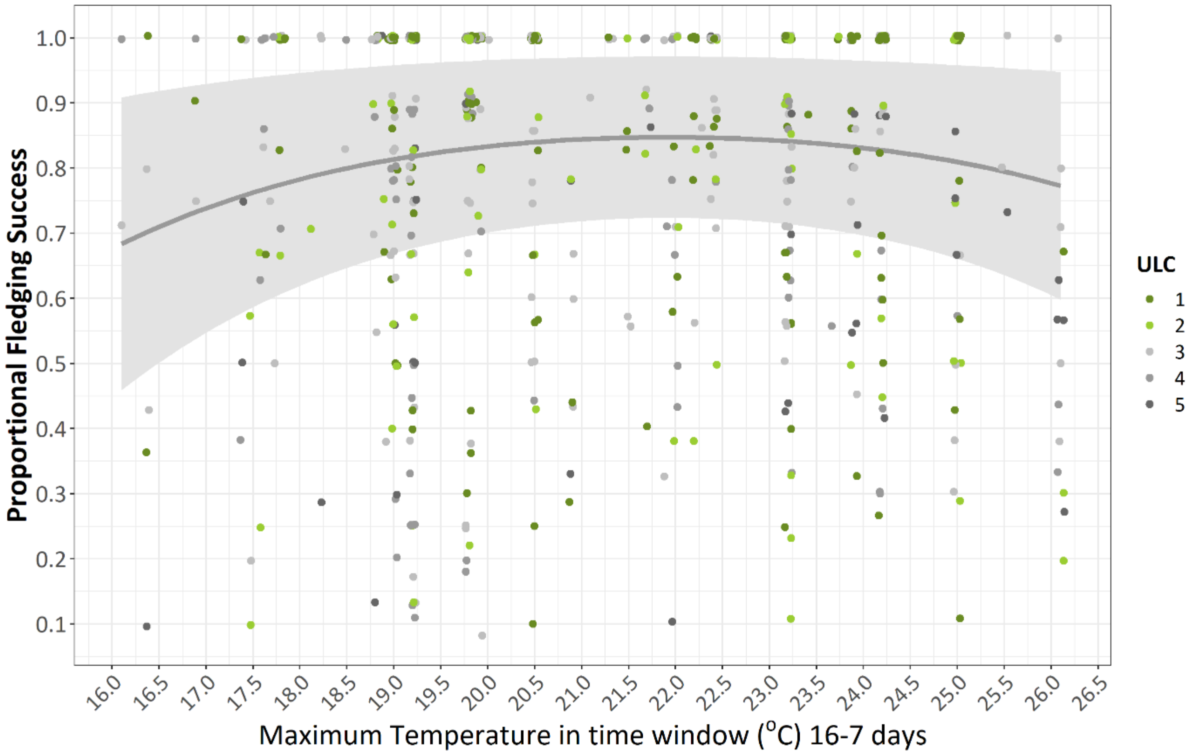


Figure 5.11. The relationship between maximum temperature during the critical climate window 16-7 days prior to fledging date and rates of fledging success for Blue Tits breeding across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points categorised by urban land class (ULC). ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = binomial) in glmmTMB and using the *predicts* function in R. (n = 554).

The probability of fledging success was best explained by the maximum temperature during the critical climate window 3 – 1 days prior to fledging, with the final model predicting a higher probability of nesting failure with increasing maximum temperature. However, the majority of breeding failures in this population was previously shown in Chapters 3 and 4 to occur during early brood-rearing, therefore it is likely that this finding is an artefact of the analytical process, in particular the dummy fledging date used to determine the predicted date that nestlings should have fledged in failed nests. Considering the biological uncertainty with this finding this potential climate effect was not considered further.

5.3.4. The effects of temperature and rainfall on nestling weight

Analysis of the maximum temperature and dry days in the global hierarchical model confirmed the strength and direction of the effects of these weather signals on nestling body mass that were detected from the *climwin* analysis (Table 5.5).

Table 5.5. Model summary from a GLMM analysis of mean body mass for Blue Tit nestlings reared along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against habitat, landscape and weather covariates. Weather signals include maximum daily temperature (window open = day 6, window close = day 0 relative to ringing date) and dry days (window open = day 8, window close = day 2 relative to ringing date). The urban gradient was specified using the linear (%BLC) metric. Intercept Year = 2013. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). • indicates a borderline sig effect (CIs crossed zero).

Nestling body mass (6 years: n = 3129)					
Fixed Term	**Coefficient**	**±SE**	**z value**	**Confidence Intervals**	
				(2.5%)	**(97.5%)**
Intercept	65.23	73.90			
Inverse Simpson's Index	0.072	0.056	**1.286**	-0.038	0.182
Inverse Simpson's Index^2	**-0.119**	**0.036**	**-3.273****	**-0.190**	**-0.047**
Built Landcover (%)	**-0.198**	**0.061**	**-3.247****	**-0.318**	**-0.078**
MaxT (^{O}C)	**0.309**	**0.069**	**4.484*****	**0.174**	**0.445**
Proportion Dry Days	**0.168**	**0.059**	**2.868****	**0.053**	**0.283**
Dry Days * MaxT	**0.218**	**0.066**	**3.288****	**0.088**	**0.349**
Occupancy	-0.107	0.058	-1.839•	-0.221	0.007
Brood Size	**-0.107**	**0.051**	**-2.092***	**-0.207**	**-0.007**
Ringing Age	**0.295**	**0.052**	**5.615*****	**0.192**	**0.398**
April Hatching Date	**-0.229**	**0.057**	**-3.997*****	**-0.342**	**-0.117**
Year (factor)	-.0.028	0.037	0.883	-0.010	0.044
Random Terms	**Coefficient**	**±SD**			
Nest ID	1.036	1.02			
Residual	0.910	0.954			

The final global model revealed a strong positive effect of both the maximum temperature (Fig. 5.12) in the six days prior to ringing date and the proportion of dry days in the period 8 – 2 days prior to ringing date on nestling body mass. Whilst no significant interactive effect of either covariate with the urban gradient was detected, a strong interactive effect between the two weather variables was revealed (β ± SE = 0.218 ± 0.066, z = -3.288, *P* ≤0.001, Table 5.5).

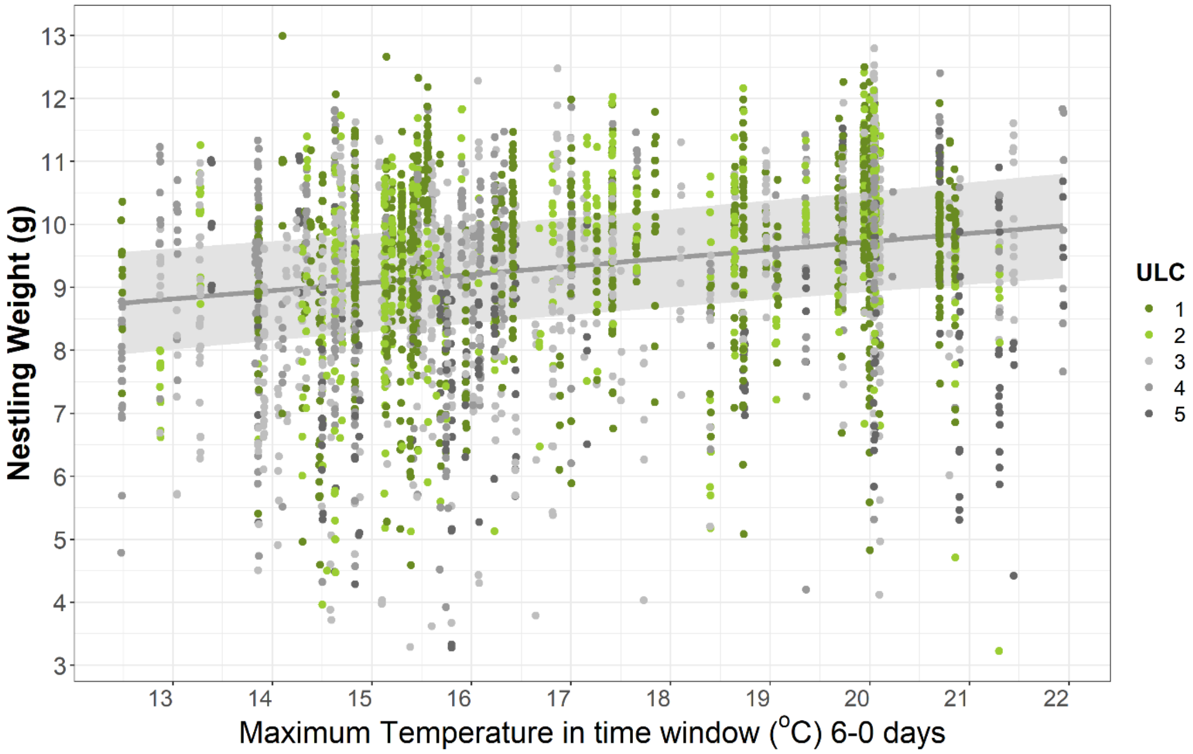


Figure 5.12. The relationship between maximum temperature during the critical climate window 6 - 0 days prior to ringing date and body mass for Blue Tit nestlings reared across 28 sites along an urban gradient in Birmingham, UK over six breeding seasons (2013-2018). Raw data are represented by coloured points categorised by urban land class (ULC). ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = binomial) in glmmTMB and using the *predicts* function in R. (n = 3129).

Similarly, the linear positive effect of maximum temperature in the 16 – 4 day critical window and the non-linear effect of mean rainfall in the period 19 – 5 days prior to ringing date on nestling body mass detected from the *climwin* analysis of the 2-year subset of data were both further confirmed when analysed in the global hierarchical model (Table 5.6).

Table 5.6. Model summary from a GLMM analysis of body mass for Blue Tit nestlings reared along an urban gradient in the city of Birmingham, UK between 2013-2018 regressed against habitat, landscape and weather covariates. Weather signals include maximum daily temperature (window open = day 16, window close = day 4 relative to ringing date) and mean daily rainfall (window open = day 19, window close = day 5 relative to ringing date). The urban gradient was specified using the linear (%BLC) metric. Intercept Year = 2013. All significant slopes (using CIs) are indicated in bold (significance codes: *P* ≤0.001***, ≤0.01**, ≤0.05*). $^{\bullet}$ indicates a borderline sig effect (CIs crossed zero).

Nestling body mass **(2 years: n = 1133)**					
Fixed Term	Coefficient	±SE	z value	Confidence Intervals (2.5%)	(97.5%)
Intercept	-401.384	357.880	-1.122		
Inverse Simpson's Index	0.232	0.127	1.832$^{\bullet}$	-0.0323	0.483
Inverse Simpson's Index^2	**-0.188**	**0.070**	**-2.671****	**-0.0329**	**-0.044**
Built Landcover (%)	-0.103	0.128	-0.802	-0.033	-0.044
MaxT (^{O}C) 6-0 days	**0.265**	**0.128**	**2.077***	**0.0179**	**0.519**
Mean Rainfall Days 19 –5 days	**-0.767**	**0.095**	**-8.087*****	**-0.954**	**-0.581**
Mean Rainfall Days 19 –5 days^2	**0.132**	**0.020**	**6.559*****	**0.093**	**0.172**
Brood Size	-0.380	0.042	-9.029***	-0.462	-0.297
Ringing Age	0.418	0.039	10.746***	0.341	0.494
April Hatching Date	-0.021	0.0916	-0.231	-0.202	0.157
Year (factor)	-.0.028	0.037	0.883	-1.446	0.551
Random Terms	**Coefficient**	**±SD**			
Site ID	0.295	0.543			
Residual	1.358	1.165			

Both critical time windows span a wider timeframe, encompassing both the late stage of incubation as well as the early development phase of nestlings, in comparison to the critical windows detected for maximum temperature and dry days using the full dataset. Increasing rainfall during the critical time window, initially had a strong negative impact on nestling body mass (β ± SE = -0.767 ± 0.095, z = -8.087, *P* ≤0.001; Fig. 5.13 and Table 5.6). However the model detected a threshold (~6mm), at which point higher mean daily rainfall had a positive effect on nestling body mass (β ± SE = 0.132 ± 0.020, z = -6.559, ≤0.001).

In contrast to the full dataset model, the two-year subset model did not detect any interactive effects, either between the climate variables and the urban gradient or with each other.

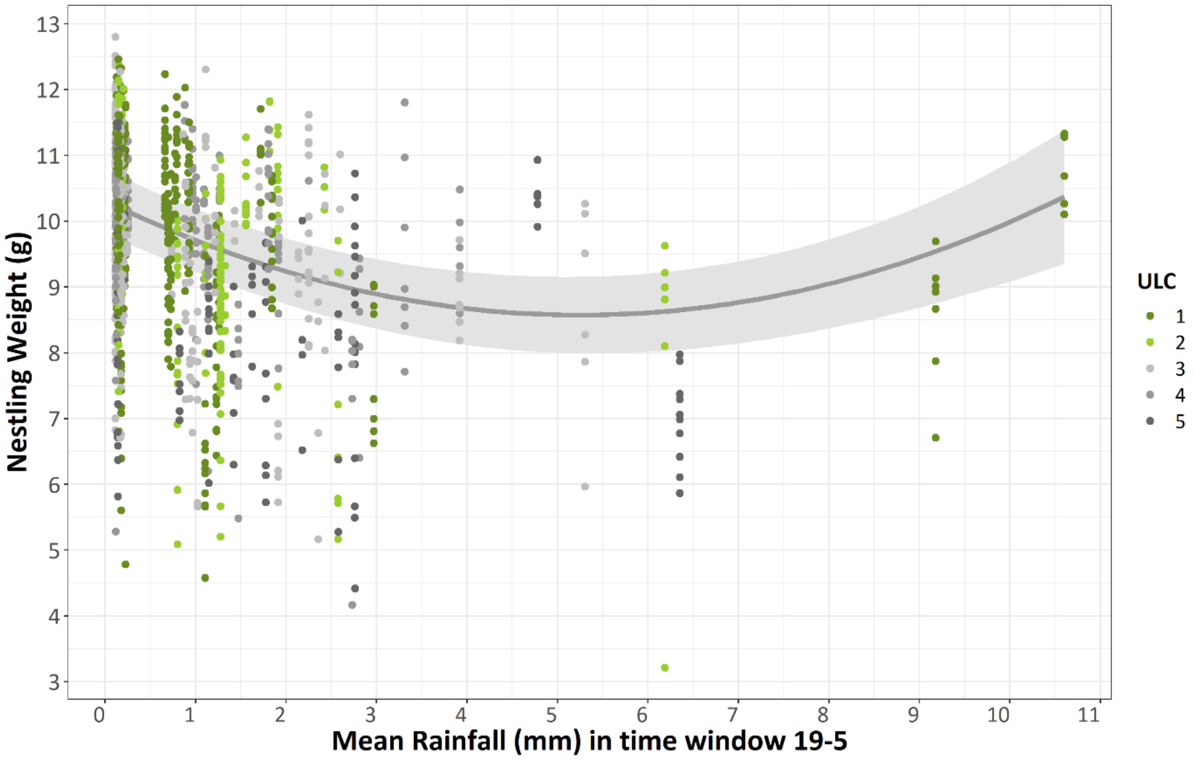


Figure 5.13. The relationship between mean daily rainfall during the critical climate window 19-5 days prior to ringing date and body mass for Blue Tit nestlings reared across 28 sites along an urban gradient in Birmingham, UK using the two years of subset data (2017-2018). Raw data are represented by coloured points categorised by urban land class (ULC). ULC1 (dark green points) = least urbanised (suburban) sites, ULC5 (dark grey) = most densely urbanised sites. The solid line is the prediction curve (and grey ribbons the 95% CIs) calculated from a generalised linear mixed model (family = binomial) in glmmTMB and using the *predicts* function in R. (n = 1133).

5.4. DISCUSSION

In this chapter I focused on how short-term variation in weather during the breeding season affects several key reproductive responses that occur after initial reproductive decisions have been made, and that may in turn impact the overall reproductive success in a population of Blue Tits nesting along an urban gradient in the city of Birmingham, UK. More specifically the potential downstream and immediate impacts of both temperature and rainfall on hatching success, fledging success, nestling body weight and the probability of total failure during both the pre-hatching (incubation) and brood-rearing phase were investigated. The study is exploratory in nature, with the main aim to identify the critical time periods and climate signals that drive variation in different breeding outcomes, and from which further hypotheses can be generated for testing in future research.

My results provide tentative evidence to suggest that at least some of the variation in breeding outcomes observed among the Blue Tit population may be correlated with prevailing weather conditions. Crucially, the main findings from these preliminary analyses suggest that variation in daily maximum temperatures, rather than mean or minimum temperatures, and the amount of rainfall both prior to and during the two reproductive stages investigated may impact breeding success. Moreover, increases in both maximum temperature and rainfall elicited negative responses in breeding traits, with the brood-rearing stage appearing the most susceptible to change in these weather signals. Overall, therefore, and as hypothesised, the brood-rearing stage appeared the most susceptible to short term variation in the weather. These results have important implications for the future reproductive success and overall fitness of this and other populations of urban-dwelling birds considering the dual impacts of higher temperatures associated with the urban heat island effect (Sumasgutner *et al.* 2020) and the intensity, frequency and duration of extreme weather events, in particular daily temperature and rainfall extremes, which are projected to increase as a result of climate change (Ummenhofer and Meehl 2017).

5.4.1 Weather effects pre – hatching

Variation in hatching success was partially explained by the maximum temperature recorded in the three days prior to hatching date (i.e. incubation) and to the mean amount of daily rainfall 31-22 days pre-hatch. Based on the mean clutch size (9 ± 1.8 eggs) and mean incubation period (15 ± 2.2 days), this latter timeframe corresponds with the nest-building and early egg laying phase (estimated as starting on average at 24 days pre-hatch for this population). Both maximum temperature and mean daily rainfall signals were negatively correlated with hatching success, intimating that weather may negatively affect the physiology of eggs and their survival to hatching both directly during incubation or indirectly prior to laying, for example via female behaviour (Marques-Santos *et al.* 2021).

The temperature of eggs during the incubation period is crucial for embryonic development and hatching success and exposure to either high or low temperatures outside of a narrow optimal window can be detrimental or even lethal (DuRant, *et al.* 2013; Vaugoyeau *et al.* 2017). For example, warmer temperatures during incubation were positively correlated with egg failure (the number of unviable or missing eggs) in a population of wild nesting Saffron Finches (*Sicalis flaveola*) breeding in sub-tropical Brazil (Marques-Santos *et al.* 2021). However, my study was conducted in a temperate climate where the maximum recorded temperatures for the critical climate window did not exceed 23.7^{o}C. This is lower than the optimal temperatures for embryonic development in passerines (36 - 40^{o}C; DuRant *et al.*

2013; Ospina *et al.* 2018) and also lower than the manipulated temperatures often used in experimental studies (e.g. Nord and Nilsson 2011, 2016). Furthermore, the negative effect of increasing maximum temperature observed here contrasts with the results from both observational (e.g. Pipoly *et al.* 2013) and experimental studies (e.g. Nilsson 2016; Vaugoyeau *et al.* 2017) which demonstrate that increasing air and nest temperatures during incubation generally confer fitness benefits on breeding success in passerines. Therefore, considering the correlative nature of this research it is difficult to determine the potential mechanisms that may drive this relationship.

The longer-lag effects of rainfall on hatching success in birds have been less well studied and are difficult to separate out from the effects of cold temperatures (Bordjan and Tome 2014). However, in studies where the negative effects of rainfall have been demonstrated, they are much more immediate and related to heavy or extreme rainfall events during the period of incubation itself. For example, extreme rainfall events during incubation led to greater nest abandonment and therefore higher rates of hatching failure in a population of Great Tits nesting in forest in Slovenia (Bordjan and Tome 2014). Here, failure was attributed to the trade-off in females between incubation and the extended periods required off the nest searching for food. In contrast, Higgott *et al.* (2020) found that whilst heavier rainfall was correlated with an increase in the length of the incubation period in Long-tailed Tits (*Aegithalos caudatus*) breeding in Sheffield, UK, variation in mean temperature and rainfall only had a marginal effect on hatching success.

To resolve these conflicting findings, further critical climate window analysis is required to disentangle the potential effects of weather signals prior to and during the incubation phase on hatching success. Furthermore, it would be beneficial to investigate incubation schedules and nest attendance patterns of females to determine their correlation with the urban gradient and weather changes (e.g. see Coe *et al.* 2015). However, it could be that the urban environment buffers the effects of lower minimum daily temperatures and heavy rainfall during incubation that have been shown to negatively impact breeding success in passerines nesting in more natural habitats. Similarly, the elevated temperatures within the city, associated with the urban heat island effect (Sumasgutner *et al.* 2020) could exacerbate the negative impacts of raised maximum temperatures leading to reduced hatching success in the Birmingham population.

5.4.2 Weather effects on nestling body mass and fledging success

Weather conditions during brood-rearing have been widely shown to play a crucial role in determining the growth and development of nestlings (Morganti *et al.* 2017). Weather may impact nestlings directly, for example through the influence of precipitation on thermoregulation (Schöll and Hille 2020) and temperature on growth and metabolism (Ospina *et al.* 2018), or indirectly by impacting foraging conditions including the availability of preferred natural food such as caterpillars or the foraging efficiency of parents (Mainwaring and Hartley 2016; Morganti *et al.*, 2017).

The analysis of nestling weight using the six years of data revealed that nestling body mass was higher when the proportion of dry days between hatching date and 10 days of age (taking into consideration the age range at ringing) increased. In contrast modelling of the two-years of spatialised climate data against nestling weight (2017-2018) revealed slightly different critical climate windows and climate signals. Hierarchical mixed modelling of the two-year data subset confirmed a significant non–linear effect of mean rainfall (window range = 19 – 5 days before ringing date) corresponding to a period encompassing the latter part of the incubation period and the early brood-rearing period. Visual inspection of the prediction curve (Fig. 5.13) revealed that increasing rainfall overall had a negative impact on nestling body mass. The positive effect of higher rainfall detected appeared to be driven by two late hatching broods (25th May and 4th June respectively) in Cannon Hill Park (a suburban site: ULC 1) in 2018. These two nests therefore may have decreased model fit when using the linear only term. As such the polynomial effect detected may be an artefact of the extrapolation of the model and therefore this result should be considered with caution. Supporting this, the best rainfall candidate model for the six years data found an unexpected linear positive effect of rainfall (window range 19 – 7 days prior to ringing date), which was confirmed as non-significant in subsequent hierarchical modelling. Consequently, future research from this study should revisit the potential impacts of increasing rainfall on nestling weight to tease out the potential for a linear negative rather than non-linear response as a result of potential outliers in the dataset: an issue that is likely to occur in studies of this type. In particular, this will be helped by the future addition of breeding and climate data as the Birmingham Blue Tit population continues to be monitored.

The negative effect of rainfall on nestling body mass is consistent with the findings of several other studies that have demonstrated the negative impacts of increasing rainfall on both nestling morphometrics and growth rates, as well as nestling survival (Öberg *et al.*, 2015; Capilla-Lasheras *et al*, 2021, except see Mainwaring and Hartley; Arct *et al.* 2022). Morganti *et al.* (2017) for example, showed that growth rates during the linear growth phase (4 – 8 days of age) of Blue Tits reared in a forest near Milan, Italy were lower on wet days compared with dry days. Similarly in a long-term study of Great Tits breeding in mixed deciduous woodland, Schöll and Hille (2020) found that heavy and persistent rainfall significantly reduced individual nestling survival, with knock on effects to brood reduction. Öberg *et al.*, (2015) demonstrated a negative correlation between the number of days with rainfall over 10mm and fledging success in a population of Northern Wheatears (*Oenanthe oenanthe*) breeding in farmland (Uppsala, Sweden).

Persistent and/or heavy rainfall can impact the growth and development of nestlings via a few different mechanisms. Heavy rainfall, particularly during the first few days after hatching when altricial nestlings are unable to maintain their own body temperature, may increase heat loss and therefore thermo-regulatory demands, with detrimental impacts to their continued growth and survival (Marques-Santos and Rodrigues 2021). The growth rate and weight of nestlings during early brood-rearing is also directly linked to parental foraging efficiency and therefore the availability of food (Naef-Daenzer and Keller, 1999; Naef-Daenzer *et al*. 2000). For example, Morganti *et al.* (2017) established that rainfall likely causes caterpillars to be knocked off from tree branches thus making them unavailable to foraging tits, thereby limiting the availability of prey and reducing foraging performance. In contrast, Mainwaring and Hartley, (2016) found a positive influence of moderate levels of rainfall, on a range of nestling body size characteristics and growth rates in Blue Tits reared in small patches of coniferous trees in Lancashire, UK. Of interest to my research, both Mainwaring and Hartle (2016) and Morganti *et al.* (2017) hypothesise that the variation detected in the effects of rainfall on nestling growth across this and other studies might be linked to the intensity of rainfall. Light rainfall, (≤13mm/day) as observed in the Mainwaring and Hartley (2016) study may through some as yet undetermined mechanism make caterpillars more available to foraging adults with positive benefits to nestling growth, whilst heavier, more intense periods of rainfall may confer the opposite effect. This hypothesis therefore could potentially explain the anomalous positive impact of higher mean daily rainfall on nestlings in the two late-hatching nests identified previously. However, further studies are required to determine more precisely how variations in rainfall impact the growth and weight of nestlings (Morganti *et al.* 2017). In particular, for my study population, continuing the collection of spatialised climate data will help to better elucidate the impacts of rainfall intensity and temperature at the site-level on nestling body mass. It would also be beneficial to increase the temporal resolution of breeding data collection (e.g. collecting nestling morphometrics over multiple visits prior to fledging) in order that variation in the growth trajectories of nestlings across the urban gradient can be determined.

In contrast to other studies investigating the impacts of climate on breeding in passerines (e.g. Marques-Santos *et al.* 2020), preliminary analyses failed to detect a significant effect of rainfall on either fledging success or the probability of nest failure. However, most previous research has been conducted in more natural deciduous forested habitats, therefore the absence of a significant rainfall signal could potentially highlight a buffering effect of the urban gradient: a phenomena that has been previously reported. For example in a study investigating the combined impacts of urbanisation and weather on breeding success in Peregrine Falcons (*Falco peregrinus*) in Cape Town, South Africa, Sumasgutner *et al.* (2020) demonstrated that more urbanised nests may be buffered against the impacts of cold and wet weather conditions resulting in reduced nesting failure. Furthermore, Whitehouse *et al.*, (2013) reported that Blue and Great Tits breeding in riparian and urban habitats in Cambridge, UK, appeared relatively less vulnerable to the impacts of an extreme cold wet event experienced during the 2017 breeding season, compared with their conspecifics breeding in deciduous woodland.

Consequently, the potential for this type of buffering effect deserves further attention in this study system.

Using the full six year dataset, a positive correlation between nestling weight and the mean maximum temperature between nestling ages 2 and 12 was predicted. Correspondingly, nestling weight in the two-year subset model was positively correlated with higher maximum temperatures, although the critical window was slightly wider, spanning a period that included the final week of incubation and early – brood rearing up to approximately 8 days of age.

The finding that higher maximum temperatures, during early development (including the linear growth phase) aligns with the results from a number of different observational (e.g. (Ambrosini *et al.* 2006; Arct *et al.* 2022) and experimental studies (Dawson *et al.* 2005; Rodríguez *et al.* 2016b except see Rodriguez et al. 2016a) that have established a positive correlation between increasing ambient and nest temperatures and the growth and body mass of altricial nestlings. Of particular relevance to this study, Marques-Santos and Dingemanse (2020) determined that the body mass of Great Tit nestlings at 14 days of age was positively related to the maximum temperatures experienced during a critical time window corresponding to ages 4-8 days post-hatch.

Whilst increasing maximum temperatures during early brood-rearing positively influenced nestling weight, the non-linear effect of maximum temperature on fledging success suggests that nestlings are sensitive to variation in high temperatures and that this can have a knock-on effect to their ultimate survival. In particular my results tentatively suggest a tipping point beyond which increased maximum temperatures lead to higher rates of nestling loss and reduced fledging success. Furthermore, there is evidence from this analysis to suggest that the influence of increasing maximum temperatures on fledging may further be exacerbated by the urban gradient.

Blue and Great Tit nestlings are unable to thermoregulate until they are approximately 9 – 11 days old (Mertens 1977; Ardia 2005; Dawson *et al.* 2005). Therefore during the earliest stages of development they are particularly vulnerable to adverse environmental conditions including suboptimal temperatures, which may lead to impaired growth and lower survival prospects (Salaberria *et al.* 2014; Arct *et al.* 2022). Moreover, females only intensively brood young during the first three days post-hatch (Sanz and Tinbergen 1999), at which point the nutritional demands of young increase and females spend progressively more time foraging and therefore away from the nest (Mainwaring and Hartley 2016; Arct *et al.* 2022). In my study, the opening of the critical maximum temperature window at day 16 (i.e. nestling ages 4-5 days) approximates the period (ages 3-6 days) when female brooding is known to rapidly decrease (Sanz and Tinbergen 1999) and therefore nestlings may be more vulnerable to weather-related stress. Under conditions of heat stress nestlings may have to trade-off limited energy resources between maintaining body temperature below potentially damaging levels and investment in development and growth (Andreasson *et al.* 2018, 2020). Although a different climate signal to this study, Marques-Santos and Dingemanse (2020) similarly hypothesised that the observed negative relationship between fledging success and minimum temperatures between 6 – 23 days in their Great Tit population may in part be attributable to the susceptibility of nestlings to cold stress in a forest environment during this same period.

Supporting the results from this study, Ardia (2013) reported reduced fledging success of Tree Swallows (*Tachycineta bicolor*) in nests that were exposed to high daytime temperatures, whilst Rodriguez *et al.* (2016) demonstrated that Great Tit nestlings subjected to artificial heating during early development had a lower estimated survival rate post-fledging.

5.5. CONCLUSIONS

In this chapter I used a sliding window analysis to identify the critical time windows of temperature and rainfall signals that are most likely to impact breeding success in an urban Blue Tit population. As other studies have previously shown (e.g. Marques-Santos *et al.* 2021; Sauve *et al.*, 2021a, 2021b), my study confirmed that variation in weather conditions prior to and during the breeding season have complex downstream effects on breeding traits, with both positive and negative impacts detected during the two phases of the reproductive cycle explored. Notwithstanding, my results provide evidence to suggest that while variation in rainfall and maximum temperatures influenced both pre-hatching and brood rearing outcomes, nestlings were particularly vulnerable to changes in weather during early development.

Overall, my findings corroborate the available literature, and suggest that periods of warmer and drier weather during the later stages of incubation and early brood rearing have a positive downstream impact on both nestling body mass and fledging success. However, temperatures may threshold at an upper limit during this period at which point fledging success is reduced. Together with the finding that higher maximum temperatures earlier in the breeding season also lead to decreased hatching success, an important, albeit tentative, outcome of this exploratory work, therefore, is that the Birmingham Blue Tit population may be more vulnerable to extremes of heat. I hypothesise that the lack of an equivalent effect of extreme minimum temperatures indicates that the urban environment may buffer the effects of variation and extremes in cold temperatures on breeding attempts, a finding that was also reported for urban breeding Peregrine Falcons (Sumasgutner *et al.* 2020).

Chapter Six

Summary and Conclusions

One of the overarching aims of this thesis was to incorporate a comprehensive, field and analytical approach to investigate the current impacts of urbanisation and weather on a population of Blue Tits (*Cyanistes caeruleus*) breeding in a highly urbanised environment (i.e. the city of Birmingham, UK) in order to begin to disentangle how the potentially complex interactions operating between these two abiotic factors shape breeding success. A key element of this study was the incorporation of a fine-scale quantitative urban gradient, which enabled the complexity of the urban landscape and variation in weather effects at a high spatial resolution to be explored.

The key objectives as laid out in the General Introduction (Chapter 1) were accomplished through an intensive six-year field work campaign carried out by Dan Hunt (2013 – 2015) and the author (2016 – 2018) for the collection of breeding data, investigative analytical techniques incorporating hierarchical mixed modelling and critical climate window analysis and finally the reporting of the approaches used and associated findings (Chapters 2 – 5).

Here I briefly evaluate the significance of the findings presented throughout the thesis according to the main themes of the research, which consider:

- The importance and relevance of the methodological approaches used and the value of this study as an example of incorporating robust analytical tools in the investigation of human-mediated environmental change on breeding in birds.
- The biological interpretation and significance of the findings relating to the effects of urbanisation and weather and their potential for interactive effects on breeding success in the Birmingham Blue Tit population.
- I consider the implications of the findings from my study in the wider context of the effects of urbanisation and climate change on breeding in birds at the national and global scale. This is followed by a discussion of the limitations of the study and suggestions for future research.

6.1. The effects of urbanisation on breeding success

To my knowledge, this is the first time that a study has explicitly investigated the effects of urbanisation within a hierarchical modelling framework and simultaneously directly compared quantitative and categorical urban gradient metrics at a high spatial resolution across such a highly urbanised gradient.

Notably, the findings of this research align with those reported from a growing suite of more recent studies that have also employed spatially-nested sampling designs, albeit these have primarily focused on urbanisation effects at broader spatial-scales and/or have investigated different ecological, demographic or life-history traits (e.g. Hedblom and Söderström 2012; Concepción *et al.*, 2015; Glądalski et al., 2017; Sprau et al. 2017; Merckx et al., 2018; Seress et al. 2018; de Satgé et al. 2019; Wawrzyniak et al. 2020 except see Corsini *et al*. 2017; 2021).

Therefore, whilst the results from this study complement findings from previous research they also provide a novel contribution, in demonstrating that across short fine-scale urban gradients, breeding is also impacted by a number of interlinked processes and effects operating at different spatial-scales. Thus providing further support for the call to consider environmental impacts of urbanisation at multiple spatial-scales and incorporate hierarchical modelling as a more reliable and robust tool in future urban ecological research (Hostetler, 2001; Clergeau *et al.*, 2006; Goddard *et al*., 2010; Moll *et al.,* 2019). Finally, these results also further substantiate how the appropriate quantification of urbanisation can influence the predictive ability of models and consequently the statistical inference of urban environmental effects (e.g. see also Satgé *et al.*, 2019; Strubbe *et al.*, 2020; Corsini *et al.*, 2021).

Overall, the results from my study suggest that, at least across a short and fine-scale spatial-resolution, the quantitative metric is a much more reliable and sensitive indicator of the effects of urbanisation on measures of breeding success across two key phases of the breeding cycle (laying and hatching, and brood rearing), compared with the categorical approach tested. In particular, the results highlight that this may be key in the detection of the more nuanced non-linear impacts of urbanisation, and for identifying potential variation in the strength and direction of breeding traits across different phases of the reproductive cycle, as well as additive or synergistic effects across multiple spatial scales.

Overall, the evidence presented from the urban research supports the hypothesis that reduced breeding success within this Blue Tit population is primarily driven by higher rates of brood reduction and complete reproductive failure, resulting in fewer nestlings surviving to fledging. In particular, the early developmental stage of nestlings appeared to be the most sensitive phase of the breeding season, with the majority of brood losses and failures occurring within the first ten days post-hatching. This accords, biologically, with what would be anticipated considering that altricial nestlings are known to be particularly vulnerable to environmental conditions during their first week post-hatching, a period when they are unable to thermoregulate and are heavily reliant on their parents to maintain body heat and for food provisioning (Mertens 1977; Ardia 2005; Blondel *et al*. 1990; Tremblay *et al.* 2003). Interestingly, however, if nestlings survived this initial period of development, their probability of surviving to fledge was high, however the reduced weight of nestlings on leaving the nest is cause for concern.

Due to the exploratory and correlative nature of the research, it is not possible to determine the exact causal mechanism driving the observed decrease in nestling growth and survival and increased rates of loss. There are potentially two hypotheses to consider for exploration and testing in future research in this population: that the results observed are potentially evidence of (1) maladaptive breeding and/or a brood reduction strategy (Gottlander 1987; Slagsvold and Amundsen 1992), with both potentially linked to the low quality of the breeding habitat and / or unpredictable breeding conditions (Gottlander 1987; Slagsvold and Amundsen, 1992).

For example, the findings from this study suggest that clutch size in the Birmingham population maybe non-adaptive (Dhondt *et al.* 1990; Hõrak 1993; Arriero *et al.* 2006). Despite smaller clutches, pairs still experienced significantly reduced hatching success, and higher brood reduction and loss. This suggests a disparity in the effects of environmental predictors between the earliest phase of reproduction (i.e. when making breeding decisions) and later post-natal breeding outcomes (Solonen and Hildén 2014; Shutt et al. 2018; Seress et al., 2018). This phenomenon may arise because pairs are unable to accurately assess the quality of breeding habitats whilst establishing territories, resulting in females laying sub-optimally large clutches, (e.g. Harrison *et al.* 2010; Seress *et al.* 2018). The potential for maladaptive breeding behaviour was tentatively supported by the distinct seasonal shifts in the influence of both garden landcover and more nuanced changes associated with the habitat surrounding nests (in particular the density and diversity of preferred native broadleaved tree species), with pre-hatching breeding traits positively correlated with these covariates, and later post-hatch breeding traits exhibiting more complex or non-linear relationships.

Although indirect, the evidence from this study, together with results from the existing literature suggests that variability in the availability and quality of food along the urban gradient is likely contributing to starvation and consequently critically influencing nestling condition and breeding success. Furthermore, the results also intimate that if alternative natural and anthropogenic foods were sourced to supplement the poor supply of caterpillars, whilst these may have benefited females during egg laying and incubating, these foods were not an adequate substitute for rearing chicks (Chamberlain *et al.*, 2009; Hedblom and Söderström 2012).

The increased risk of nestling loss is a significant concern since this directly impacts fledgling numbers, with knock-on effects to recruitment and population stability, e.g. as already observed in House Sparrows (*Passer domesticus*; Peach *et al.* 2008; Shaw *et al*. 2008; Meillère *et al.* 2015). Furthermore, there are potentially other more subtle yet serious consequences. Foremost, is the implied reduced capacity of urban parents to compensate for poor breeding decisions and/or additional environmental stresses that may be experienced earlier in the season, for example extreme weather: an issue that was also recently highlighted by Satgé *et al.* (2019).

6.1.1. Directions for future research

A particularly important point for consideration related to the maladaptation hypothesis above, is whether reduced but variable clutch sizes, and concomitant poor breeding success observed across Birmingham were evidence for a lack of adaptation driven by high gene flow, (Dhondt *et al.* 1990; Hinsley e*t al.* 1999; Shutt *et al.* 2018), between the city and surrounding landscape and/or along the urban gradient. Since genetic data was not collected for this study, it is not possible to differentiate whether egg laying, for example was mediated by directional selection or phenotypic plasticity. An interesting direction, for future research therefore, would be to investigate the genetic structure of the population and the direction of gene flow to determine fluxes in genotypes and test for potential source-sink dynamics (Björklund *et al.* 2010; Charmantier *et al.* 2017; Perrier *et al.* 2018). Since egg quality is a reflection of maternal condition and the environmental pressures experienced by individuals, it would also be useful in the future to investigate how maternal investment in egg laying varies (i.e. measuring egg shell thickness, egg mass and the deposition of diet derived antioxidants), across the urban gradient and if this is linked with carry-over effects on hatching success and chick survival (Plummer *et al.* 2013a; Bailly *et al.* 2016).

On the other hand, the high rate of nestling loss during the first ten days post-hatch could be due to females selectively starving their young to ensure the successful fledging of at least some of the brood. This hypothesis, also presents the opportunity for future research within this study system. More targeted, regular monitoring of nestboxes during brood rearing to determine provisioning rates and the type and abundance of food delivered to nestlings, as well as the growth trajectories of nestlings, for example using faecal metabarcoding and RFID technology could help to elucidate the mechanisms linking the environment with reduced breeding success within this study system (for example see Demeyrier *et al.* 2017; Seress *et al.* 2018; Jarrett *et al.* 2020; Shutt *et al*. 2021). Finally the potential influence of gardens on breeding success is also an intriguing finding to potentially further explore in the future and would be an excellent opportunity to engage in citizen/public science projects locally (e.g. see Narango *et al*. 2017; Plummer *et al*. 2019).

The incorporation of genetic analyses and biotelemetry, would also provide an insight into the movement of birds across the landscape and provide an assessment as to how dynamic and/or linked the populations of Blue Tits are across the wider metropolitan area and surrounding woodland (e.g. Chaddesley woodland). Furthermore, the incorporation of such techniques could help in the future assessment of recruitment rates into the population and determine which fledglings reached adulthood and subsequently bred: outcomes that we were unable to track due to the nature of the current demographic survey work and in particular the time constraints and difficulties in tracking individuals post-fledging across a project area of this size.

Finally, an important restriction of the current study was the inability to differentiate between potential extrinsic and intrinsic influences on breeding. Whilst it proved difficult to capture and collect data on adults, the inclusion of biotic covariates associated with parental identity, experience and condition (Saarikivi and Herczeg, 2014) in models could also help to identify the underlying factors driving the high levels of intra-site variability in breeding outcomes observed both within and among sites.

The results reported here thus far support the growing consensus in the literature that urban greenspace planning and management needs to carefully balance the size trees can grow to with the total number of trees planted with the diversity of species considered. More in-depth habitat surveys considering all nestboxes within sites, and further analyses incorporating measures of individual "priority species", variation in tree girth and total canopy cover would enable a more thorough understanding of the quality of nesting habitat within sites and enable us to investigate food availability in more detail.

6.1.2. Management Implications

Urban ecology has evolved dramatically since the turn of the century, and cities are now increasingly considered as dynamic and complex but also adaptive landscapes (Grimm 2008). Urban greenspaces are an important component of the urban fabric, in particular acting as refugia for many different species, e.g. see (McKinney 2008a; Hutto and Barrett, 2021; Toffolo et al. 2021) and delivering crucial ecosystem services (Grimm 2008; Leveau et al., 2019). Moreover, the provision of high quality greenspace is increasingly being recognised as key in the creation of environmentally healthy cities and promoting well-being for the growing numbers of people living there (Barton and Pretty 2010; Apfelbeck *et al*. 2020). Therefore the conservation, expansion and increased connectivity of greenspace is crucial for biodiversity conservation (Lepczyk *et al*. 2017).

Unravelling the complex effects of fine-scale changes in the urban environment on breeding success at the individual and site levels, as undertaken here, can help to guide and inform the planning, design and management of urban greenspaces and the conservation of species in cities undergoing further expansion and densification, with the aim of enhancing the possibility of people encountering wildlife on their doorstep (Cox et al. 2016), potentially enhancing the cultural ecological services this provides (Shanahan et al. 2015; Cox et al. 2015; 2017). More specifically, this research builds on the growing body of evidence demonstrating that mitigating actions need to be considered at multiple spatial scales if they are to be effective (Pollock et al. 2017; Satgé et al. 2019; Plummer et al. 2020; Strubbe et al. 2020). In particular, evidence from this and other studies demonstrates that greenspaces do not necessarily buffer the detrimental effects of urbanisation (Saarikivi and Herczeg, 2014; Satgé et al. 2019). Therefore, future planning and management strategies will need to prioritise improving and maintaining the quality of greenspaces such as through the careful selection and planting of native tree and shrub species that can support diverse and abundant insect populations (Pollock et al. 2017; Seress et al. 2018; Dekeukeleire et al. 2019; Satgé et al. 2019; Strubbe et al. 2020). Mitigating the effects of key abiotic factors within the wider urban matrix (including predation, pollution, noise, light and temperature) will also be imperative if wildlife-friendly city designs are to be effective and will need to consider the connectivity (both structural and functional) within cities and towns as well as suburban and smaller urban centres.

In particular, the UK government has recently backed the development of more than 30 new garden cities and towns (MCHLG 2018 and as reported by Plummer *et al.* 2020). Furthermore, changes to UK law also mean that new developments will need to enhance habitat value for wildlife if they are to achieve the mandatory guidelines set down (DEFRA 2019). Therefore studies such as this provide an ideal opportunity to work with stakeholders to improve the planning, development and management of urban greenspace to maximise its potential for biodiversity and for the people that will be living in these increasingly urbanised areas.

6.2. Climate-urbanisation interactions

In chapter five I used a sliding window analysis to explore and identify potential critical time windows of both temperature and rainfall weather signals that may influence breeding success in this urban-breeding Blue Tit population. The results from this initial stage of analyses provide tentative evidence to suggest that at least some of the variation in breeding outcomes observed among the Blue Tit population may be correlated with prevailing weather conditions, specifically variation in daily maximum temperatures, rather than mean or minimum temperatures, and the amount of rainfall both prior to and during the two reproductive stages. Moreover, increases in both maximum temperature and rainfall elicited negative responses in breeding traits, with the brood-rearing stage again appearing the most susceptible to change in these weather signals. In particular, nestlings appeared particularly vulnerable to variation in maximum temperatures and the amount of rainfall during the early developmental stage (approximately the first ten days post hatching), a period when they are unable to thermoregulate properly and provisioning rates by the female concomitantly increase to keep up with nutritional demands, thus meaning brooding bouts become increasingly irregular (Mertens 1977; Sans and Tinbergen 1999; Ardia 2005; Dawson *et al.* 2005).

Weather conditions during brood-rearing play an important role in determining the growth and development of nestlings (Morganti *et al*. 2017). They may impact nestlings directly, via thermoregulation (Schöll and Hille 2020) and temperature on growth and metabolism (Ospina *et al*. 2018), or indirectly by impacting the foraging conditions of parents and the availability of preferred natural food such as caterpillars during periods of rainfall (Mainwaring and Hartley 2016; Morganti *et al*. 2017). Both impacts are suggested by this research.

As with other emerging correlative research investigating the impacts of weather using sliding window analysis tools such as *climwin* (e.g. Marques-Santos and Dingemanse, 2020; Marques-Santos *et al.* 2021), the underlying mechanisms that drive breeding behaviour and success cannot be established. However, these preliminary exploratory analyses identified weather signals and critical climate windows that will be crucial in directing future research and hypothesis testing and considered some of the mechanisms that might be driving the relationships.

The identification of a potential maximum threshold temperature and interactive effect between the urban gradient and rainfall on fledging success, in particular could be key to further understanding the mechanisms driving breeding success. Furthermore, considering the effects of climate change and associated extreme weather events are likely to be more acute in urban areas (Diamond *et al.* 2014; Sumasgutner *et al.*, 2020), these findings have potentially significant implications for the future breeding success and stability of this population and other populations of passerines considered adapted to living in urban areas.

Importantly, the results presented here also demonstrate that the downstream effects of variation in prevailing weather conditions, and, therefore by implication extreme weather events are likely complex, particularly in already human-mediated environments such as urbanised areas. As such, the results of this study, further advocate the need for continuous intensive research in the future, that focuses on how weather conditions, and especially unpredictable extreme weather events, impact breeding behaviour and success in birds once initial reproductive decisions have been made. Such studies are likely to be crucial if we are to understand how different species and populations are likely to respond to changing environmental conditions in the future, and the long-term consequences to the evolution of life-histories. With respect to this study system, as an immediate next step, further analyses should consider investigating the within-year versus among-year variation in weather effects (e.g. see Marques-Santos and Dingemanse, 2020) using the method of within-subject centering (van de Pol and Wright, 2009; Bailey and van de Pol, 2015).

Understanding how anthropogenic-mediated environmental change interact antagonistically with climate change in urban areas at an individual level of breeding responses in birds is therefore vital if we are to accurately model and predict how increasing urbanisation (Cole et al., 2015; Shutt et al., 2018; Plummer et al, 2020) and weather extremes may influence population dynamics in the long-term and prevent future population crashes (Pollock et al., 2017).This will require the continued long-term collection of weather and biological data at both high temporal and spatial resolutions and the collaboration of scientists across multiple study systems in order to refine analytical techniques and modelling capabilities.

References

Abbas, T. (2006) *Muslims in Birmingham, UK: Background paper for the University of Oxford, Centre on Migration Policy and Society*.

Alberti, M. (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology and Evolution* **30**: 114 - 126. doi: 10.1016/j.tree.2014.11.007.

Alberti, M., Marzluff, J.M. and Hunt, V.M. (2017) Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **372**: 20160029. doi: 10.1098/rstb.2016.0029.

Alexander, L.V. (2016) Global observed long-term changes in temperature and precipitation extremes: A review of progress and limitations in IPCC assessments and beyond. *Weather and Climate Extremes* **11**: 4 – 16. doi: 10.1016/j.wace.2015.10.007.

Ambrosini, R., Ferraro, R.P., Martinelli, R., Romano, M. & Saino, N. (2006) Seasonal, meteorological, and microhabitat effects on breeding success and offspring phenotype in the barn swallow, *Hirundo rustica. Ecoscience* **13**: 298–307. doi: 10.2980/ i1195-6860-13-3-298.1.

Amininasab, S.M., Vedder, O., Schut, E., de Jong, B., Magrath, M.J.L., Korsten, P. & Komdeur, J. (2016a) Influence of fine-scale habitat structure on nest-site occupancy, laying date and clutch size in Blue Tits *Cyanistes caeruleus*. *Acta Oecologica* **70**: 37–44. doi: 10.1016/j.actao.2015.11.006.

Amininasab, S.M., Kingma, S.A., Birker, M., Hildenbrandt, H & Komdeur, J. (2016b) The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behavioral Ecology and Sociobiology* **70**: 1591 - 1600. doi: 10.1007/s00265-016-2167-2.

Amrhein, V. (2014) Wild bird feeding (probably) affects avian urban ecology. In: Gil, D. and Brumm, H. (eds.) *Avian Urban Ecology: Behavioural and Physiological Adaptations*. Oxford University Press (OUP), Oxford, UK, pp. 29–37.

Amundsen, T. and Slagsvold, T. (1998) Hatching asynchrony in Great Tits: A bet hedging strategy? *Ecology* **79(1)**: 295 - 304.

Anderies, J.M., Katti, M. & Shochat, E. (2007) Living in the city: Resource availability, predation, and bird population dynamics in urban areas. *Journal of Theoretical Biology* **247**: 36 - 49. doi: 10.1016/j.jtbi.2007.01.030.

Andreasson,F., Nord, A & Nilsson, J.Å. (2016) Brood size constrains the development of endothermy in Blue Tits. *Journal of Experimental Biology* **219 (14)**: 2212 – 2219. doi: 10.1242/jeb.135350.

Andreasson, F., Nilsson, J.Å. & Nord, A. (2020) Avian Reproduction in a Warming World. *Frontiers in Ecology and Evolution* **8**: 1 – 8. doi: 10.3389/fevo.2020.576331.

Angelstam, P. (1986) Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* **47**:365 – 373.

Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R & Thompson, K. (2006) Biodiversity in urban habitat patches. *Science of the Total Environment* **360**: 196 – 204. doi:10.1016/j.scitotenv.2005.08.035.

Apfelbeck, B., Snep, R.P.H., Hauck, T.E., Ferguson, J., Holy, M. , Jakoby, C., MacIvor, J. S., Schär, L., Taylor, M.. & Weisser, W.W. (2020) Designing wildlife-inclusive cities that support human- animal co-existence. *Landscape and Urban Planning* **200**: 103817. doi: 10.1016/j.landurbplan.2020.103817.

Arct, A., Drobniak, S.M., Dubiec, A., Martyka, R., Sudyka, J., Gustafsson, L., & Cichoń, M. (2022) The interactive effect of ambient temperature and brood size manipulation on nestling body mass in Blue Tits: an exploratory analysis of a long-term study. *Frontiers in Zoology* **19(9)**: 1- 8. doi: 10.1186/s12983-022-00456-x.

Ardia, D.R. (2005) Super size me: an experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. *Functional Ecology* **19**: 414 –420.

Ardia, D.R. (2013) The effects of nestbox thermal environment on fledging success and haematocrit in Tree Swallows. *Avian Biology Research* **6(2)**: 99 - 103 doi: 10.3184/175815513X13609528031394.

Arnfield, A.J. (2003) Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. *International Journal of Climatology*. **23(1)**:1–26. doi: 10.1002/joc.859.

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., Pyšek, P., Siebert, S., Sushinsky, J., Werner, P. & Winter, M. (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* **281(1780)**: 20133330 doi: 10.1098/rspb.2013.3330.

Arriero, E., Sanz, J.J. & Romero-Pujante, M. (2006) Habitat structure in Mediterranean deciduous oak forests in relation to reproductive success in the Blue Tit *Parus caeruleus. Bird Study* **53**: 12 - 19. doi: 10.1080/00063650609461411.

Atiénzar, F., Visser, M.E., Greño, J.L., Holleman, L.J.M., Belda, E.J. & Barba, E. (2010) Across and within-forest effects on breeding success in Mediterranean Great Tits *Parus major Ardea* **98(1)**: 77 – 89. doi: 10.5253/078.098.0110.

Bailey, L. and van de Pol, M. (2016) climwin: An R Toolbox for Climate Window Analysis. *PLoS ONE* **11(12)**: e0167980. doi:10.1371/journal.pone.0167980. [Computer software].

Bailey, L.D. and van de Pol, M. (2016) Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology* **85**: 85 - 96. doi: doi.org/10.1111/1365-2656.12451

Bailly, J., Scheifler, R., Berthe, S., Clément-Demange, V., Leblond, M., Pasteur, B., & Faivre, B. (2016) From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. *Journal of Ornithology* **157**: 377 - 392. doi: 10.1007/s10336-015-1293-3.

Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review* **35**: 302 - 312. doi: 10.1111/j.1365-2907.2005.00071.x.

Balogh, A.L., Ryder, T.B. and Marra, P.P. (2011) Population demography of gray catbirds in the suburban matrix: sources, sinks and domestic cats. *Journal of Ornithology* **152**: 717 - 726. doi: 10.1007/s10336011-0648-7.

Bańbura, J. and Bańbura, M. (2012) Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*) as urban habitat breeders. *International Studies on Sparrows* **36**: 66 –72. doi: 10.1515/isspar-2015-0014.

Bańbura, J., Blondel, J., de Wilde-Lambrechts, H., Galan, M.J., & Maistre, M. (1994) Nestling diet variation in an insular Mediterranean population of Blue Tits *Parus caeruleus*: effects of years, territories and individuals. *Oecologia* **100(4)**: 413 - 420. https://www.jstor.org/stable/4220834.

Barba, E., Gil-Delgado, J.A. and Monros, J.S. (1995) The Costs of Being Late: Consequences of Delaying Great Tit *Parus major* First Clutches. *Journal of Animal Ecology* **64(5)**: 642 – 651. doi: 10.2307/5806.

Barber, A. and Hall, S. (2008) Birmingham: whose urban renaissance? Regeneration as a response to economic restructuring. *Policy Studies* **29(3)**: 281 – 292. doi: 10.1080/01442870802159871.

Barriga, G.D.C. and Louzada, F. (2014) The zero-inflated Conway-Maxwell-Poisson distLyribution: Bayesian inference, regression modeling and influence diagnostic. *Statistical Methodology* **21**: 23 – 34. doi: 10.1016/j.stamet.2013.11.003.

Barton, J. and Pretty, J. (2010) What is the best dose of nature and green exercise for improving mental health? A multi-study analysis. *Environmental science and Technology* **15(44)**: 3947 – 3955. doi: 10.1021/es903183r.

Batáry, P. and Báldi, A. (2004) Evidence of an edge effect on avian nest success. *Conservation Biology* **18(2)**: 389 – 400. doi: 10.1111/j.1523-1739.2004.00184.x.

Batáry, P., Fronczek, S., Normann, C., Scherber, C. & Tscharntke, T. (2014) How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest? *Forest Ecology and Management*, **319**: 44 – 50. doi: 10.1016/j.foreco.2014.02.004.

Batáry, P., Kurucz, K., Suarez-Rubio, M. & Chamberlain, D.E. (2018) Non-linearities in bird responses across urbanization gradients: A meta-analysis. *Global Change Biology* **24(3)**: 1046 – 1054. doi: 10.1111/gcb.13964.

Bateman, P.W. and Fleming, P.A. (2014) Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? Journal of Zoology **294**: 93 - 98. doi: 10.1111/jzo.12156.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67(1)**: 1 - 48. doi: 10.18637/jss.v067.i01.

Battin, J. (2004) When Good Animals Love Bad Habitats: Ecological traps and the Conservation of Animal Populations. *Conservation Biology* **18(6)**: 1482 – 1491. doi: 10.1111/j.1523-1739.2004.00417.x.

Beninde, J., Veith, M. and Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters* **18**: 581 – 592. doi: 10.1111/ele.12427.

Beniston, M. (2015) Ratios of record high to record low temperatures in Europe exhibit sharp increases since 2000 despite a slowdown in the rise of mean temperatures. *Climatic Change* **129**: 225 – 237. doi: 10.1007/s10584-015-1325-2.

Berthouly, A., Cassier, A., and Richner, H. (2008) Carotenoid-induced maternal effects interact with ectoparasite burden and brood size to shape the trade-off between growth and immunity in nestling Great Tits. *Functional Ecology* **22(5)**: 854 - 863. doi: 10.1111/j.1365-2435.2008.01439.x.

Bélisle, M. (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* **86(8)**: 1988 - 1995. doi: 10.1890/04-0923.

Bélisle, M. and Desrochers, A. (2002) Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* **17**: 219 - 231.

Bell, S.C., Owens, I.P.F. and Lord, A.M. (2014) Quality of breeding territory mediates the influence of paternal quality on sex ratio bias in a free-living bird population. *Behavioral Ecology* **25(2)**: 352 - 358. doi: 10.1093/beheco/art112.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology letters* **15(4)**: 365 - 377.

Betts, M.M. (1955) The food of titmice in oak woodland. *The Journal of Animal Ecology* **24(2)**: 282 - 323. doi: 10.2307/1715.

Beyer, H.L. (2004) Hawth's Analysis Tools for ArcGIS.

Biard, C., Brischoux, F., Meillère, A., Michaud, B., Nivière, M., Ruault, S., Vaugoyeau, M. and Angelier, F. (2017) Growing in cities: An urban penalty for wild birds? A study of phenotypic differences between urban and rural great tit chicks (*Parus major*). *Frontiers in Ecology and Evolution* **5(79)** doi: 10.3389/fevo.2017.00079.

Biophillic Cities. https://biophiliccities.org (accessed 05/03/2023).

Birmingham City Council (2022) Population and Census Information. Available at: https://www.birmingham.gov.uk/info/20057/about_birmingham/1294/population_and_census/2 (accessed 28/06/2022).

Bivand, R.S. and Wong, D.W.S. (2018) Comparing implementations of global and local indicators of spatial association. *TEST* **27**: 716 – 748. doi: 10.1007/s11749-018-0599-x.

Björklund, M., Ruiz, I. and Senar, J.C. (2010) Genetic differentiation in the urban habitat: the Great Tits (*Parus major*) of the parks of Barcelona city. *Biological Journal of the Linnean Society* **99**: 9 – 19.

Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications* **6(2)**: 506 - 519. doi: 10.2307/2269387.

Bland, R.L., Tully, J. and Greenwood, J.J.D. (2004) Birds breeding in British gardens: an underestimated population? *Bird Study* **51**: 97 – 106.

Blondel, J. (2007) Coping with habitat heterogeneity: The story of Mediterranean Blue Tits. *Journal of Ornithology* **148**: 3 - 15.doi: 10.1007/s10336-007-0161-1.

Blondel, J., Dervieux, A., Maistre, M. & Perret P. (1991) Feeding ecology and life history variation of the Blue Tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia* **88(1)**: 9 – 14. doi: 10.1007/BF00328397.

Blondel, J., Dias, P.C., Maistre, M. & Perret, P. (1993) Habitat Heterogeneity and Life-History Variation of Mediterranean Blue Tits (*Parus caeruleus*). *The Auk* **110(3)**: 511 – 520. doi: 10.2307/4088415.

Blondel, J., Thomas, D.W., Charmantier, A., Perret, P., Bourgault, P., & Lambrechts, M.M. (2006). A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. *Bioscience* **56(8)**: 661 - 673.

Bolker, B.M. (2017) Getting started with the glmmTMB package. *Cran.R-Project Vignette* 1 - 9. Available at: https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf. (accessed 06/04/2019).

Bonier, F., Martin, P.R. and Wingfield, J.C. (2007) Urban birds have broader environmental tolerance. *Biology Letters* **3(6)**: 670 – 673. doi: 10.1098/rsbl.2007.0349.

Borden, J.B. and Flory, S.L. (2021) Urban evolution of invasive species. *Frontiers in Ecology and the Environment* **19(3)**: 141 – 196. doi: 10.1002/fee.2295.

Bordjan, D. and Tome, D. (2014) Rain may have more influence than temperature on nest abandonment in the Great Tit *Parus major*. *Ardea* **102(1)**: 79 – 86. doi: 10.5253/078.102.0107.

Both, C. (1998) Density dependence of clutch size: Habitat heterogeneity or individual adjustment? *Journal of Animal Ecology* **67(4)**: 659 – 666. doi: 10.1046/j.1365-2656.1998.00227.x.

Both, C., Visser, M.E. and Verboven, N. (1999) Density-dependent recruitment rates in Great Tits: the importance of being heavier. *Proceedings of the Royal Society B: Biological Sciences* **266(1418)**: 465 – 469. doi: 10.1098/rspb.1999.0660.

Boutin, S., and Lane, J.E. (2014) Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications* **7(1)**: 29 - 41. doi: Boutin, S., & Lane, J. E. (2014).

Climate change and mammals: evolutionary versus plastic responses. Evolutionary Applications, 7(1), 29-41. doi: 0.1111/eva.12121.

Bradley, C.A. & Altizer, S. (2007) Urbanisation and the ecology of wildlife diseases. *Trends in Ecology and Evolution* **22(2)**: 95 - 102. doi: 10.1016/j.tree.2006.11.001.

Brahmia, Z., Scheifler, R., Crini, N. & Maas, S. (2013) Breeding performance of Blue Tits (*Cyanistes cæruleus ultramarinus*) in relation to lead pollution and nest failure rates in rural, intermediate, and urban sites in Algeria. *Environmental Pollution* **174**: 171 – 178. doi: 10.1016/j.envpol.2012.11.028.

Bramer, I., Anderson, B.J., Bennie, J., Bladon, A.J., De Frenne, P., Hemming, D., Hill, R.A., Kearney, M.R., Kömer, C., Korstjens, A.H. et al. (2018) Chapter three-advances in monitoring and modelling climate at ecologically relevant scales. In: Bohan, D.A., Dumbrell, A.J., Woodward, G. & Jackson, M. (eds.) *Advances in Ecological Research*, Academic Press. pp. 101 – 161.

Brischoux, F., Meillère, A., Dupoué, A., Lourdais, O. & Angelier, F. (2017) Traffic noise decreases nestlings' metabolic rates in an urban exploiter. *Journal of Avian Biology* **48(7)**: 905 - 909. doi: 10.1111/jav.01139.

British Trust for Ornithology (2023) BTO Bird Facts: Blue Tit (*Cyanistes caeruleus*). Available at: https://app.bto.org/birdfacts/results/bob14629.htm (accessed 14/01/2023).

British Trust for Ornithology (2023) BTO Maps of popluation density and trends. Available at: https://bto.org/our-science/projects/breeding-bird-survey/latest-results/maps-population-density-and-trends (accessed 14/01/2023).

Brittingham, M.C. and Temple, S.A. (1986) A survey of avian mortality at winter feeders. *Wildlife Society Bulletin* **14(4)**: 445 – 450.

Brooks, M. E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H. J., Mächler, M. & Bolker, B.M. (2017) The R Journal: glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9(2)**: 378 - 400. doi: 10.32614/rj-2017-066.

Brooks, M. E., Kristensen, K., Darrigo, M.R., Rubim, P., Uriarte, M., Bruna, E. & Bolker, B.M. (2019) Statistical modeling of patterns in annual reproductive rates. *Ecology* **100(7)**: e02706. doi: 10.1002/ecy.2706.

Brown, M.E. (1996) Assessing body condition in birds. In: Nolan, V., Ketterson, E.D. (eds.) *Current Ornithology*, vol 13. Springer, Boston, MA. pp. 67-135. doi: 10.1007/978-1-4615-5881-1_3.

Buchholz, R., Banusiewicz, J.D., Burgess, S., Crocker-Buta, S., Eveland, L. & Fuller, L. (2019) Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour* **150:** 127 - 137. doi: 10.1016/j.anbehav.2019.02.005.

Bueno-Enciso, J., Ferrer, E.S., Barrientos, R. & Sanz, J.J. (2016) Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. *Journal of Ornithology*, **157(3)**: 759–772. doi: 10.1007/s10336-016-1339-1.

Bueno-Enciso, J., Ferrer, E.S., Barrientos, R., Serrano-Davies, E. & Sanz, J.J. (2016) Habitat fragmentation influences nestling growth in Mediterranean Blue and Great Tits. *Acta Oecologica*, **70**: 129–137. doi: 10.1016/j.actao.2015.12.008.

Buonomo, E., Jones, R., Huntingford, C. and Hannaford, J. (2007) On the robustness of changes in extreme precipitation over Europe from two high resolution climate change simulations. *Quarterly.Journal of the Royal Meteorological Society* **133**: 65 - 81. doi: 10.1002/qj.13.

Burgess, M.D., Smith, K.W., Evans, K.L., Leech, D., Pearce-Higgins, J.W., Branston, C.J., Briggs, K., Clark, J.R., du Feu, C.R., Lewthwaite, K., Nager, R.G., Sheldon, B.C., Smith, J.A., Whytock, R.C., Willis, S.T. & Phillimore, A.B. (2018) Tritrophic phenological match – mismatch in space and time. *Nature Ecology & Evolution* **2(6)**: 970 - 975. doi: 10.1038/s41559-018-0543-1

Burness, G. P., McClelland, G.B., Wardrop, S.L. & Hochachka, P.W. (2000) Effect of brood size manipulation on offspring physiology: an experiment with passerine birds. *Journal of Experimental Biology* **203(22)**: 3513–3520. doi: 10.1242/jeb.203.22.3513.

Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multi-model inference: A practical information-theoretic approach*. 2nd Edition. Springer, New York, NY.

Burnham, K. P. and Anderson, D. R. (2004) Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* **33(2)**: 261 – 304. doi: 10.1177/0049124104 268644.

Buse, A., Drury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G. (1999) Effects of elevated temperature on multi-speciesinteractions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* **13(Supp. 1)**: 74 – 82. doi: 10.1046/j.1365-2435.1999.00010.x.

Buxton, V.L. and Benson, T.J. (2015) Do natural areas in urban landscapes support successful reproduction by a group of conservation priority birds? *Animal Conservation* **18(5)**: 471 - 479. doi: 10.1111/acv.12198.

Camacho-Cervantes, M., Ojanguren, A.F. and MacGregor-Fors, I. (2018) Birds from the burgh: bird diversity and its relation with urban traits in a small town. *Journal of Urban Ecology* **4(1)**: 1 -7. doi: 10.1093/jue/juy011.

Canal and River Trust. https://canalrivertrust.org.uk/enjoy-the-waterways/canal-and-river-network/birmingham-canal-navigations (accessed: 05/03/2023).

Capilla-Lasheras, P., Dominoni, D., Babayan, S., O'Shaughnessy, P., Mladenova, M., Woodford, L., Pollock, C., Barr, T., Baldini, F. & Helm, B. (2017) Elevated immune gene expression is associated with poor reproductive success of urban Blue Tits. *Frontiers in Ecology and Evolution* **5**. doi: 10.3389/fevo.2017.00064.

Capilla-Lasheras, P., Bondía, B. and Aguirre, J.I. (2021) Environmental conditions but not nest composition affect reproductive success in an urban bird. *Ecology and Evolution* **11(7)**: 3084 – 3092. doi: 10.1002/ece3.7234.

CaraDonna, P.J., Cunningham, J.L., & Iler, A.M. (2018) Experimental warming in the field delays phenology and reduces body mass, fat content and survival: Implications for the persistence of a pollinator under climate change. *Functional Ecology* **32(10)**: 2345 -

2356. doi: 10.1111/1365-2435.13151.

Carbó-Ramírez, P., & Zuria, I. (2011) The value of small urban greenspaces for birds in a Mexican city. *Landscape and Urban Planning* **100(3)**: 213 - 222. doi: 10.1016/j.landurbplan.2010.12.008.

Caro, S.P., Lambrechts, M.M., Balthazart, J., & Perret, P. (2007) Non-photoperiodic factors and timing of breeding in Blue Tits: impact of environmental and social influences in semi-natural conditions. *Behavioural Processes* **75(1)**: 1 - 7. doi: 10.1016/j.beproc.2007.02.011.

Chace, J.F. and Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning***74(1)**: 46 – 69. doi: 10.1016/j.landurbplan.2004.08.007.

Chace, J.F., Walsh, J.J., Cruz, A., Prather, J.W. & Swanson, H.M. (2003). Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. *Landscape and Urban Planning* ***64*****(3)**: 179 - 190.

Chalfoun, A.D. and Schmidt, K.A. (2012) Adaptive Breeding-Habitat Selection: Is it for the Birds? *The Auk* **129(4)**: Pages 589 – 599. doi: 10.1525/auk.2012.129.4.589.

Chamberlain, D.E., Cannon, A.R., Toms, M.P., Leech, D.I., Hatchwell, B.J. & Gaston, K.J. (2009) Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* **151**: 1 - 18. doi: 10.1111/j.1474-919X.2008.00899.x.

Chapman, S., Watson, J.E.M., Salazar, A. & McAlpine, C.A. (2017) The impact of urbanization and climate change on urban temperatures: a systematic review. *Landscape Ecology* **32**: 1921 – 1935. doi: 10.1007/s10980-017-0561-4.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L. E. & Sheldon, B.C. (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320(5877)**: 800 - 803. doi: 10.1126/science.1157174.

Charmantier, A., Demeyrier, V., Lambrechts, M.M., Perret, S., & Grégoire, A. (2017) Urbanization is associated with divergence in pace-of-life in Great Tits. *Frontiers in Ecology and Evolution* **5**. doi: 10.3389/fevo.2017.00053.

Charmantier, A., & Gienapp, P. (2014) Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications* **7(1)**: 15 - 28. doi: 0.1111/eva.12126.

Chen, I-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**: 1024 – 1026. doi: 10.1126/science.1206432.

Chevin, L. M., Visser, M. E., & Tufto, J. (2015) Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. Evolution 69(9): 2319 - 2332. doi: 10.1111/evo.12741.

Chinn, C. and Dick, M. (eds.) (2016) *Birmingham: The Workshop of the World*. Liverpool University Press, Liverpool, uk. pp. 334. doi: 10.1017/jbr.2018.30.

Clark, A.B. and Wilson, D.S. (1991) Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Quarterly Review of Biology* **56**: 253 - 277.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M. & Dinetti, M. (2006a) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation* **127**:336 – 344. doi: 10.1016/j.biocon.2005.06.035

Clergeau, P., Jokimäki, J. and Snep, R. (2006b) Using hierarchical levels for urban ecology. *Trends in Ecology and Evolution* **21(12)**: 660 – 661. doi: 10.1016/j.tree.2006.09.006.

Clergeau, P., Savard, J-P. L., Mennechez, G. & Falardeau, G. (1998) Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *The Condor* **100(3)**: 413 – 425.

Cody, M.L. (ed.). (1985) *Habitat selection in birds.* Academic Press, Orlando, FL.

Coe, B.H., Beck, M.L., Chin, S.Y., Jachowski, C.M.B. & Hopkins, W.A. (2015) Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology* **46(4)**: 385 – 394. doi: 10.1111/jav.00581.

Cole, E.F., Morand-Ferron, J., Hinks, A.E., & Quinn, J.L. (2012) Cognitive ability influences reproductive life history variation in the wild. *Current Biology* **22(19)**: 1808 - 1812. doi: 10.1016/j.cub.2012.07.051.

Cole, E.F., Long, P.R., Zelazowski, P., Szulkin, M. & Sheldon, B.C. (2015) Predicting bird phenology from space: satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment. *Ecology and Evolution*, **5(21)**: 5057 – 5074. doi: 10.1002/ece3.1745.

Cooper, C.B., Hochachka, W.M., Butcher, G., & Dhondt, A.A. (2005) Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. *Ecology* **86(8)**: 2018 - 2031.

Cornelis, J. and Hermy, M. (2004) Biodiversity relationships in urban and suburban parks in Flanders. *Landscape and Urban Planning* **69(4)**: 385 – 401. doi: 10.1016/j.landurbplan.2003.10.038.

Corsini, M., Dubiec, A., Marrot, P. & Szulkin, M. (2017) Humans and tits in the city: Quantifying the effects of human presence on great tit and blue tit reproductive trait variation. *Frontiers in Ecology and Evolution* **5**. doi: 10.3389/fevo.2017.00082.

Corsini, M., Schöll, E.M., Di Lecce, I., Chatelain, M., Dubiec, A. & Szulkin, M. (2021) Growing in the city: Urban evolutionary ecology of avian growth rates. *Evolutionary Applications* **14(1)**: 69 – 84. doi: 10.1111/eva.13081.

Coulson, A. and Ferrario, C. (2007) “Institutional Thickness”: Local Governance and Economic Development in Birmingham,England. *International Journal of Urban and Regional Research* **31(3)**: 591 – 615. doi: 10.1111/j.1468-2427.2007.00739.x.

Coumou, D., Rahmstorf, S. (2012) A decade of weather extremes. *Nature Climate Change* 2: 491 – 496. doi: https://doi.org/10.1038/nclimate1452.

Cuervo, J. J., Soler, J. J., Avilés, J. M., Pérez-Contreras, T., & Navarro, C. (2011). Experimental feeding affects the relationship between hematocrit and body mass in Spotless

Starling (*Sturnus unicolor*) nestlings. *Journal of Ornithology* **152**: 201 - 206.

Cowie, R.J. and Hinsley, S.A. (1987) Breeding Success of Blue Tits and Great Tits in surburban gardens. *Ardea* **75**: 81 – 90.

Cowie, R.J., and Hinsley, S.A. (1988) Feeding Ecology of Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*), Breeding in Suburban Gardens. *Journal of Animal Ecology* **57(2)**: 611 – 626. doi: 10.2307/4928.

Cox, D. T. C. *et al.* (2016) Movement of feeder-using songbirds: the influence of urban features. *Scientific Reports* **6**: 37669. doi: 10.1038/srep37669.

Cramp, S. and Perrins, C.M. (1993) *The Birds of the Western Palearctic*, *Volume 7: Flycatchers to Shrikes.* Oxford University Press, Oxford.

Crates, R.A., Firth, J.A., Farine, D.R., Garroway, C.J., Kidd, L.R., Aplin, L.M., Radersma, R., Milligan, N.D., Voelkl, B., Culina, A., Verhelst, B.L., Hinde, C.A. & Sheldon, B. C. (2016) Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds. *Journal of Avian Biology* ***47*****(5)**: 678-689. doi: 10.1111/jav.00936.

Crawley, M.J. (2007) *The R Book.* John Wiley & Sons Ltd, Chichester, UK.

Crawley, M. J. and Akhteruzzaman, M. (1988) Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology* **2(3)**: 409 - 415. doi: 10.2307/2389414.

Creegan, H.P., and Osborne, P.E. (2005) Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach*. Journal of Applied Ecology* **42(4)**: 678-687. https://www.jstor.org/stable/3505901.

Cresswell, W. and McCleery, R. (2003) How Great Tits maintain synchronisation of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* **72**: 356 - 366. doi: 10.1111/j.1365-2664.2005.01057.x.

Crick, H.Q.P. (2004) The impact of climate change on birds. *Ibis* **146**: 48 - 56. Doi: 10.1111/j.1474-919X.2004.00327.x.

Croci, S., Butet, A. and Clergeau, P. (2008) Does urbanization filter birds on the basis of their biological traits? *Condor* **110(2)**: 223 – 240. doi: 10.1525/cond.2008.8409.

Croghan, D., Van Loon, A.F., Sadler, J.P., Bradley, C. & Hannah, D.M. (2019) Prediction of river temperature surges is dependent on precipitation method. *Hydrological Processes* **33:** 144 – 159. doi: https://doi.org/10.1002/hyp.13317.

Crooks, K.R., & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400(6744)**: 563 - 566.

Dallimer, M., Tang, Z., Bibby, P.R., Brindley, P., Gaston, K.J. & Davies, Z.G. (2011) Temporal changes in greenspace in a highly urbanized region. *Biology letters* ***7*****(5)**: 763 - 766. doi: 10.1098/rsbl.2011.0025.

D'Amelio, P.B., Ferreira, A.C., Fortuna, R., Paquet, M., Silva, L.R., Theron, F., et al. (2022) Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird. *Ecology Letters* **25**: 151 – 162. doi: 10.1111/ele.13913.

Davies, Z.G., Fuller, R.A., Dallimer M., Loram, A. & Gaston K.J. (2012) Household factors influencing participation in bird feeding activity: a national scale analysis. *PLoS ONE* **7(6)**: e39692. doi: 10.1371/journal.pone.0039692.

Dawson, A., King, V.M., Bentley, G.E., & Ball, G.F. (2001) Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms*, **16(4)**:365 - 380.

Dawson, R.D., Lawrie, C.C. and O'Brien, E.L. (2005) The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Behavioral Ecology* **144**: 499 – 507. doi: 10.1007/s00442-005-0075-7.

Dearborn, D.C. and Kark, S. (2010) Motivations for conserving urban biodiversity. *Conservation Biology* **24(2)**: 432 – 440. doi: 10.1111/j.1523-1739.2009.01328.x.

de Jong, M., Ouyang, J.Q., Da Silva, A., van Grunsven, R.H.A., Kempenaers, B., Visser, M.E. & Spoelstra, K. (2015) Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **370**: 20140128. doi: 10.1098/rstb.2014.0128.

de Jong, M., van den Eertwegh, L., Beskers, R.E., de Vries, P.P., Spoelstra, K. & Visser, M.E. (2018) Timing of Avian Breeding in an Urbanised World. *Ardea* **106(1)**: 31 - 38,doi: 10.5253/arde.v106i1.a4.

Dekeukeleire, D., van Schrojenstein Lantman, I.M., Hertzog, L.R., Vandegehuchte, M.L., Strubbe, D., Vantieghem, P., Martel, A., Verheyen, K., Bonte, D. & Lens, L. (2019a) Avian top-down control affects invertebrate herbivory and sapling growth more strongly than overstorey species composition in temperate forest fragments. *Forest Ecology and Management* **442**: 1 – 9. doi: 10.1016/j.foreco.2019.03.055.

Dekeukeleire, D., Hertzog, L.R., Vantieghem, P., van Schrojenstein Lantman, I.M., Sercu, B.K., Boonyarittichaikij, R., Martel, A., Verheyen, K., Bonte, D., Strubbe, D. & Lens, L. (2019b) Forest fragmentation and tree species composition jointly shape breeding performance of two avian insectivores. *Forest Ecology and Management* **443**: 95 - 105. doi: 10.1016/j.foreco.2019.04.023.

Delaney, K.S. (2014) Landscape genetics of urban bird populations. In: Gil, D. and Brumm, H. (eds.) *Avian Urban Ecology: Behavioural and Physiological Adaptations*. Oxford University Press (OUP), Oxford, UK, pp. 143-154.

Demeyrier, V*.*, Lambrechts, M.M., Perret, P. & Grégoire, A. (2016) Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. *Animal Behaviour*, **118**: 181 – 190. doi: 10.1016/j.anbehav.2016.06.007.

Demeyrier, V., Charmantier, A., Lambrechts, M.M. & Grégoire A. (2017) Disentangling drivers of reproductive performance in urban Great Tits: a food supplementation experiment. *Journal of Experimental Biology* **220(Pt 22)**: 4195 - 4203. doi: 10.1242/jeb.161067.

Derryberry, E.P. and Coomes, C.M. (2020) Providing urban birds nutritious food to feed chicks reduces urban versus rural breeding success disparities. *Journal of Animal Ecology* **89(7)**: 1546 - 1548. doi: 10.1111/1365-2656.13277.

de Satgé, J., Strubbe, D., Elst, J., De Laet, J., Adriaensen, F. & Mattheysen, E. (2019) Urbanisation lowers Great Tit (*Parus major*) breeding success at multiple spatial scales. *Journal of Avian Biology* **50**: e02108, 1 - 15. doi: 10.1111/jav.02108.

Desrochers, A. and Hannon, S.J. (1997) Gap Crossing Decisions by Forest Songbirds during the Post-Fledging Period: Decisíones de Cruce de Claros por Aves Paserinas de Bosques Durante el Periodo Post-Juvenil. *Conservation Biology* **11(5)**: 1204 - 1210. doi: 10.1046/j.1523-1739.1997.96187.x.

Desrochers, A., Bélisle, M. and Bourque, J. (2002) Do mobbing calls affect the perception of predation risk by forest birds? *Animal Behaviour* **64**: 709 – 714. doi: 10.1006/anbe.2002.4013.

Deviche, P. and Davies, S. (2014) Reproductive phenology of urban birds: environmental cues and mechanisms. In: Gil, D. and Brumm, H. (eds.) *Avian Urban Ecology: Behavioural and Physiological Adaptations.* Oxford University Press (OUP), Oxford, UK, pp. 99 - 115.

de Zwaan D.R., Drake, A., Greenwood, J.L. and Martin, K. (2020) Timing and Intensity of Weather Events Shape Nestling Development Strategies in Three Alpine Breeding Songbirds. Frontiers in Ecology and Evolution 8: 570034. doi: https://doi.org/10.3389/fevo.2020.570034.

Dhondt, A. A. (1989) Blue tit. In: *Lifetime reproduction in birds* (Edited by Newton, I.) Academic Press, London, UK.

Dhondt, A.A., Adriaensen, F., Matthysen, E. & Kempenaers, B. (1990) Nonadaptive clutch sizes in tits. *Nature* **348**: 723 - 725.doi: 10.1038/348723a0.

Dhondt, A. A. (2010) Effects of competition on Great and Blue Tit reproduction: intensity and importance in relation to habitat quality. *Journal of Animal Ecology* **79(1)**: 257 - 265.doi: 10.1111/j.1365-2656.2009.01624.x.

Dhondt, A.A., Kempenaers, B. and Adriaensen, F. (1992) Density-dependent clutch size caused by habitat heterogeneity. *The Journal of Animal Ecology* **61(3)**: 643 - 648. doi: 10.2307/5619.

Diamond, S.E., Cayton, H., Wepprich, T., Jenkins, C.N., Dunn, R.R., Haddad, N.M. & Ries, L. (2014) Unexpected phenological responses of butterflies to the interaction of urbanization and geographic temperature. *Ecology* **95(9)**:2613 – 21. doi: 10.1890/13-1848.1.

Diamond, S.E. and Martin, R.A. (2020) Evolutionary Consequences of the Urban Heat Island. In: Szulkin, M., Munshi-South, J. and Charmantier, A. (eds) *Urban Evolutionary Biology.* Oxford Academic online edition, Oxford, UK, pp. 91 –110. doi: 10.1093/oso/9780198836841.003.0006.

Dijkstra, C., Bult, A., Bijlsma, S, Serge, D., Meijer, T., & Zijlstra, M. (1990) Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology* **59(1)**: 269 – 285.

Di Pietro, S., Mantoni, C. and Fattorini, S. (2020) Influence of urbanization on the avian species-area relationship: insights from the breeding birds of Rome. *Urban Ecosystems* **24**: 779 - 788. doi: 10.1007/s11252-020-01081-4.

Dias, P.C. and Blondel, J. (1996) Breeding time, food supply and fitness components of Blue Tits *Parus caeruleus* in Meditteranean habitats. *Ibis* **138(4)**: 664 – 649. doi: 10.1111/j.1474-919X.1996.tb04766.x.

Dominoni, D. M. (2015) The effects of light pollution on biological rhythms of birds: an integrated, mechanistic perspective. *Journal of Ornithology* **156:** 409 - 418. doi: 10.1007/s10336-015-1196-3.

Dominoni, D.M., Jensen, J.K., de Jong, M., Visser, M.E., & Spoelstra, K. (2020) Artificial light at night, in interaction with spring temperature, modulates timing of reproduction in a passerine bird. *Ecological Applications* **30(3)**: e02062. doi: 10.1002/eap.2062.

Dominoni, D., Quetting, M. and Partecke, J. (2013) Artificial light at night advances avian reproductive physiology. *Proceedings of the Royal Society B: Biological Sciences* **280(1756)**. doi: 10.1098/rspb.2012.3017.

Douglas W. Tallamy and Shriver, G. W. (2021) Are declines in insects and insectivorous birds related? *Ornithological Applications* **123(1)**: 1 – 8. doi: 10.1093/ornithapp/duaa059.

Doutrelant, C., Grégoire, A., Grnac, N., Gomez, D., Lambrechts, M.M. & Perret. P. (2008) Female coloration indicates female reproductive capacity in Blue Tits. *Journal of Evolutionary Biology* **21(1)**: 226 - 233. doi: 10.1111/j.1420-9101.2007.01451.x.

DuRant, S. E., Hopkins, W.A., Hepp, G.R. & Walters, J.R. (2013) Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews* **88**: 499 – 509. doi: 10.1111/brv.12015.

Eaton, M.A., Noble, D.G., Cranswick, P.A., Carter, N., Wotton, S., Ratcliffe, N., Wilson, A., Hilton, G.M. & Gregory, R.D. (2004) *The State of the UK's Birds 2003.* Sandy: BTO, the RSPB and WWT.

Eeva, T., Lehikoinen, E. and Pohjalainen, T. (1997) Pollution-related variation in food supply and breeding success in two hole-nesting passerines. Ecology **78(4)**: 1120 – 1131. doi: 10.2307/2265863.

Eeva, T., Ryömä, M. and Riihimäki, J. (2005) Pollution-related changes in diets of two insectivorous passerines. Oecologia, **145**:629 – 639. doi: 10.1007/s00442-005-0145-x.

Eeva, T., Sillanpää, S., Salminen, J. P., Nikkinen, L., Tuominen, A., Toivonen, E., Pihlaja, K., & Lehikoinen, E. (2008) Environmental pollution affects the plumage color of Great Tit nestlings through carotenoid availability. *EcoHealth* **5(3)**: 328 – 337. doi: 10.1007/s10393-008-0184-y.

ESRI Green Cities: Resource Centre UK & Ireland Available at https://resource.esriuk.com/maps-gallery/green-cities/ (accessed 18/09/2017).

Evans, B.S., Ryder, T.B., Reitsma, R., Hurlbert, A.H., & Marra, P.P. (2015) Characterizing avian survival along a rural-to-urban land use gradient. *Ecology* **96(6)**: 1631 - 1640. http://www.jstor.org/stable/43495125.

Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D. & Gaston, K.J. (2011) What makes an urban bird? *Global Change Biology* **17**: 32 – 44. doi: 10.1111/j.1365-2486.2010.02247.x.

Evans, K.L., Gaston, K.J., Sharp, S.P., McGowan, A., Simeoni, M. & Hatchwell. B.J. (2009a) Effects of urbanisation on disease prevalence and age structure in blackbird *Turdus merula* populations. *Oikos*, **118(5)**: 774 – 782. doi: 10.1111/j.1600-0706.2008.17226.x.

Evans, K.L., Gaston, K.J., Sharp, S.P., McGowan, A. & Hatchwell. B.J. (2009b) The effect of urbanisation on avian morphology and latitudinal gradients in body size. *Oikos*, **118(2)**: 251 - 259. doi: 10.1111/j.1600-0706.2008.17092.x.

Evans, K.L., Van Rensburg, B.J., Gaston, K.J., & Chown, S.L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography* **15(6)**: 625 - 636.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C., Elvidge, C. D., Baugh, K., Portnov, B. A., Rybnikova, N. A., & Furgoni, R. (2016) The new world atlas of artificial night sky brightness. *Science advances* **2(6)**: e1600377. doi: 10.1126/sciadv.1600377.

Fenoglio, M.S., Rossetti, M.R. and Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. *Global Ecology and Biogeography* **29**: 1412 – 1429. doi: 10.1111/geb.13107.

Fenoglio, M.S., Calviño, A., González, E., Salvo, A. & Videla, M. (2021) Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecological Entomology* **46**: 757-771. doi: 10.1111/een.13041.

Fernández-Juricic, E. (2000a) Avifaunal Use of Wooded Streets in an Urban Landscape. *Conservation Biology* **14**: 513 – 521. doi: 10.1046/j.1523-1739.2000.98600.x.

Fernández-Juricic, E. (2000b) Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation. *Ecological Research* **15**: 373 - 383. doi: 10.1046/j.1440-1703.2000.00358.x.

Fernández-Juricic, E. (2001) Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodiversity and Conservation* **10**: 1303 - 1316. doi: 10.1023/A:1016614625675.

Fernández-Juricic, E. and Jokimäki, J. (2001) A habitat island approach to conserving birds in urban landscapes : case studies from southern and northern Europe. *Biodiversity and Conservation* **10**: 2023 – 2043. doi: 10.1023/A:1013133308987.

Fernández-Juricic, E. and Tellería, J.L. (2000) Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* **47(1)**: 13 – 21. doi: 10.1080/00063650009461156.

Filloy, J., Zurita, G. A. and Bellocq, M. I. (2019) Bird Diversity in Urban Ecosystems: The Role of the Biome and Land Use Along Urbanization Gradients. *Ecosystems* **22**: 213 - 227. doi: 10.1007/s10021-018-0264-y.

Fink, D.,T., Johnston, A.A., Strimas-Mackey, M., Ligocki, S., Robinson, O., Hochachka, W.M., Jaromczyk, L., Rodewald, A., Wood, C., Davies, I. & Spencer A. (2022) *eBird Status and Trends, Data Version: 2021;* Released: 2022. Cornell Lab of Ornithology, Ithaca, New

York. Available at: https://doi.org/10.2173/ebirdst.2021 (accessed 28/02/2023).

Fischer, J.D., Schneider, S.C., Ahlers, A.A., & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology* **29(4)**: 1246 – 1248. http://www.jstor.org/stable/24483200. doi: 10.1111/cobi.12451.

Fox, J. and Weisberg, S. (2019) Package 'car': An {R} Companion to Applied Regression, Third Edition. Sage, Thousand Oaks, CA, USA. Available at: https://socialsciences.mcmaster.ca/jfox/Books/Companion/ [Computer software].

Fuller, R.A. and Gaston, K.J. (2009) The scaling of green space coverage in European cities. *Biology Letters* **5(3)**: 352 - 355. doi: 10.1098/rsbl.2009.0010.

Fuller, R.A., Warren, P.H., & Gaston, K.J. (2007) Daytime noise predicts nocturnal singing in urban robins. *Biology Letters* **3(4)**: 368 - 370. doi: 10.1098/rsbl.2007.0134.

Fuller, R.A., Warren, P.H., Armsworth, P.R., Barbosa, O. & Gaston, K.J. (2008) Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and distributions* **14(1)**: 131 - 137.

Gaertner, M., Wilson, J.R.U., Cadotte, M.W., MacIvor, J.S., Zenni, R.D. & Richardson, D.M. (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. *Biological Invasions* **19**: 3461 – 3469. doi: 10.1007/s10530-017-1598-7

Galbraith, J. A., Beggs, J.R., Jones, D.N. & Stanley, M.C. (2015) Supplementary feeding restructures urban bird communities. *Proceedings of the National Academy of Sciences of the United States of America* **112(20)**: E2648-E2657. doi: 10.1073/pnas.1501489112.

Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological reviews of the Cambridge Philosophical Society* **88(4)**: 912 – 927. doi: 10.1111/brv.12036.

Gaston, K. J., Visser, M. E. and Hölker, F. (2015) The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **370(1667)**: 20140133. doi: 10.1098/rstb.2014.0133.

Gazzard, A., Yarnell, R.W. and Baker, P.J. (2022) Fine-scale habitat selection of a small mammalian urban adapter: the West European hedgehog (*Erinaceus europaeus*) *Mammalian Biology* **102**: 387–403 https://doi.org/10.1007/s42991-022-00251-5.

Germain, R.R. & Arcese, P. (2014) Distinguishing individual quality from habitat preference and quality in a territorial passerine. *Ecology* **95(2)**: 436 - 445. doi: 10.1890/13-0467.1.

Gibb., J. (1950) The breeding biology of the Great and Blue Titmice. *Ibis* **92**: 507 - 539. doi: 10.1111/j.1474-919X.1950.tb01759.x.

Gibb, J. (1954) Feeding Ecology of Tits, With Notes on Treecreeper and Goldcrest. *Ibis* **96(4)**: 513 – 543. doi: 10.1111/j.1474-919X.1954.tb05476.x.

Gibb, J. A. (1955) Feeding rates of Great Tits. *British birds* **48(2)**: 49 - 58.

Gil, D. and Brumm, H. (eds.) (2013) *Avian Urban Ecology*. Oxford University Press (OUP), Oxford, UK. doi: 10.1093/acprof:osobl/9780199661572.001.0001.

Gilbert, O.L. (1989) The ecology of urban habitats. Chapman and Hall, London, UK. Chapman & Hall, London.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., Cyzewska, I. & Bańbura, J. (2015) Inter-annual and inter-habitat variation in breeding performance of Blue Tits (*Cyanistes caeruleus*) in central Poland. *Ornis Fennica* **92**: 34–42.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., Cyżewska, I., Mańkowska, D., & Bańbura, J. (2016a) Effects of human-related disturbance on breeding success of urban and non-urban Blue Tits (*Cyanistes caeruleus*). *Urban Ecosystems* **19(3)**: 1325 – 1334. doi: 10.1007/s11252-016-0543-3.

Glądalski, M., Wawrzyniak, J., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Zieliński, P., & Bańbura, J. (2016b) Long-term changes in population density of nest-box breeding Great Tits and Blue Tits in two contrasting habitats in central Poland. *Polish Journal of Ecology.* doi: 10.3161/15052249PJE2016.64.3.009.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., Cyżewska, I. & Bańbura, J. (2017) Differences in the breeding success of Blue Tits *Cyanistes caeruleus* between a forest and an urban area: A long-term study. *Acta Ornithologica***52(1)**: 59 – 68. doi: 10.3161/00016454AO2017.52.1.006.

Goddard, M.A., Dougill, A.J. and Benton, T.G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution* **25(2)**: 90 - 98. doi: 10.1016/j.tree.2009.07.016.

Goodenough, A.E., Hart, A.G. and Elliot, S.L. (2011) What prevents phenological adjustment to climate change in migrant bird species? Evidence against the Barrival constraint hypothesis. *International Journal of Biometeorology* **55**: 97 – 102.

Gosler, A., Clement, P. and D.A. Christie (2020) Eurasian Blue Tit (*Cyanistes caeruleus*), version 1.0. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.) *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.blutit.01.

Gottlander, K. (1987) Parental feeding behaviour and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica* **18**: 269–276. doi: 10.2307/3676895.

Greenberg, R. (1989) Neophobia, aversion to open space, and ecological plasticity in song and swamp sparrows. *Canadian Journal of Zoology* **67**: 1194 – 1199.

Greño, J. L., Belda, E. J., & Barba, E. (2008). Influence of temperatures during the nestling period on post-fledging survival of great tit Parus major in a Mediterranean habitat. Journal of Avian Biology, 39(1), 41-49.

Grieco, F., Van Noordwijk, A. J. and Visser, M. E. (2002) Evidence for the effect of learning on timing of reproduction in Blue Tits. *Science* **296(5565)**: 136 – 138. doi: 10.1126/science.1068287.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M.

(2008) Global change and the ecology of cities. (2014). *Science* **319(5864)**: 756 - 760. doi: 10.1126/science.1150195.

Grimmond, S. (2007) Urbanization and global environmental change: local effects of urban warming. *The Geographical Journal* **173**: 83 – 88. doi: 10.1111/J.1475-4959.2007.232_3.X.

Guibert, F., Richard-Yris, M.A., Lumineau, S., Kotrschal, K., Möstl, E., & Houdelier, C. (2012) Yolk testosterone levels and offspring phenotype correlate with parental age in a precocial bird. *Physiology & behavior* **105(2)**: 242 - 250. doi: 10.1016/j.physbeh.2011.08,..009.

Gustafsson, L. (1988) Foraging behaviour of individual Coal Tits, *Parus ater*, in relation to their age, sex and morphology. *Animal Behaviour* **36(3)**: 696 - 704.

Gustafsson, L., Nordling, D., Andersson, M. S., Sheldon, B. C. & Qvarnstrom, A. (1994) Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **346(1317):** 323 – 331. http://www.jstor.org/stable/55965. doi: 10.1098/rstb.1994.0149.

Hagen, O.E., Hagen, O., Ibáñez-Álamo, J.D., Petchey, O.L. & Evans, K.L.(2017) Impacts of urban areas and their characteristics on avian functional diversity. *Frontiers in Ecology and Evolution* **5(84)**: 1 - 15. doi: 10.3389/fevo.2017.00084.

Hager, S.B., Cosentino, B.J., McKay, K.J., Monson, C., Zuurdeeg, W. & Blevins, B. (2013) Window Area and Development Drive Spatial Variation in Bird-Window Collisions in an Urban Landscape. *PLoS ONE* **8(1)**: e53371 doi: 10.1371/journal.pone.0053371.

Hager, S.B. and Craig, M.E. (2014) Bird-window collisions in the summer breeding season. *PeerJ 2,* e460. doi: 10.7717/peerj.460.

Haggard, W.H. (1990) Urban weather. *International Journal of Environmental Studies* **36(1–2)**: 73 – 82. doi: 10.1080/00207239008710584.

Hahs, A.K. and McDonnell, M.J. (2006) Selecting independent measures to quantify Melbourne's urban-rural gradient. *Landscape and Urban Planning* **78(4)**: 435 - 448. doi: 10.1016/j.landurbplan.2005.12.005.

Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W. & Williams, N. S. (2009) A global synthesis of plant extinction rates in urban areas. *Ecology letters* **12(11)**: 1165 - 1173. doi:10.1111/j.1461-0248.2009.01372.x.

Hajdasz, A.C., Otter, K.A., Baldwin, L.K. & Reudink, M.W. (2019) Caterpillar phenology predicts differences in timing of mountain chickadee breeding in urban and rural habitats. *Urban Ecosystems*. **22(6)**:1113–1122. doi: 10.1007/s11252-019-00884-4.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., & Sadler, J.P. (2012) Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. *PLoS ONE* **7(3)**: e33300. doi: 10.1371/journal.pone.0033300.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G. & Sadler, J.P. (2015) The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology* **21(7)**: 2467 – 2478. doi: 10.1111/gcb.12884.

Halfwerk, W.H., Holleman, L.J.M., Lessells, C.M. & Slabbekoorn, H. (2011) Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* **48**: 210 - 219. doi: 10.1111/j.1365-2664.2010.01914.x.

Hall, S., Harriss, S., Kerwin, B. & Fowell, M. (2022) *Statistical Digest of Rural England*, August 2022 Edition, Department for Environment, Food and Rural Affairs. Available at: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/1100175/07_Statistical_Digest_of_Rural_England_2022_August_edition.pdf (accessed 07/02/2023).

Hamer, A.J. (2022) A multi-scale, multi-species approach highlights the importance of urban greenspace and pond design for amphibian communities. *Urban Ecosyst*ems **25**: 393 – 409. doi: 10.1007/s11252-021-01162-y.

Hamer, A.J. and McDonnell, M.J. (2008) Amphibian ecology and conservation in the urbanising world: A review. *Biological Conservation* **141(10)**: 2432 - 2449. doi: 10.1016/j.biocon.2008.07.020.

Hamer, A.J. and McDonnell, M.J. (2010) The response of herpetofauna to urbanization: Inferring patterns of persistence from wildlife databases *Austral Ecology* **35**: 568 - 580. doi: 10.1111/j.1442-9993.2009.02068.x.

Hanmer, H.J., Thomas, R. L. and Fellowes, M.D.E. (2016) Provision of supplementary food for wild birds may increase the risk of local nest predation. *Ibis* **159(1)**: 158 – 167. doi: 10.1111/ibi.12432.

Harrison, T.J.E., Smith, J.A., Martin, G.R., Chamberlain, D.E., Bearhop, S., Robb, G.N. & Reynolds, S. J. (2010) Does food supplementation really enhance productivity of breeding birds?, *Oecologia* **164(2)**: 311 - 320. doi: 10.1007/s00442-010-1645-x.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**: 4 - 18. doi: 10.1111/j.1365-2656.2010.01740.x.

Hartig, F. & Lohse, L. (2020) DHARMa: Residual diagnostics for hierarchical regression models (0.3. 3.0) [Computer software].

Hartig, F. (2022) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.5. https://CRAN.R-project.org/package=DHARMa [Computer software].

Hartmann, D.L., and Stocker, T.F. (2013) Observations: atmosphere and surface. In Stocker, T.F. *et al*. (eds.) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Haskell, D.G., Knupp, A.M. and Schneider, M.C. (2001) Nest predator abundance and urbanization. In: Marzluff, J. M., Bowman, R., and Donnelly, R. (eds.) *Avian Ecology and Conservation in an Urbanizing World.* Springer US, Boston, MA, pp. 243–258. doi: 10.1007/978-1-4615-1531-9_11.

Hedblom, M. and Söderström, B. (2010) Landscape effects on birds in urban woodlands: an analysis of 34 Swedish cities. *Journal of Biogeography* **37(7)**: 1302 - 1316. doi: 10.1111/j.1365-2699.2010.02299.x.

Hedblom, M. and Söderström, B. (2012) Effects of urban matrix on reproductive performance of Great Tit (*Parus major*) in urban woodlands. *Urban Ecosystems***15(1)**: 167 – 180. doi: 10.1007/s11252-011-0204-5.

Heim, R.R. (2015) An overview of weather and climate extremes – Products and trends. *Weather and Climate Extremes* **10(B)**: 1 – 9. doi: 10.1016/j.wace.2015.11.001.

Hetem, R.S., Fuller, A., Maloney, S.K., & Mitchell, D. (2014) Responses of large mammals to climate change. *Temperature* **1(2)**: 115 - 127. doi: 10.4161/temp.29651.

Hidalgo Aranzamendi, N., Hall, M. L., Kingma, S. A., van de Pol, M., & Peters, A. (2019). Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. Journal of Animal Ecology, 88(11), 1799-1811. doi: 10.1111/1365-2656.13068.

Higgot, C.G., Evans, K.L. and Hatchwell, B.J. (2020) Incubation in a temperate passerine: do environmental conditions affect incubation period duration and hatching success? *Frontiers in Ecology and Evolution* **8**. doi: 10.3389/fevo.2020.542179.

Hildén, O. (1982) Proportion of juveniles as a measure of adult mortality in a breeding population of Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*). *Ornis Fennica* **59**: 149 - 151.

Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. (2015) Scale-Dependent Phenological Synchrony between Songbirds and Their Caterpillar Food Source. *The American Naturalist* **186(1)**:84 – 97. doi: 10.1086/681572.

Hinsley, S.A. (2000) The costs of multiple patch use by birds. *Landscape Ecology* **15**: 765 - 775. doi: 10.1023/A:1008149403852.

Hinsley, S.A., Bellamy, P.E., Newton, I., & Sparks, T.H. (1995) Habitat and Landscape Factors Influencing the Presence of Individual Breeding Bird Species in Woodland Fragments. *Journal of Avian Biology* **26(2**): 94 - 104. doi: 10.2307/3677057.

Hinsley, S.A., Bellamy, P.E., Hill, R.A & Dawson, A. (2002) Birds and habitat quality: effects of wood size and spatial arrangement in the landscape. In: *Avian landscape ecology: pure and applied issues in the large-scale ecology of birds. Proceedings of the eleventh annual IALE (UK) conference.* University of East Anglia, UK, 10-13 September 2002. International Association for Landscape Ecology (IALE, UK), Norwich, UK, pp. 15–24.

Hinsley, S.A., Hill, R.A., Bellamy, P.E., Harrison, N.M., Speakman, J.R., Wilson, A.K. & Ferns, P.N. (2008) Effects of structural and functional habitat gaps on breeding woodland birds: working harder for less. *Landscape Ecology* **23**: 615 - 626. doi: 10.1007/s10980-008-9225-8.

Hinsley, S.A., Rothery, P. and Bellamy, P.E. (1999) Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *Journal of Avian Biology* **30**: 271 - 281. doi: 10.2307/3677353.

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

Hochachka, W.M. and Smith, J.N.M. (1991) Determinants and consequences of nestling condition in Song Sparrows. *Journal of Animal Ecology Ecology* **60**: 995 – 1008. doi: 10.2307/5427.

Hohtola, E. and Visser, G. H. (1998) *Development of locomotion and endothermy in altricial and precocial birds.* In Avian Growth and Development. Evolution Within the Altricial-precocial Spectrum (ed. J. M. Starck and R. E. Ricklefs), pp. 157-173. Oxford: Oxford University Press.

Hollander, F.A., Titeux, N. and Van Dyck, H. (2013) Habitat-dependent prey availability and offspring provisioning explain an ecological trap in a migratory bird. *Functional Ecology* **27**: 702 – 709. doi: 10.1111/1365-2435.12077.

Hõrak, P. (1993) Low fledging success of urban Great Tits. *Ornis Fennica*, **70(3)**:168 – 172.

Hostetler, M. (2001) The importance of multi-scale analyses in avian habitat selection studies in urban environments. In: Marzluff, J.M., Bowman, R. and Donelly, R. (eds.) *Avian Ecology and Conservation in an Urbanizing World*. Springer US, Boston, MA, pp. 139 – 154. doi: 10.1007/978-1-4615-1531-9_7.

Hostetler, M., Allen, W. and Meurk, C. (2011) Conserving urban biodiversity? Creating green infrastructure is only the first step. *Landscape and Urban Planning* **100**: 369 – 371. doi: 10.1016/J.LANDURBPLAN.2011.01.011.

Hostetler, M. and Holling, C.S. (2000) Detecting the scales at which birds respond to structure in urban landscapes. *Urban Ecosystems* **4**: 25 - 54. doi: 10.1023/A:1009587719462.

Huang, Y., Zhao, Y., Li, S. & von Gadow, K. (2015) The effects of habitat area, vegetation structure and insect richness on breeding bird populations in Beijing urban parks. *Urban Forestry and Urban Greening***14(4)**: 1027 – 1039. doi: 10.1016/j.ufug.2015.09.010.

Hunter, A. F., and Lechowicz, M. J. (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology* **29(3)**: 597 - 604. doi: 10.2307/2404467.

Hutto, D. J. and Barrett, K. (2021) Do urban spaces provide refugia for frogs in urban environments? *PLoS ONE* **16(1):** e0244932. doi: 10.1371/journal.pone.0244932.

Ibáñez-Álamo, J.D., Rubio, E., Benedetti, Y. & Morelli, F. (2017) Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biology* **23**: 2990 - 2998. doi: 10.1111/gcb.13567.

Imhoff, M.L., Zhang, P., Wolfe, R.E. & Bounoua, L. (2010) Remote sensing of the urban heat island effect across biomes in the continental USA. *Remote Sensing of Environment*. **114(3)**: 504 – 513. doi: 10.1016/j.rse.2009.10.008.

Injaian, A.S., Taff, C.C., Pearson, K.L., Gin, M.M.Y., Patricelli, G.L. & Vitousek, M.N. (2018a)

Effects of experimental chronic traffic noise exposure on adult and nestling corticosterone levels, and nestling body condition in a free-living bird. *Hormones and Behavior* **106**: 19 - 27. doi: 10.1016/j.yhbeh.2018.07.012.

Injaian, A. S., Taff, C. C. and Patricelli, G. L. (2018b) Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress. *Animal Behaviour* **136**: 31 - 39. doi: 10.1016/j.anbehav.2017.12.003.

IPCC. (2012) *Managing the risks of extreme events and disasters to advance climate change adaptation. In: A special report of working groups I and II of the intergovernmental panel on climate change* (eds. CB Field et al.). Cambridge University Press, Cambridge, UK. pp. 582.

IPCC (2018) Summary for Policymakers. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 3 – 24. doi: 10.1017/9781009157940.001.

IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V.,P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, doi:10.1017/9781009157896.

Isaksson, C. (2010) Pollution and its impact on wild animals : a meta-analysis on oxidative stress. *EcoHealth* **7(3)**: 342 – 350. doi: 10.1007/s10393-010-0345-7.

Isaksson, C. (2018) Impact of Urbanization on Birds. In: Tieze, D.T. (ed.) *Bird Species. Fascinating Life Sciences.* Springer, Cham, pp. 235–257. doi: 10.1007/978-3-319-91689-7_13.

Isaksson, C. and Andersson, S. (2007) Carotenoid diet and nestling provisioning in urban and rural Great Tits *Parus major*. *Journal of Avian Biology* **38(5)**: 564 - 572. doi: 10.1111/j.0908-8857.2007.04030.x.

Isaksson, C., Uller, T., and Andersson, S. (2006) Parental effects on carotenoid-based plumage coloration in nestling great tits, *Parus major*. *Behavioral Ecology and Sociobiology* **60**: 556-562.

Jakob, E.M., Marshall, S.D., and Uetz, G. W. (1996) Estimating fitness: a comparison of body condition indices. Oikos **7(1)**: 61 - 67. doi: 10.2307/3545585.

Jarrett, C., Powell, L.L., McDevitt, H., Helm, B. & Welch, A.J. (2020) Bitter fruits of hard labour: diet metabarcoding and telemetry reveal that urban songbirds travel further for lower-quality food. *Oecologia* **193(2)**: 377–388. doi: 10.1007/s00442-020-04678-w.

Johnson, M.D. (2007) Measuring habitat quality: a review. *The Condor* **109(3)**: 489 - 504.

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

Jokimäki, J. and Suhonen, J. (1993) Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison. *Ornis Fennica* **70**: 71 - 71.

Jones, D.N. and Reynolds, S.J. (2008) Feeding birds in our towns and cities: a global research opportunity. *Journal of Avian Biology* **39(3)**: 265 – 271. doi: 10.1111/j.0908-8857.2008.04271.x.

Jones, E.L. and Leather, S.R. (2012) Invertebrates in urban areas: A review. *European Journal of Entomology* **109**: 463 - 478. doi: 10.14411/EJE.2012.060.

Joys, A.C. and Crick, H.Q.P. (2004) *Breeding periods for selected bird species in England.* BTO Research Report No. 352. British Trust for Ornithology, Thetford, UK.

Jukka, S. and Jokimäki, J. (1988) A biogeographical comparison of the breeding bird species assemblages in twenty Finnish urban parks. *Ornis Fennica* **65(2)**: 76 – 83.

Kaiser, A., Merckx, T. and Van Dyck, H. (2018) Urbanisation and sex affect the consistency of butterfly personality across metamorphosis. *Behavioural Ecology and Sociobiology* **72**: 188. doi: 10.1007/s00265-018-2616-1.

Kaliński, A.,Wawrzyniak, J., Bańbura, M., Skwarska, J., Zieliński, P. & Bańbura, J. (2009) Haemoglobin concentration and body condition of nestling Great Tits *Parus major*: a comparison of first and second broods in two contrasting seasons. *Ibis*, **151(4)**: 667–676. doi: https://doi.org/10.1111/j.1474-919X.2009.00959.x.

Kaliński, A., Bańbura, M., Glądalski, M., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P. & Bańbura, J. (2019) Physiological condition of nestling Great Tits (*Parus major*) declines with the date of brood initiation: a long term study of first clutches. *Scientific Reports* **9(1):** 9843. doi: https://doi.org/10.1038/s41598-019-46263-z.

Keller, L.F. and Van Noordwijk, A.J. (1994) Effects of local environmental conditions on nestling growth in the Great Tit *Parus major L. Ardea* **82**: 349 – 362.

Kempenaers, B., Adriaensen, F., Van Noordwijk, A.J. & Dhondt, A.A. (1996) Genetic similarity, inbreeding and hatching failure in Blue Tits: are unhatched eggs infertile? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **263(1367)**: 179 – 185. https://www.jstor.org/stable/50471. doi: 10.1098/rspb.1996.0029.

Kempenaers, B., Adriaensen, F. and Dhondt, A.A. (1998) Inbreeding and divorce in Blue and Great Tits. *Animal Behaviour* **56**: 737 – 740. doi: 10.1006/anbe.1998.0800.

Kennedy, C.E.J. and Southwood, T.R.E. (1984) The number of species of insects associated with British trees: a re-analysis. *The Journal of Animal Ecology* **53(2)**: 455-478.

Kiritani, K. (2013) Different effects of climate change on the population dynamics of insects. *Applied Entomology and Zoology* 48(2): 97 - 104. doi:10.1007/s13355-012-0158-y.

Koenig, J., Shine, R. and Shea, G. (2001) The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? *Wildlife Research* **28**: 215 – 227. doi: 10. .1071/WR00068.

Knowles, S.C.L., Wood, M.J. and Sheldon, B.C. (2010) Context-dependent effects of parental effort on malaria infection in a wild bird population, and their role in reproductive trade-offs. *Oecologia* **164**: 87 - 97. doi: 10.1007/s00442-010-1706-1.

Kruger, D.J.D., Hamer, A.J. & Du Preez, L.H. (2015) Urbanization affects frog communities at multiple scales in a rapidly developing African city. *Urban Ecosystems* **18**: 1333 – 1352 doi: 10.1007/s11252-015-0443-y.

Labocha, M.K., & Hayes, J.P. (2012) Morphometric indices of body condition in birds: a review. *Journal of Ornithology* **153**: 1 - 22. doi: 10.1007/s10336-011-0706-1.

Lack, D. (1954) *The natural regulation of animal numbers.* Clarendon Press, Oxford, UK.

Lahti, D.C. (2001) The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99(3)**: 365 - 374. doi: 10.1016/S0006-3207(00)00222-6.

Lambrechts, M.M., Blondel, J., Maistre, M. & Perret, P. (1997) A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proceedings of the National Academy of Sciences* **94(10)**: 5153 - 5155. doi: 10.1073/pnas.94.10.5153.

Lambrechts, M.M., Caro, S., Charmantier, A., Gross, N., Galan, M.-J., Perret, P., Cartan-Son, M., Dias, P.C., Blondel, J. & Thomas, D.W. (2004) Habitat quality as a predictor of spatial variation in Blue Tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. *Oecologia* **141(4)**: 555 – 561. http://www.jstor.org/stable/40005615. doi: 10.1007/s00442-004-1681-5.

LaPoint, S., Balkenhol, N., Hale, J., Sadler, J.P. & van der Ree, R. (2015) Ecological connectivity research in urban areas. *Functional Ecology* **29**: 868 – 878. doi: 10.1111/1365-2435.12489.

Learmonth, J.A., MacLeod, C.D., Santos, M.B., Pierce, G.J., Crick, H.Q.P., & Robinson, R.A. (2006) Potential effects of climate change on marine mammals. *Oceanography and Marine Biology* **44**: 431 - 464.

Leech, D.I., and Crick, H.Q.P. (2007) Influence of climate change on the abundance, distribution and phenology of woodland bird species in temperate regions. *Ibis* **149**: 128 – 145. doi: 10.1111/j.1474-919X.2007.00729.x.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P., & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320(5884)**: 1768 - 1771. doi: 10.1126/science.11568.

Lepczyk, C.A., Aronson, M.F.J., Evans, K.L., Goddard, M.A., Lerman, S.B.J. & MacIvor, S. (2017) Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. *BioScience* **67(9)**: 799 – 807. doi: 10.1093/biosci/bix079.

Lepczyk, C. A., & Warren, P. S. (Eds.). (2012) *Urban bird ecology and conservation* (Vol. 45). Univ of California Press, USA.

Leveau, L.M., Ruggiero, A., Matthews, T.J. & Isabel Bellocq, M. (2019) A global consistent positive effect of urban green area size on bird richness.. *Avian Research* **10(1)**: 1 - 14. doi: 10.1186/s40657-019-0168-3.

Li, B., Zhang, W., Shu,. X, Pei, E., Yuan, X., Wang, T. & Wang, Z. (2018) Infuence of breeding habitat characteristics and landscape heterogeneity on anuran species richness and abundance in urban parks of Shanghai, China. *Urban For Urban Green* **32**: 56 – 63.

doi: 10.1016/j.ufug.2018.03.017.

Li, G., Wan, X., Yin, B., Wei, W., Hou, X., Zhang, X., Batsuren, E., Zhao, J., Huang, S., Xu, X, Song, Y., Ozgul, A., Dickman, C.R., Wang, G, Krebs, C.J. & Zhang, Z. (2021). Timing outweighs magnitude of rainfall in shaping population dynamics of a small mammal species in steppe grassland. *Proceedings of the National Academy of Sciences* **118(42)**: e2023691118. doi: https://doi.org/10.1073/pnas.2023691118.

Liker, A., Papp, Z., Bókony, V. & Lendvai, Á.Z. (2008) Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology* **77**: 789 - 795. doi: 10.1111/j.1365-2656.2008.01402.x.

Lombardi, R.D., Porter, L., Barber, A. & Rogers, C.D.F. (2011) Conceptualising Sustainability in UK Urban Regeneration: a Discursive Formation. *Urban Studies* 4**8(2)**: 273–296. doi: 10.1177/0042098009360690.

Łopucki, R., Klich, D. and Kiersztyn, A. (2021) Changes in the social behavior of urban animals: more aggression or tolerance? *Mammalian Biology* **101**: 1 – 10. doi: 10.1007/s42991-020-00075-1.

Loram, A., Tratalos, J., Warren, P.H. & Gaston, K.J. (2007) Urban domestic gardens (X): the extent and structure of the resource in five major cities. *Landscape Ecology* **22**: 601 – 615. doi: 10.1007/s10980-006-9051-9.

Loss, S. R., Will, T., Loss, S.S. & Marra, P.P. (2014a) Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. *The Condor* **116(1)**: 8 - 23. doi: 10.1650/condor-13-090.1.

Loss, S.R., Will, T. and Marra, P.P. (2014b) Estimation of bird-vehicle collision mortality on U.S. roads. *Journal of Wildlife Management* **78(5)**: 763 - 771. doi: 10.1002/jwmg.721.

Lowry, H., Lill, A., & Wong, B.B. (2013) Behavioural responses of wildlife to urban environments. *Biological reviews* **88(3)**: 537 - 549. doi: 10.1111/brv.12012.

Lynch, H.J., Thorson, J.T. and Shelton, A.O. (2014) Dealing with under- and over-dispersed count data in life history, spatial, and community ecology. *Ecology* **95**: 3173 - 3180. doi: 10.1890/13-1912.1.

MacArthur, R.H. and Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist* **100(916)**: 603 – 609.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, USA.

MacGregor-Fors, I., Ortega-Álvarez, R. and Schondube, J. E. (2009). On the ecological quality of urban systems: An ornithological perspective. In: Graber, D. S. & Birmingham, K. A. (eds.) *Urban planning in the 21st century*, pp. 51–66, Nova Science Publishing, New York, NY, USA.

MacGregor-Fors, I. (2011) Misconceptions or misunderstandings? On the standardisation of basic terms and definitions in urban ecology. *Lanscape and urban planning* **100(4)**: 347 – 349. doi: 10.1016/j.landurbplan.2011.01.013.

MacGregor-Fors, I. and Schondube, J.E. (2011) Gray vs. green urbanisation: Relative importance of urban features for urban bird communities. *Basic and Applied Ecology* **12**: 372 – 381. doi: 10.1016/j.baae.2011.04.003.

Mackay, B., Lee, A.T.K., Barnard, P., Møller, A.P. & Brown, M. (2017) Urbanization, climate and ecological stress indicators in an endemic nectarivore, the Cape Sugarbird. *Journal of Ornithology* **158(4)**: 1013 – 1024. doi: 10.1007/s10336-017-1460-9.

Mackenzie, J.A., Hinsley, S.A. and Harrison, N.M. (2014) Parid foraging choices in urban habitat and their consequences for fitness. *Ibis* **156(3)**: 591 - 605. doi: 10.1111/ibi.12166.

Mainwaring, M.C., Dickens, M., and Hartley, I.R. (2010) Environmental and not maternal effects determine variation in offspring phenotypes in a passerine bird. *Journal of Evolutionary Biology* **23(6)**: 1302 - 1311. doi: 10.1111/j.1420-9101.2010.01997.x.

Mainwaring, M.C., Dickens, M., & Hartley, I.R. (2011) Sexual dimorphism and growth trade-offs in Blue Tit Cyanistes caeruleus nestlings. *Ibis* **153(1)**: 175 - 179.

Mainwaring, M.C. and Hartley, I.R. (2016) Local weather conditions have complex effects on the growth of Blue Tit nestlings. *Journal of Thermal Biology* **60**: 12 – 19. doi: 10.1016/j.jtherbio.2016.05.005.

Manley, G. (1958) On the frequency of snowfall in metropolitan England. *Quarterly Journal of the Royal Meteorological Society* **84(359)**: 70 - 72.

Marciniak, B., Nadolski, J., Nowakowska, M., Loga, B. & Bańbura, J. (2007) Habitat and annual variation in arthropod abundance affects Blue Tit *Cyanistes caeruleus* reproduction. *Acta Ornithologica* **42(1)**: 53 - 62. doi: 10.3161/000164507781646870.

Marín-Gómez, O.H. and McGregor-Fors, I. (2021) Review: A global synthesis of the impacts of urbanization on bird dawn choruses. *Ibis* **163(4)**: 1133 – 1154. doi: 10.1111/ibi.12949.

Markowski, M., Bańbura, M., Kaliński, A., Markowski, J., Skwarska, J., Wawrzyniak, J., Zieliński, P & Bańbura, J. (2014) Spatial and Temporal Variation of Lead, Cadmium, and Zinc in Feathers of Great Tit and Blue Tit Nestlings in Central Poland. *Archives of Environmental Contamination and Toxicology* **67**: 507 – 518. doi: 10.1007/s00244-014-0028-4.

Marques-Santos, F. and Dingemanse, N.J. (2020) Weather effects on nestling survival of Great Tits vary according to the developmental stage. *Journal of Avian Biology* **51(10)**: 1 - 12, e02421. doi: 10.1111/jav.02421.

Marques-Santos, F., Wischhoff, U. and Rodrigues, M. (2021) Weather fluctuations are linked to nesting success and renesting decisions in Saffron Finches. *Journal of Avian Biology* **52:** 1 - 12, e02323,. doi: 10.1111/jav.02323.

Marrot, P., Charmantier, A., Blondel, J., & Garant, D. (2018) Current spring warming as a driver of selection on reproductive timing in a wild passerine. *Journal of Animal Ecology* **87(3)**: 754 – 764. doi: 10.1111/1365-2656.12794.

Marrot, P., Garant, D. and Charmantier, A. (2017) Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **372(1723)**: 20160372. doi: 10.1098/rstb.2016.0372.

Martin, K., Wilson, S., MacDonald, E.C., Camfield, A.F., Martin, M., & Trefry, S.A. (2017) Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. *The Auk* **134(3)**: 696 - 709. doi: 10.1642/AUK-16-271.1.

Marvel, K. and Bonfils, C. (2013) Identifying external influences on global precipitation. *Proceedings of the National Academy of Sciences USA* **110(48)**: 19301 – 19306. doi: 10.1073/pnas.1314382110.

Marzluff, J.M. (2001) Worldwide urbanization and its effects on birds. In: Marzluff, J.M., Bowman, R., and Donnelly, R. (eds.) *Avian Ecology and Conservation in an Urbanizing World.* Springer US, Boston, MA, pp. 19 - 47. doi: 10.1007/978-1-4615-1531-9_2.

Marzluff, J.M. (2008) *Urban* ec*ology: an international perspective on the interaction between humans and nature.* New York: Springer.

Marzluff, J.M. (2016) A decadal review of urban ornithology and a prospectus for the future. *Ibis* **159(1)**: 1 - 13. /doi: 10.1111/ibi.12430.

Marzluff, J.M., DeLap, J.H., Oleyar, M.D., Whittaker, K.A. & Gardner, B. (2016) Breeding dispersal by birds in a dynamic urban ecosystem. *PLoS ONE* **11(12)**: e0167829, 1 - 20. doi: 10.1371/journal.pone.0167829.

Mason, C.F. (2008) Thrushes now largely restricted to the built environment in eastern England. *Diversity and Distributions* **6(4)**: 189 – 194. doi: 10.1046/j.1472-4642.2000.00084.x.

Matthews, T. (2015) Analysing and modelling the impact of habitat fragmentation on species diversity: a macroecological perspective. *Frontiers of Biogeography* **7(2)**: 60 – 68. doi: 10.21425/F5FBG25942.

Matthysen, E. and Currie, D. (1996) Habitat fragmentation reduces disperser success in juvenile Nuthatches *Sitta europaea*: evidence from patterns of territory establishment. *Ecography* **19(1)**: 67 - 72.

Matthysen, E., Adriaensen, F. and Dhondt, A.A. (2011) Multiple responses to increasing spring temperatures in the breeding cycle of Blue and Great Tits (*Cyanistes caeruleus, Parus major*). *Global Change Biology*, **17(1)**: 1 - 16. doi: 10.1111/j.1365-2486.2010.02213.x.

Mayor, S. J., Schneider, D. C., Schaefer, J. A. & Mahoney, S. P. (2009) Habitat selection at multiple scales. *Ecoscience* **16(2)**: 238 - 247. doi: 10.2980/16-2-3238.

Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., Andrew, M.E., Leyk, S., Pearse, I.S. & Schneider, D.C. (2017) Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports* **7(1)**:1902, 1 - 10. doi: 10.1038/s41598-017-02045-z.

Maziarz, M., Wesołowski, T., Hebda, G. *& Cholewa* (2015) Natural nest-sites of Great Tits (*Parus major*) in a primeval temperate forest (Białowieża National Park, Poland). *Journal of Ornithology* **156**: 613–623. https://doi.org/10.1007/s10336-015-1169-6.

McCaffrey, R.E. and Mannan, R. W. (2012) How scale influences birds' responses to habitat features in urban residential areas. *Landscape and Urban Planning* **105(3)**: 274 - 280.

McDonald, R.I., Kareiva, P. and Forman, R.T.T. (2008) The implications of current and future urbanisation for global protected areas and biodiversity conservation. *Biological Conservation* **141(6):** 1695-1703. doi: 10.1016/j.biocon.2008.04.025.

McDonald, R., Guneralp, B., Zipperer, W., & Marcotullio, P. (2014) The future of global urbanization and the environment. Solutions **5(6)**: 60 - 69. doi: 10.1016/j.biocon.2008.04.025.

McDonnell, M.J. and Hahs, A.K. (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecology* **23**: 1143 - 1155. doi: 10.1007/s10980-008-9253-4.

McDonnell, M.J. and Hahs, A.K. (2015) Adaptation and adaptedness of organisms to urban environments. *Annual review of ecology, evolution, and systematics* **46**: 261 - 280. doi: 10.1146/annurev-ecolsys-112414-054258.

McDonnell, M.J. and Pickett, S.T.A. (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* **71(4)**: 1232 –1237. doi: 10.2307/1938259.

McDonnell, M. J., Pickett, S. T. A. and Pouyat, R. V. (1993) The application of the ecological gradient paradigm to the study of urban effects. In: McDonnell, M. J. and Pickett, S. T. A. (eds.) *Humans as components of ecosystems*. Pages 175-189, Springer-Verlag, New York, New York, USA.

McEwan, C., Pollard, J. and Henry, N. (2005) The "Global" in the City Economy: Multicultural Economic Development in Birmingham. *International Journal of Urban and Regional Research* **29(4)**: 916 – 933. doi: 10.1111/j.1468-2427.2005.00628.x.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C. & Cushman, S.A. (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* **31**: 1161 - 1175. doi: 10.1007/s10980-016-0374-x.

McIntyre, N.E. (2000) Ecology of urban arthropods: a review and a call to action. *Annals of the Entomological Society of America* **93**: 825 – 835. doi: 10.1603/0013-8746(2000)093[0825:EOUAAR]2.0.CO;2.

McKinney, M.L. (2002) Urbanization, biodiversity, and conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* **52(10)**: 883 – 890. doi: 10.1641/0006-3568.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127(3)**: 247 – 260. doi: 10.1016/j.biocon.2005.09.005.

McKinney, M.L. (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* **11**: 161–176. doi: 10.1007/s11252-007-0045-4.

McMahon, C.R., and Burton, H.R. (2005) Climate change and seal survival: evidence for environmentally mediated changes in Elephant Seal, *Mirounga leonina*, pup survival. *Proceedings of the Royal Society B: Biological Sciences* **272(1566)**: 923 - 928.

Meillère, A., Brischoux, F., Parenteau, C. & Angelier, F. (2015) Influence of urbanization on body size, condition, and physiology in an urban exploiter: A multi-component approach. *PLoS ONE* **10(8)**: e0135685, 1 - 19. doi: 10.1371/journal.pone.0135685.

Meillère, A., Brischoux, F., Henry, P-Y., Michaud, B., Garcin, R. & Angelier, F. (2017) Growing in a city: Consequences on body size and plumage quality in an urban dweller, the House Sparrow (*Passer domesticus*). *Landscape and Urban Planning* **160**: 127 - 138/ doi: 10.1016/j.landurbplan.2016.12.014.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N., De Wolf, K., Engelen, J.M.T., Fontaneto, D., Gianuca, A.T., Govaert, L., Hendrickx, F., Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Piano, E., Sablon, R., Schön, I., Van Doninck, K., De Meester, L. & Van Dyck, H. (2018) Body-size shifts in aquatic and terrestrial urban communities. *Nature* **558(7708)**: 113 - 116. doi: 10.1038/s41586-018-0140-0.

Mertens, J. A.L. (1977) Thermal conditions for successful breeding in Great Tits *Parus major L.*): I. Relation of growth and development of temperature regulation in nestling Great Tits. *Oecologia* **28(1)**: 1 - 29. doi: 10.1007/BF00346834.

Met Office (2003) Met Office Rain Radar Data from the NIMROD System. NCAS British Atmospheric Data Centre. Available at: http://catalogue.ceda.ac.uk/uuid/82adec1f896af6169112d09cc1174499.

Met Office (2006) UK Daily Temperature Data, Part of the Met Office Integrated Data Archive System (MIDAS). NCAS British Atmospheric Data Centre. Available at: http://catalogue.ceda.ac.uk/uuid/1bb479d3b1e38c339adb9c82c15579d8 (accessed from 28/10/2017).

Met Office Hadley Centre (2015) Our changing climate – the current science. *Climate Service UK*. Available at: http://www.metoffice.gov.uk/media/pdf/4/b/Our_changing_climate_-_the_current_science.pdf. (accessed 18/06/2019).

Metcalfe, N.B. and Monaghan, P. (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* **16(5)**: 254 – 260. doi: 10.1016/S0169-5347(01)02124-3.

Millán, M.F., Carranza, J., Perez-Gonzalez, J., Valencia, J., Torres-Porras, J., Seoane, J. M., de la Peña, E., Alarcos, S., Sánchez-Prieto, C.B., Castillo, L., Flores, A. & Membrillo, A. (2021) Rainfall decrease and red deer rutting behaviour: Weaker and delayed rutting activity though higher opportunity for sexual selection. *Plos one* **16(1)**: e0244802. doi: 10.1371/journal.pone.0244802.

Miranda, A.C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013) Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology* **19(9)**: 2634 - 2644. doi: 10.1111/gcb.12258.

Møller, A. P., Fiedler, W., & Berthold, P. (eds.). (2010) *Effects of climate change on birds*. Oxford University Press, Oxford, UK.

Møller, A.P. (2013) Biological consequences of global change for birds. *Integrative Zoology* **8(2)**: 136 – 144. doi: 10.1111/1749-4877.12006.

Moll, R. J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Tans, E., Robison, T., Millspaugh, J.J. & Montgomery, R.A. (2019) What does urbanization actually mean? A framework for urban metrics in wildlife research. *Journal of Applied Ecology* **56(5)**: 1289 - 1300. doi: 10.1111/1365-2664.13358.

Monaghan, P. and Nager, R. G. (1997) Why don't birds lay more eggs? *Trends in Ecology and Evol*ution **12**: 270 – 274. doi: 10.1016/S01695347(97)01094-X.

Monaghan, P. (2008) Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **363**: 1635 – 1645. doi: .1098/rstb.2007.0011.

Morganti, M., Rubolini, D., Caprioli, M., Saino, N. & Ambrosini, A. (2017) Rainfall, but not temperature, negatively affects the growth of Blue Tit *Cyanistes caeruleus* nestlings. *Bird Study* **64(2)**: 159 – 167. doi: 10.1080/00063657.2017.1309006.

Mörtberg, U.M. (2001) Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landscape Ecology* **16**: 193 – 203. doi: 10.1023/A:1011190902041

Mueller, M.A., Drake, D. and Allen, M.L. (2018) Coexistence of coyotes (*Canis latrans*) and red foxes (V*ulpes vulpes*) in an urban landscape. PLoS ONE **13(1)**: e0190971. doi: 10.1371/journal.pone.0190971

Muller, R., Amar, A., Sumasgutner, P., McPherson, S.C. & Downs, C.T. (2020) Urbanization is associated with increased breeding rate, but decreased breeding success, in an urban population of near-threatened African Crowned Eagles. *Condor* **122(3)**: 1 - 11. doi: 10.1093/condor/duaa024.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation.*Trends in Ecology & Evolution* **10(2)**: 58 - 62.doi: 10.1016/S0169-5347(00)88977-6.

Murgui, E. (2007) Effects of seasonality on the species–area relationship: a case study with birds in urban parks. *Global Ecology and Biogeography* **16**:319 – 329. doi:

10.1111/j.1466-8238.2006.00304.x.

Murton, R.K. and Westwood, N.J. (1977) *Avian breeding cycles* Clarendon, Oxford, UK.

Naef-Daenzer, B. (2000) Patch time allocation and patch sampling by foraging Great and Blue Tits. *Animal Behaviour* **59(5)**: 989 – 999. doi: 10.1006/anbe.1999.1380.

Naef-Daenzer, B. and Keller, L.F. (1999) The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology* **68(4)**: 708 - 718. doi: 10.1046/j.1365-2656.1999.00318.x.

Naef-Daenzer, B., Widmer, F. and Nuber, M. (2001) Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70(5)**:730 – 738. doi: 10.1046/j.0021-8790.2001.00533.x.

Naef-Daenzer, L., Naef-Daenzer, B. and Nager, R.G. (2000) Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* **31(2)**: 206 - 214.doi: 10.1034/j.1600-048X.2000.310212.x.

Narango, D.L., Tallamy, D.W. and Marra, P.P. (2017) Native plants improve breeding and foraging habitat for an insectivorous bird. *Biological Conservation* Elsevier, **213(Part A)**: 42 – 50. doi: 10.1016/j.biocon.2017.06.029.

Narango, D.L., Tallamy, D.W.and Marra, P.P. (2018) Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences* **115(45)**: 11549 – 11554. doi: 10.1073/pnas.180925911.

Neuenschwander, S., Brinkhof, M.W., Kölliker, M., & Richner, H. (2003) Brood size, sibling competition, and the cost of begging in Great Tits (*Parus major*). *Behavioral Ecology* **14(4)**: 457 – 462. doi: 10.1093/beheco/arg025.

New, T.R. (2015) Insects in Urban Environments. In: *Insect Conservation and Urban Environments*. Springer, Cham. pp. 21 - 31. doi: 10.1007/978-3-319-21224-1_2

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L., Alhusseini, T., Ingram, D. J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips,H.R., Purves, D.W., Robinson, A., Simpson,J., Tuck, S.L., Weiher,E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P. & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature* **520 (7545)**: 45 - 50. doi: 10.1038/nature14324.

Niemelä, J. (1999a) Ecology and urban planning. *Biodiversity and Conservation* **8**: 119 – 131. doi: /10.1023/A:1008817325994.

Niemelä, J. (1999b) Is there a need for a theory for urban ecology? *Urban Ecosystems* **3**: 57 – 65. doi: 10.1023/A:1009595932440.

Nilsson, J. Å., and Källander, H. (2006) Leafing phenology and timing of egg laying in Great Tits *Parus major* and Blue Tits *P. caeruleus*. *Journal of Avian Biology* **37(4)**: 357 - 363. doi: 10.1111/j.2006.0908-8857.03604.x.

Nooker, J.K., Dunn, P.O., & Whittingham, L.A. (2005) Effects of food abundance, weather, and female condition on reproduction in Tree Swallows (*Tachycineta bicolor*). *The Auk* **122(4)**: 1225 - 1238.

Nord, A., & Nilsson, J. Å. (2011) Incubation temperature affects growth and energy metabolism in Blue Tit nestlings. *The American Naturalist* **178(5)**: 639 - 651. doi: 10.1086/662172.

Nord, A. and Nilsson, J-Å. (2016) Long-term consequences of high incubation temperature in a wild bird population. *Biology Letters* **12(4)**: 20160087. doi: https://doi.org/10.1098/rsbl.2016.0087.

Norris, K. (1993) Seasonal Variation in the Reproductive Success of Blue Tits: An Experimental Study. *The Journal of Animal Ecology* **62(2)**: 287 - 294. doi: 10.2307/5360.

Norte, A.C., Araújo, P.M., Sampaio, H. L., Sousa, J.P. & Ramos, J. A. (2009) Haematozoa infections in a Great Tit *Parus major* population in Central Portugal: Relationships with breeding effort and health. *Ibis* **151(4)**: 677 - 688. doi: 10.1111/j.1474-919X.2009.00960.x.

Nuissl, H., Haase, D., Lanzendorf, M. & Wittmer, H. (2009) Environmental impact assessment of urban land use transitions—A context-sensitive approach. *Land Use Policy* **26(2)**: 414 – 424. doi: https://doi.org/10.1016/j.landusepol.2008.05.006.

Nur, N. (1984) The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology* **53(2)**: 497 – 517, https://www.jstor.org/stable/4530. doi: 10.2307/4530.

Nur, N. (1988) The consequences of brood size for breeding Blue Tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution* **42(2)**: 351 – 362. doi: 10.1111/j.1558-5646.1988.tb04138.x.

Öberg, M., Arlt, D., Pärt, T., Laugen, A.T., Eggers, S. & Low, M. (2015) Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution* **5(2)**: 345 - 356. doi: 10.1002/ece3.1345.

Office for National Statistics (ONS) (2022) *ONS Statistical Bulletin: Population and household estimates, England and Wales: Census 2021, unrounded data.* Available at: https://Population and household estimates, England and Wales - Office for National Statistics (ons.gov.uk) (accessed 28/07/2022 & 03/03/2023).

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Sólymos, P., Stevens, M.H.H., Szöcs, E. & Wagner, H.H. (2020) vegan: community ecology package. R package version 2.5-7.

Oke, T.R. (1973) City size and the urban heat island. *Atmospheric Environment* **7(8)**: 769 – 779. doi: 10.1016/0004-6981(73)90140-6.

Oke, T.R. (1982) The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society* **108**: 1 - 24. doi: 10.1002/qj.49710845502.

Oliver, A.J., Hong-Wa, X., Devonshire, J., Olea, K.R., Rivas, G.F. & Gahl, M.K. (2011) Avifauna richness enhanced in large, isolated urban parks. *Landscape and Urban Planning* **102(4)**: 215 – 225. doi: 10.1016/j.landurbplan.2011.04.007.

Orros, M.E. and Fellowes, M.D.E. (2015) Wild bird feeding in an urban area: intensity, economics and numbers of individuals supported. *Acta Ornithologica* **50(1)**: 43 – 58. doi: 10.3161/00016454AO2015.50.1.006.

Ortega-Álvarez, R. and MacGregor-Fors, I. (2009) Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. *Landscape and Urban Planning* **90 (3 - 4)**: 189 - 195. doi: 10.1016/j.landurbplan.2008.11.003.

Ortega, C.P. (2012) Chapter 2: Effects of noise pollution on birds: A brief review of our knowledge - Efectos de la Polución Sonora en Aves: una Breve Revisión de Nuestro Conocimiento. *Ornithological Monographs***74(1)**: 6 – 22, https://www.jstor.org/stable/10.1525/om.2012.74.1.6. doi: 10.1525/om.2012.74.1.6.

Ospina, E., Merril, L. and Benson, T.J. (2018) Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. *Ecology and Evolution* **8(6)**: 3270 – 3279. doi: 10.1002/ece3.3911.

Owen, S.M., MacKenzie, A.R., Bunce, R.G.H., Stewart, H.E., Donovan, R.G., Stark, G. & Hewitt, C.N. (2006) Urban land classification and its uncertainties using principal component and cluster analyses: A case study for the UK West Midlands. *Landscape and Urban Planning* **78(4):** 311 - 321. doi: 10.1016/j.landurbplan.2005.11.002.

Pagani-Núñez, E. and Senar, J.C. (2014) Are colorful males of Great Tits *Parus major* better parents? Parental investment is a matter of quality. *Acta Oecologica* **55**: 23 - 28. doi: 10.1016/j.actao.2013.11.001.

Pall, P., Aina, T., Stone, D.A., Stott, P.A., Nozawa, T., Hilberts A.G.J., Lohmann, D. & Allen, M.R. (2011) Anthropogenic greenhouse gas contribution to flood risk in England and Wales in autumn 2000. *Nature* **470**: 382 –385. doi: 10.1038/nature09762.

Pampus, M., Schmidt, K.-H. and Wiltschko, W. (2005) Pair bond and breeding success in Blue Tits *Parus caeruleus* and Great Tits *Parus major*. *Ibis* **147**: 92 - 108. doi: 10.1111/j.1474-919x.2004.00376.x.

Parmesan, C., and Hanley, M.E. (2015) Plants and climate change: complexities and surprises. *Annals of Botany*, **116(6)**: 849 - 864.

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37 – 42. doi: 10.1038/nature01286.

Pärt,T. (1995) Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society B: Biological Sciences* **260(1357)**: 113 – 117. doi: 10.1098/rspb.1995.0067.

Partecke, J., Hof, V. and Gwinner, E. (2004) Differences in the timing of reproduction between urban and forest European Blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society B: Biological Sciences* **271(1552)**: 1995 – 2001. doi: 10.1098/rspb.2004.2821.

Partecke, J., Schwabl, I. and Gwinner, E. (2006). Stress and the city: urbanization and its effects on the stress physiology in European Blackbirds. *Ecology* **87(8)**: 1945 - 1952.

Pavisse, R., Vangeluwe, D. and Clergeau, P. (2019) Domestic Cat Predation on Garden Birds: An Analysis from European Ringing Programmes. *Ardea* **107**: 103 - 109.doi: 10.5253/arde.v107i1.a6.

Peach, W.J., Vincent, K.E., Fowler, J.A. & Grice, P.V. (2008) Reproductive success of House Sparrows along an urban gradient. *Animal Conservation* **11(6)**: 493 - 503. doi: 10.1111/j.1469-1795.2008.00209.x.

Peach, W.J., Mallord, J.W., Ockendon, N., Orsman, C.J. & Haines, W.G. (2015) Invertebrate prey availability limits reproductive success but not breeding population size in suburban House Sparrows *Passer domesticus*. *Ibis* **157**: 601 – 613. doi: 10.1111/IBI.12264.

Pennington, D. N. and Blair, R. B. (2011) Habitat and selection of breeding riparian birds in an urban environment: untangling the relative importance of biophysical elements and spatial scale. *Diversity and Distributions* **17(3)**: 506 – 518. doi: 10.1111/j.1472-4642.2011.00750.x.

Pennington, D.N. and Blair, R.B. (2012) *Using Gradient Analysis to Uncover Pattern and Process in Urban Bird Communities*. In: Lepczyk, C.A. and Warren, PS. (eds.) *Urban Bird Ecology and Conservation*. Oakland, CA, online edn, California Scholarship Online, 23 May 2013). doi: 10.1525/california/9780520273092.003.000.

Perrier, C., Lozano del Campo, A., Szulkin, M., Demeyrier, V., Gregoire, A. & Charmantier, A. (2018) Great tits and the city: Distribution of genomic diversity and gene–environment associations along an urbanization gradient. *Evolutionary Applications* **11(5)**: 593 - 613. doi: 10.1111/eva.12580.

Perrins, C. M. (1965) Population Fluctuations and Clutch-Size in the Great Tit, *Parus Major L.*, *Journal of Animal Ecology* **34(3)**: 601 – 647.

Perrins, C. M. (1979) British tits. Collins, London, UK.

Perrins, C. M. (1991) Tits and their caterpillar food supply. *Ibis* **133(1)**: 49 – 54. doi: 10.1111/j.1474-919X.1991.tb07668.x.

Perrins, C.M. and McCleery, R.H. (1989) Laying dates and clutch size in the Great Tit. *The Wilson Bulletin (Wilson Ornithological Society)* **101(2)**: 236 - 253. https://www.jstor.org/stable/4162727.

Perrins, C.M. and Moss, D. (1975) Reproductive rates in the Great Tit. *Journal of Animal Ecology* **44(3)**: 695 – 706. https://www.jstor.org/stable/3712. doi: 10.2307/3712.

Pettifor, R.A., Perrins, C.M. and McCleery, R.H. (2008) The individual optimization of fitness: Variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of Great Tits (*Parus major*). *Journal of Animal Ecology* **70(1)**: 62 - 79, https://www.jstor.org/stable/2693480. doi: 10.1046/j.1365-2656.2001.00465.x.

Phillimore, A.B., Leech, D.I., Pearce-Higgins, J.W. & Hadfield, J. D. (2016) Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global* *change biology* **22(10)**: 3259 - 3272. doi: 10.1111/gcb.13302.

Piersma, T. (2012) What is habitat quality? Dissecting a research portfolio on shorebirds. Birds and habitat: Relationships in changing landscapes, 383-407.

Pipoly, I. Bókony, V., Seress, G., Szabó, K. & Liker, A. (2013) Effects of Extreme Weather on Reproductive Success in a Temperate-Breeding Songbird. *PLoS ONE* **8(11):** e80033, 1 - 11. doi: 10.1371/journal.pone.0080033.

Pipoly, I.*,* Preiszner, B., Sándor, K., Sinkovics, C., Seress, G., Vincze, E., Bókony, V. & Liker A. (2022) Extreme Hot Weather Has Stronger Impacts on Avian Reproduction in Forests Than in Cities. *Frontiers in Ecology and Evolution* **10**: 825410, 1 - 11. doi: 10.3389/fevo.2022.825410.

Plummer, K. E., Bearhop, S., Leech, D.I., Chamberlain, D.E. & Blount, J.D. (2013a) Fat provisioning in winter impairs egg production during the following spring: A landscape-scale study of Blue Tits. *Journal of Animal Ecology* **82(3)**: 673 - 682. doi: 10.1111/1365-2656.12025.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. & Blount J.D. (2013b) Winter food provisioning reduces future breeding performance in a wild bird. *Scientific Reports* **3(2002).** doi: 10.1038/srep02002.

Plummer, K.E.*,* Bearhop, S., Leech, D.I., Chamberlain, D.E. & Blount, J.D. (2018) Effects of winter food provisioning on the phenotypes of breeding Blue Tits. *Ecology and Evolution* **8(10)**: 5059 – 5068. doi: 10.1002/ece3.4048.

Plummer, K.E., Risely, K., Toms, M.P. & Siriwardena, G.M. (2019) The composition of British bird communities is associated with long-term garden bird feeding. *Nature Communications* **10(1)**: 2088, 1 - 8. doi: 10.1038/s41467-019-10111-5.

Plummer, K. E., Gillings, S. and Siriwardena, G.M. (2020) Evaluating the potential for bird-habitat models to support biodiversity-friendly urban planning. *Journal of Applied Ecology* **57(10)**: 1902 - 1914. doi: 10.1111/1365-2664.13703.

Podmokła, E., Dubiec, A., Drobniak, S.M., Arct, A., Gustafsson, L. & Cichoń, M. (2014) Avian malaria is associated with increased reproductive investment in the Blue Tit. *Journal of Avian Biology* **45(3)**: 219 – 224. doi: 10.1111/j.1600-048X.2013.00284.x.

Pollock, C. J., Capilla-Lasheras, P., McGill, R.A.R., Helm, B. & Dominoni, D.M. (2017) Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling Blue Tits (*Cyanistes caeruleus*). *Scientific Reports* **7**: 5014, 1 -14/ doi: 10.1038/s41598-017-04575-y.

Prokosch, J., Bernitz, Z., Bernitz, H., Erni, B. & Altwegg, R. (2019) Are animals shrinking due to climate change? Temperature-mediated selection on body mass in mountain wagtails. *Oecologia* **189(3)**: 841 - 849. doi: 10.1007/s00442-019-04368-2.

Przybylo, R., Wiggins, D. A. and Merilä, J. (2001) Breeding success in Blue Tits: Good territories or good parents? *Journal of Avian Biology* **32(3)**: 214 - 218, https://www.jstor.org/stable/3677366. doi: 10.1111/j.0908-8857.2001.320302.x.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*

132(5): 652 - 661.

Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography* **25**: 155–163.

Quattrochi, D.A. and Ridd, M.K. (1994) Measurement and analysis of thermal energy responses from discrete urban surfaces using remote sensing data. *International Journal of Remote Sensing* **15(10)**: 1991 – 2022. doi: 10.1080/01431169408954224.

Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M.P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K.S., Borras, A., Burthe, S., Clobert, J., Dehnhard, N., Lope, F. de, Dhondt, A.A., Dingemanse, N.J., Doi, H., Eeva, T., Fickel, J., Filella, I., Fossøy, F., Goodenough, A.E., Hall, S.J.G., Hansson, B., Harris, M., Hasselquist, D., Hickler, T., Joshi, J., Kharouba, H., Martínez, J. G., Mihoub, J.-B., Mills, J. A., Molina-Morales, M., Moksnes, A., Ozgul, A., Parejo, D., Pilard, P., Poisbleau, M., Rousset, F., Rödel, M.-O., Scott, D., Senar, J.C., Stefanescu, C., Stokke, B.G., Kusano, T., Tarka, M., Tarwater, C.E., Thonicke, K., Thorley, J., Wilting, A., Tryjanowski, P., Merilä, J., Sheldon, B. C., Møller, A.P., Matthysen, E., Janzen, F., Dobson, F.S., Visser, M.E., Beissinger, S.R., Courtiol, A. & Kramer-Schadt,S. (2019) Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* **10**: 3109. doi: 10.1038/s41467-019-10924-4.

Rae, A. (2017) *A Land Cover Atlas of the United Kingdom* The University of Sheffield. Journal contribution. Available at: https://doi.org/10.15131/shef.data.5266495.v1 (accessed 07/02/2023).

Rebele, F. (1994) Urban Ecology and Special Features of Urban Ecosystems. *Global Ecology and Biogeography Letters* **4(6)**: 173 – 187. https://doi.org/10.2307/2997649.

Redfern, C. P. and Clark, J. A. (2001) *Ringers' Manual*. Thetford, UK: British Trust for Ornithology.

Redhead, J. W., Pywell, R.F., Bellamy, P.E., Broughton, R.K., Hill, R.A. & Hinsley, S.A. (2013) Great Tits *Parus major* and Blue Tits *Cyanistes caeruleus* as indicators of agri-environmental habitat quality. *Agriculture, Ecosystems and Environment* **178**: 31 - 38. doi: 10.1016/j.agee.2013.06.015.

Reed, T. E., Jenouvrier, S. and Visser, M. E. (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology* **82(1)**: 131 - 144. doi: 10.1111/j.1365-2656.2012.02020.x.

Remeš, V. and Matysioková, B. (2013) More ornamented females produce higher-quality offspring in a socially monogamous bird: An experimental study in the Great Tit (*Parus major*). *Frontiers in Zoology* **10(1):** 14, 1 - 10. doi: 10.1186/1742-9994-10-14.

Ren, S., Vitasse, Y., Chen, X., Peichl, M. & An, S. (2022) Assessing the relative importance of sunshine, temperature, precipitation, and spring phenology in regulating leaf senescence timing of herbaceous species in China. *Agricultural and Forest Meteorology* **313**: 108770. doi: 0.1016/j.agrformet.2021.108770.

Reynolds, S.J., Davies, C.S., Elwell E. & Hunt, D. (2016) Does the Urban Gradient Influence the Composition and Ectoparasite Load of Nests of an Urban Bird Species? *Avian*

Biology Research **9(4)**: 244–234. doi: 10.3184/175815516X14725499175665.

Reynolds, S.J., Galbraith, J.A., Smith, J.A. & Jones, D.N. (2017) Garden bird feeding: Insights and prospects from a north-south comparison of this global urban phenomenon. *Frontiers in Ecology and Evolution* **5(24)**. doi: 10.3389/fevo.2017.00024.

Reynolds, S.J., Ibáñez-Álamo, J.D., Sumasgutner, P. & Mainwaring, M.C. (2019) Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology* **160**: 841 – 860. doi: 10.1007/s10336-019-01657-8.

Ricklefs, R. E. (1969) An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**: 1–48.

Riddington, R. and Gosler, A.G. (1995) Differences in reproductive success and parental qualities between habitats in the Great Tit Parus major. Ibis 137: 371 – 378.

Riitters, K. H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B. & Jackson, B.L. (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* **10(1)**: 23–39. doi: 10.1007/BF00158551.

Robb, G.N., McDonald, R.A., Chamberlain, D.E. and Bearhop, S. (2008a) Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* **6(9)**: 476 – 484, https://www.jstor.org/stable/20440990. doi: 10.1890/060152.

Robb, G.N., McDonald, R.A., Chamberlain, D.E., Reynolds, S.J., Harrison, T.J.E. & Bearhop, S. (2008b) Winter feeding of birds increases productivity in the subsequent breeding season. *Biology Letters* **4**: 220 - 223. doi: 10.1098/rsbl.2007.0622.

Robertson, B.A. and Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of exisiting evidence.. *Ecology* **87(5)**: 1075 –1085. doi: 10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2.

Robinson, S. and Hoover, J. (2011) Does forest fragmentation and loss generate sources, sinks, and ecological traps in migratory songbirds? In: Liu, J., Hull, V., Morzillo, A. & Wiens, J. (eds.) *Sources, Sinks and Sustainability (Cambridge Studies in Landscape Ecology)*. Cambridge University Press, Cambridge, pp. 423-449. doi:10.1017/CBO9780511842399.022.

Robinet, C., and Roques, A. (2010) Direct impacts of recent climate warming on insect populations. *Integrative zoology* **5(2)**: 132 - 142. doi: 10.1111/j.1749-4877.2010.00196.x.

Rodríguez, S., van Noordwijk, A.J., Álvarez, E. & Barba, E. (2016a) A recipe for postfledging survival in Great Tits *Parus major*: be large and be early (but not too much). *Ecology and Evolution* **6(13)**: 4458 - 4467. doi: 10.1002/ece3.2192.

Rodriguez, S., Diez-Mendez, D. and Barba, E. (2016b) Negative effects of high temperatures during development on immediate post-fledging survival in Great Tits *Parus major*. *Acta Ornithologica* **51(2)**: 235 – 244. doi: 10.3161/00016454AO2016.51.2.009.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57 –60.

Rosenfeld, E.J. (2012) Assessing the Ecological Significance of Linkage and Connectivity for Avian Populations in Urban Areas. PhD thesis, University of Birmingham, Birmingham, UK.

Ruffino, L., Salo, P., Koivisto, E., Banks, P.B. & Korpimäki, E. (2014) Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology* **11(80)**: 1 - 13. doi: 10.1186/s12983-014-0080-y.

Russ, A., Lučeničová, T. and Klenke, R. (2017) Altered breeding biology of the European Blackbird under artificial light at night. *Journal of Avian Biology* **48(8)**: 1114 – 1125. doi: 10.1111/jav.01210.

Saarikivi, J. and Herczeg, G. (2014) Do hole-nesting passerine birds fare well at artificial suburban forest edges? *Annales Zoologici Fennici* **51(6)**: 488 - 494, https://www.jstor.org/stable/43923498. doi: 10.5735/086.051.0603.

Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M.G. & Niemelä, J. (2006) Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *Journal of Biogeography* **33(6)**: 1126 – 1138. doi: 10.1111/j.1365-2699.2006.01476.x.

Sæther, B.E., Engen, S., Møller, A.P., Matthysen, E., Adriaensen, F., Fiedler, W., Leivits, A., Lambrechts, M.M., Visser, M.E., Anker-Nilssen, T., Both, C., Dhondt, A.A., McCleery, R.H., McMeeking, J., Potti, J., Røstad, O.W. & Thomson, D. (2003) Climate variation and regional gradients in population dynamics of two hole-nesting passerines. *Proceedings of the Royal Society of London B: Biological Sciences* **270(1531)**: 2397 - 2404. doi: 0.1098/rspb.2003.2499.

Salaberria, C., Celis, P., López-Rull, I. & Gil, D. (2014) Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. *Ibis* **156(2)**: 265 –275. doi: 10.1111/ibi.12121.

Salmón, P., Nilsson, J. F., Nord, A., Bensch, S. & Isaksson, C. (2016) Urban environment shortens telomere length in nestling great tits, *Parus major*. *Biology Letters* **12(6)**: 20160155. doi: 10.1098/rsbl.2016.0155.

Salmón, P., Stroh, E., Herrera-Dueñas, A., von Post, M. & Isaksson, C. (2018a) Oxidative stress in birds along a NOx and urbanisation gradient: An interspecific approach. *Science of the Total Environment* **622 - 623**: 635 - 643. doi: 10.1016/j.scitotenv.2017.11.354.

Salmón, P., Watson, H., Nord, A. & Isaksson, C. (2018b) Effects of the urban environment on oxidative stress in early life: insights from a cross-fostering experiment. *Integrative and Comparative Biology* **58(5)**: 986 - 994. doi: 10.1093/icb/icy099.

Samia, D.S., Blumstein, D.T., Díaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Tätte, K., Markó, G., Tryjanowski, P. and Møller, A.P. (2017) Rural-urban differences in escape behavior of European birds across a latitudinal gradient. *Frontiers in Ecology and Evolution* **5(66)**. doi: 10.3389/fevo.2017.00066.

Samplonius, J.M., Kappers, E. F., Brands, S. & Both, C. (2016) Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *The*

Journal of Animal Ecology **85(5)**: 1255 – 1264. doi: 10.1111/1365-2656.12554.

Samplonius, J. M., Bartošová, L., Burgess, M.D., Bushuev, A.V., Eeva, T., Ivankina, E.V., Kerimov, A.B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M.E., Zang, H. & Both, C. (2018) Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. *Global Change Biology* **24(8)**: 3780 – 3790. doi: 10.1111/gcb.14160.

Sánchez, S., Cuervo, J. J. and Moreno, E. (2007) Does habitat structure affect body condition of nestlings? A case study with woodland Great Tits *Parus major*. *Acta Ornithologica* **42(2)**: 200 – 204. doi: 10.3161/068.042.0204.

Santos, B. A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.P. & Tabarelli, M. (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation* **141(1)**: 249 – 260. doi: 10.1016/j.biocon.2007.09.018.

Sanz, J.J*.,* Arriero, E., Moreno, J. & Merino, S. (2001) Interactions between hemoparasite status and female age in the primary reproductive output of Pied Flycatchers. *Oecologia* **126**: 339 - 344. doi: 10.1007/s004420000530.

Sanz, J.J. and Tinbergen, J.M. (1999) Energy expenditure in, nestling age and brood size: an experimental study of parental behaviour in the Great Tit *Parus Major*. *BehaviouralEecology* **10(5)**: 598 – 606. doi: 10.1093/beheco/10.5.598.

Sauve, D., Charmantier, A., Hatch, S.A. & Friesen, V.L. (2021a) Environmental conditions variably affect growth across the breeding season in a subarctic seabird. *Oecologia* **198(2)**: 307 - 318. doi: https://doi.org/10.1007/s00442-021-05063-x.

Sauve, D., Friesen, V. L. and Charmantier, A. (2021b) The Effects of Weather on Avian Growth and Implications for Adaptation to Climate Change. *Frontiers in Ecology and Evolution* **9**: 569741. doi: 10.3389/fevo.2021.569741.

Schaper, S.V*.,* Dawson, A., Sharp, P.J., Gienapp, P., Caro, S.P. & Visser, M.E. (2012) Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. *The American Naturalist* **179(2)**: E55–E69. doi: 10.1086/663675.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* **1(2)**: 103 - 113. doi: 10.1111/j.2041-210x.2010.00012.x.

Schlaepfer, M.A., Runge, M.C. and Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology and Evolution* **17**: 474 – 480. doi: 10.1016/S0169-5347(02)02580-6.

Schöll, E.M., Ohm, J., Hoffmann, K.F. and Hille, S. M. (2016) Caterpillar biomass depends on temperature and precipitation, but does not affect bird reproduction. *Acta Oecologica* **74**: 28 – 36. doi: 10.1016/j.actao.2016.06.004.

Schöll, E.M. and Hille, S.M. (2020) Heavy and persistent rainfall leads to brood reduction and nest failure in a passerine bird. *Journal of Avian Biology* **51(7)**: 1 – 11. doi: 10.1111/jav.02418.

Schroeder J, Nakagawa S, Cleasby IR, Burke T (2012) Passerine Birds Breeding under Chronic

Noise Experience Reduced Fitness. *PLoS ONE* **7(7)**: e39200. doi: 10.1371/journal.pone.0039200.

Şekercioğlu, Ç.H., Primack, R.B., & Wormworth, J. (2012) The effects of climate change on tropical birds. *Biological conservation* **148(1)**: 1 - 18. doi: 10.1016/j.biocon.2011.10.019.

Selwood, K.E., McGeoch, M.A. & MacNally, R. (2015) The effects of climate change and land-use change on demographic rates and population viability. *Biological Reviews* **90(3)**: 837 - 853. doi: 10.1111/brv.12136.

Sepp, T., McGraw, K.J., Kaasik, A. & Giraudeau, M. (2018) A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? *Global Change Biology* **24(4)**: 1452 – 1469. doi: 10.1111/gcb.13969.

Seress, G., Bókony, V., Heszberger, J. and Liker, A. (2011) Response to predation risk in urban and rural House Sparrows. *Ethology* **117(10)**: 896 - 907. doi: 10.1111/j.1439-0310.2011.01944.x.

Seress, G., Bókony, V., Pipoly, I., Szép, T., Nagy, K. and Liker, A. (2012) Urbanization, nestling growth and reproductive success in a moderately declining House Sparrow population. *Journal of Avian Biology* **43(5)**: 403 - 414. doi: 10.1111/j.1600-048X.2012.05527.x.

Seress, G., Lipovits, Á., Bókony, V. & Czúni, L. (2014) Quantifying the urban gradient: A practical method for broad measurements. *Landscape and Urban Planning*. **131**: 42 – 50. doi: 10.1016/j.landurbplan.2014.07.010.

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K. L. & Liker, A. (2018) Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecological Applications: a publication of the Ecological Society of America* **28(5)**: 1143 – 1156. doi: 10.1002/eap.1730.

Seress, G., Sándor, K., Evans, K.L. & Liker, A. (2020) Food availability limits avian reproduction in the city: An experimental study on Great tits *Parus major*. *Journal of Animal Ecology* **89(7)**: 1570 – 1580. doi: 10.1111/1365-2656.13211.

Seress, G. and Liker, A. (2015) Habitat urbanization and its effects on birds., *Acta Zoologica Academiae Scientiarum Hungaricae* **61(4)**: 373 – 408. doi: 10.17109/AZH.61.4.373.2015.

Seto, K.C., Fragkias, M., Güneralp, B. & Reilly, M.K. (2011) A meta-analysis of global urban land expansion. *PLoS ONE* **6(8)**: e23777, 1 - 9. doi: 10.1371/journal.pone.0023777.

Seto, K.C., Güneralp, B. and Hutyra, L.R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America* **109(40)**: 16083 - 16088. doi: 10.1073/pnas.1211658109.

Shanahan, D.F., Miller, C., Possingham, H.P. & Fuller, R.A. (2011) The influence of patch area and connectivity on avian communities in urban revegetation. *Biological Conservation* **144(2)**: 722 – 729. doi: 10.1016/j.biocon.2010.10.014.

Shanahan, D.F., Strohbach, M.W., Warren, P.S. & Fuller, R.A. (2014) *The challenges of urban living.* In: Avian Urban Ecology Behavioural and Physiological Adaptations. Edited by Gil D, Brumm H. Oxford University Press: Oxford, UK, 3–20.

Shaw, L.M., Chamberlain, D. and Evans, M. (2008) The House Sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. *Journal of Ornithology* **149**: 293 – 299.

Sheridan, J.A., and Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature climate change* **1(8)**: 401 - 406. doi: 10.1038/nclimate1259

Shmueli, G., Minka, T.P., Kadane, J.B., Borle, S. & Boatwright, P. (2005) A Useful Distribution for Fitting Discrete Data: Revival of the Conway-Maxwell-Poisson Distribution. *Journal of the Royal Statistical Society. Series C (Applied Statistics)* **54(1)**: 127 – 142. http://www.jstor.org/stable/3592603.

Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H. & Nilon, C.H. (2010a) Invasion, Competition, and Biodiversity Loss in Urban Ecosystems *BioScience* **60(3)**: 199 – 208. doi: 10.1525/bio.2010.60.3.6.

Shochat, E., Lerman, S. and Fernández-Juricic, E. (2010b). Birds in Urban Ecosystems: Population Dynamics, Community Structure, Biodiversity, and Conservation. In: Aitkenhead-Peterson, J. and Volder, A. (eds.) *Agronomy Monographs: Urban Ecosystem Ecology,*Volume 55, pp 75 - 86. doi: 10.2134/agronmonogr55.c4.

Short, F.T., & Neckles, H.A. (1999) The effects of global climate change on seagrasses. *Aquatic Botany* **63(3-4)**: 169 - 196.

Shryock, B., Marzluff, J.M. and Moskal, L.M. (2017) Urbanization Alters the Influence of Weather and an Index of Forest Productivity on Avian Community Richness and Guild Abundance in the Seattle Metropolitan Area. *Frontiers in Ecology and Evolution* **5(40)**: 1 – 14. doi: 10.3389/fevo.2017.00040.

Shutt, J. D*.,* Bolton, M., Benedicto Cabello, I., Burgess, M.D., & Phillimore, A.B. (2018) The effects of woodland habitat and biogeography on Blue Tit *Cyanistes caeruleus* territory occupancy and productivity along a 220 km transect. *Ecography* **41(12)**: 1967 - 1978. doi: 10.1111/ecog.03573.

Shutt, J.D., Cabello, I.B., Keogan, K., Leech, D.I., Samplonius, J.M., Whittle, L., Burgess, M.D. & Phillimore A.B. (2019) The environmental predictors of spatio-temporal variation in the breeding phenology of a passerine bird. *Proceedings of the Royal Society Series B: Biological Sciences* **286(1908)**: 20190952, 1 - 9. doi: 10.1098/rspb.2019.0952.

Shutt, J.D., Nicholls, J.A., Trivedi, U.H., Burgess, M.D., Stone, G.N., Hadfield, J.D., & Phillimore, A.D. (2020) Gradients in richness and turnover of a forest passerine's diet prior to breeding: A mixed model approach applied to faecal metabarcoding data. *Molecular Ecology* **29(6)**: 1199 - 1213. doi: /10.1111/mec.15394.

Shutt, J.D., Trivedi, U.H. & Nicholls, J.A. (2021) Faecal metabarcoding reveals pervasive long-distance impacts of garden bird feeding. *Proceedings of the Royal Society Series B: Biological Sciences* **288(1951)**: 20210480, 1 - 10. doi: 10.1098/rspb.2021.0480.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour* **85(5)**:1077 - 1088. doi: 10.1016/j.anbehav.2013.02.017.

Siikamäki, P. (1996) Nestling growth and mortality of Pied Flycatchers *Ficedula hypoleuca* in relation to weather and breeding effort. *The Ibis* **138**: 471–478.

Silva, C.P., Sepúlveda, R.D. and Barbosa, O. (2016) Nonrandom filtering effect on birds: species and guilds response to urbanization. *Ecology and evolution* **6(11)**: 3711 - 3720. doi: https://doi.org/10.1002/ece3.2144.

Simmons, R.E., Barnard, P., Dean, W.R.J., Midgley, G.F., Thuiller, W., & Hughes, G. (2004) Climate change and birds: perspectives and prospects from southern Africa. *Ostrich-Journal of African Ornithology* **75(4)**: 295 - 308. doi: 10.2989/00306520409485458.

Siriwardena, G.M., Robinson, R.A. & Crick, H.Q.P. (2002) Investigation into the causes of the decline of Starlings and House Sparrows in Great Britain. In: Crick, H.Q.P., Robinson, R.A., Appleton, G.F., Clark, N.A. & Rickard, A.D. (eds.) *Investigation into the causes of the decline of Starlings and House Sparrows in Great Britain.* BTO Research Report No. 290, British Trust for Ornithology, Thetford, UK, pp 33–52.

Slabbekoorn, H. and Ripmeester, E.P. (2008) Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* **17(1)**: 72 - 83. doi:10.1111/j.1365-294X.2007.03487.x.

Slagsvold, T. and Amundsen, T. (1992) Do Great Tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? *Journal of Animal Ecology*, **61(2):** 249 – 258, https://www.jstor.org/stable/5318. doi: 10.2307/5318.

Slagsvold, T., Amundsen, T., and Dale, S. (1995) Costs and Benefits of Hatching Asynchrony in Blue Tits *Parus caeruleus*. *Journal of Animal Ecology* **64(5)**: 563 - 578. doi: 10.2307/5800.

Smith, H.G., Kallander, H. and Nilsson, J.A. (1989) The Trade-Off Between Offspring Number and Quality in the Great Tit *Parus major*. *Journal of Animal Ecology* **58(2)**: 383 – 401, https://www.jstor.org/stable/4837. doi: 10.2307/4837.

Smith, J.A. (2010) From nest buiding to life-history patterns: Does food supplementation influence reproductive behaviour of birds?. PhD thesis, University of Birmingham, Birmingham, UK.

Smith, J.A., Harrison, T.J.E., Martin, G.E. & Reynolds, S.J. (2013) Feathering the nest: food supplementation influences nest construction by Blue (*Cyanistes caeruleus*) and Great Tits (Parus major). *Avian Biology Research* **6(1)**: 18 – 25. doi: 10.3184/175815512X13530764553094.

Snell, K.R.S., Jensen, R.B.E., Ortvad,T.E., Willemoes, M. & Thorup, K. (2020) Multiple fragmented habitat-patch use in an urban breeding passerine, the Short-toed Treecreeper. *PLoS ONE* **15(1)**: e0227731. doi: 10.1371/journal.pone.0227731.

Snow, D.W. (1956) The annual mortality of the Blue Tit in different parts of its range. *British Birds* **49**: 174 - 177.

Socolar, J.B., Epanchin, P.N., Beissinger, S.R. & Tingley, M.W. (2017) Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences* **114(49)**: 12976 - 12981. doi: 10.1073/pnas.170589711.

Sol, D., Lapiedra, O. and González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour* **85(2)**: 1101 – 1112. doi: 10.1016/j.anbehav.2013.01.023.

Sol, D., González-Lagos, C., Moreira, D., Maspons, J. & Lapiedra, O. (2014) Urbanisation tolerance and the loss of avian diversity. *Ecology Letters* **17(8)**: 942 – 950. doi: 10.1111/ele.12297.

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot, A.L., Ricotta, C., Swan, C.M., Tobias, J.A. & Pavoine, S. (2020) The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters* **23(6)**: 962 – 972. doi: 10.1111/ele.13495.

Solonen, T. (2001) Breeding of the Great Tit and Blue Tit in urban and rural habitats in Southern Finland. *Ornis Fennica* **78(2)**: 49 - 60.

Solonen, T. and Hildén, M. (2014) Breeding phenology in Great and Blue Tits (*Parus* spp.): Are urban populations more resistant to climate change than rural ones? *Ornis Fennica* **91(4)**: 209 - 219.

Sorace, A. (2002) High density of bird and pest species in urban habitats and the role of predator abundance. *Ornis Fennica*, **79(2)**: 60 – 71.

Southwood, T.R.E., Wint, G.W., Kennedy, C.E., & Greenwood, S.R. (2004) Seasonality abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology* **101(1)**: 43 - 50. doi: 10.14411/EJE.2004.011.

Sprau, P., Mouchet, A. and Dingemanse, N.J. (2017) Multidimensional environmental predictors of variation in avian forest and city life histories., *Behavioral Ecology* **28(1)**: 59 – 68. doi: 10.1093/beheco/arw130.

Stanbury, A., Eaton, M., Aebischer, N., Balmer, D., Brown, A., Douse, A., Lindley, P., McCulloch, N., Noble, D. & Win, I. (2021) The status of our bird populations: the fifth Birds of Conservation Concern in the United Kingdom, Channel Islands and Isle of Man and second IUCN Red List assessment of extinction risk for Great Britain. *British Birds* **114 (12)**: 723 - 747.

Stauss, M. J., Burkhardt, J. F. and Tomiuk, J. (2005) Foraging flight distances as a measure of parental effort in Blue Tits *Parus caeruleus* differ with environmental conditions. *Journal of Avian Biolog*y **36(1)**: 47 - 56. doi: 10.1111/j.0908-8857.2005.02855.x.

Stenning, M. (2018) *The Blue Tit,* T & A D Poyser (Bloomsbury Publishing), London, UK.

Stephens, S.E., Koons, D.N., Rotella, J.J. & Willey, D.W. (2004) Effects of habitat fragmentation on avian nesting success: A review of the evidence at multiple spatial scales. *Biological Conservation* **115(1)**: 101 - 110. doi: 10.1016/S0006-3207(03)00098-3.

Stracey, C.M. and Robinson, S.K. (2012) Are urban habitats ecological traps for a native songbird? Season-long productivity, apparent survival, and site fidelity in urban and rural habitats. *Journal of Avian Biology* **43**: 50 – 60. doi: 10.1111/j.1600-048X.2011.05520.x.

Strubbe, D., Hudin, N.S., Teyssier, A., Vantieghem, P., Aerts, J. & Lens, L. (2020) Phenotypic signatures of urbanization are scale-dependent: A multi-trait study on a classic urban exploiter. *Landscape and Urban Planning* **197**: 103767, 1 - 10. doi: 10.1016/j.landurbplan.2020.103767.

Sullivan, M.J.P., Newson, S.E. and Pearce-Higgins, J.W. (2015) Using habitat-specific population trends to evaluate the consistency of the effect of species traits on bird population change. *Biological Conservation* **192**: 343–352. doi: 10.1016/j.biocon.2015.10.009.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. & Gamauf, A. (2014) Hard times in the city- attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology* **11(48)**: 1 - 13. doi: 10.1186/1742-9994-11-48.

Sumasgutner, P., Jenkins, A., Amar, A. & Altwegg, R. (2020) Nest boxes buffer the effects of climate on breeding performance in an African urban raptor. *PLoS ONE* **15(6)**: e0234503, 1 - 24**.** doi: 10.1371/journal.pone.0234503.

Sutherland, W. (1996) *From individual behaviour to population ecology* (Oxford series in ecology and evolution). Oxford University Press, Oxford.

Svensson, L. (1992) *Identification Guide to European Passerines*. Stockholm, Sweden.

Szulkin, M., Garroway, C.J., Corsini, M., Kotarba, A.Z., & Dominoni, D. (2020) How to quantify urbanisation when testing for urban evolution? In: Szulkin, M., Munshi-South, J., and Charmantier, A. (eds.) *Urban Evolutionary Biology*. Oxford University Press (OUP), Oxford, UK, pp. 13–35. doi: 10.1093/oso/97801 98836 841.003.0002.

Tallamy, D. W. and Shriver, W. G. (2021) Are declines in insects and insectivorous birds related? *The Condor* **123(1)**: 1 - 8. doi: 10.1093/ornithapp/duaa059.

Telve, K., Mägi, M., Lodjak, J., Kilgas, P., Remm, J. & Mänd, R. (2020) Looking at the forest through the eyes of birds: A radio-tracking study of microhabitat use in provisioning Great Tits. *Acta Oecologica* **103**: 103531, 1 - 7. doi: 10.1016/j.actao.2020.103531.

Ter Braak, C.J., & Prentice, I.C. (1988) *A theory of gradient analysis*. *Advances in Ecological Research* **18**: 271 - 317. doi: 10.1016/S0065-2504(08)60183-X.

Thackeray, S. J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T, Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I, Winfield, I.J. & Wanless, S. (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535(7611)**: 241 - 245.

Theodorou, P. (2022) The effects of urbanisation on ecological interactions. *Current Opinion in Insect Science* **52**: 100922, 1 - 9. doi: 10.1016/j.cois.2022.100922.

Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M. & Speakman, J.R. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291(5513)**: 2598 - 2600. doi: 10.1126/science.1057487.

Thompson, C.F., Flux, J.E.C. and Tetzlaff, V.T. (1999) The Heaviest Nestlings Are Not Necessarily the Fattest Nestlings (Los polluelos más pesados no necesariamente son los más gordos). *Journal of Field Ornithology*, **64(4)**: 426 – 432, https://www.jstor.org/stable/4513851.

Thompson, M.J., Capilla-Lasheras, P., Dominoni, D.M., Réale, D. & Charmantier, A. (2022) Phenotypic variation in urban environments: mechanisms and implications. *Trends in ecology & evolution* **37(2)**: 171 - 182. doi: 10.1016/j.tree.2021.09.009.

Thorpe, K. (2017) UK Urban Regeneration Policy for Competitiveness: A Government Perspective. *LHI Journal of Land, Housing and Urban Affairs* **8(2)**: 33 - 53. doi: 10.5804/LHIJ.2017.8.2.033.

Toffolo, C., Gentili, R., Banfi, E., Montagnani, C., Caronni, S., Citterio, S. & Galasso, G. (2021) Urban plant assemblages by land use type in Milan: Floristic, ecological and functional diversities and refugium role of railway areas. *Urban Forestry and Urban Greening* **62(7)**: 127175, 1 - 11. doi: 10.1016/j.ufug.2021.127175.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D. & Gaston, K.J. (2007a) Bird densities are associated with household densities. *Global Change Biology* **13(8)**: 1685 - 1695. doi: 10.1111/j.1365-2486.2007.01390.x

Tratalos, J., Fuller, R.A., Warren, P.H., Davies, R.G. & Gaston, K.J. (2007b) Urban form, biodiversity potential and ecosystem services. *Landscape and Urban Planning* **83**: 308 – 317. doi: 10.1016/j.landurbplan.2007.05.003.

Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J. & Perret, P. (2003) Variation in Blue Tit breeding performance across gradients in habitat richness. *Ecology* **84(11)**: 3033 - 3043. doi: 10.1890/02-0663.

Tremblay, I., Thomas, D.W., Blondel, J., Perret, P. & Lambrechts, M.M. (2005) The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. *Ibis* **147(1)**: 17 - 24. doi: 10.1111/j.1474-919x.2004.00312.x.

Trepl, L. (1995) Towards a theory of urban biocoenoses: some hypotheses and research questions. In: Sukopp, H., Numata, M., and Huber, A. (eds.) *Urban Ecology as the Basis for Urban Planning*. SPB Academic Publishing, The Hague, pp. 3–21.

Turak, E., Bush, A., Dela-Cruz, J. and Powell M. (2020) Freshwater Reptile Persistence and Conservation in Cities: Insights from Species Occurrence Records. Water. **12(3)**: 651. doi: 10.3390/w12030651.

Uezu, A., Metzger, J.P., and Vielliard, J.M. (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological conservation* **123(4)**: 507 - 519.

Ummenhofer, C.C. and Meehl, G.A. (2017) Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **372 (1723)**: 20160135. doi:

10.1098/rstb.2016.0135.

United Nations (2019) Department of Economic and Social Affairs (UN DESA); Population Division. *World Urbanization Prospects: The 2018 Revision*; United Nations: New York, NY, USA. Available at: https://esa.un.org/unpd/wup/Publications. (accessed 02/02/2023).

Van Balen, J. H. (1973) A Comparative Sudy of the Breeding Ecology of the Great Tit *Parus major* in Different Habitats. *Ardea* **55 (1–2)**: 1 – 93. doi: 10.5253/arde.v61.p1.

Van Balen, J.H. and Potting R.P. (1990) Comparative reproductive biology of four Blue Tit populations in the Netherlands. In: Blondel, J., Gosler, A., Lebreton, J.D. & McCleery, R. (eds.) *Population biology of passerine birds: An integrated approach.* Springer, Berlin, Heidelberg. pp. 19 - 38.

Van der Putten, W.H., Macel, M. and Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365(1549)**: 2025 - 2034. doi: 10.1098/rstb.2010.0037.

Van Dongen, S., Backeljau, T., Matthysen, E., & Dhondt, A.A. (1997) Synchronization of hatching date with budburst of individual host trees (*Quercus robur*) in the Winter Moth (*Operophtera brumata*) and its fitness consequences. *Journal of Animal Ecology* **66(1)**: 113 - 121. doi: 10.2307/5969.

van de Pol, M. and Wright, J. (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour* **77**: 753 – 758. doi: 10.1016/j.anbehav.2008.11.006.

van de Pol, M. and Cockburn, A. (2011) Identifying the critical climatic time window that affects trait expression. *American Naturalist* **177(5)**: 698 – 707. doi: 10.1086/659101.

van de Pol, M., Bailey, L., McLean, N., Rijsdijk, L., Lawson, C. & Brouwer, L. (2016) Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution* **7(10)**: 1246 – 1257. doi:10.1111/2041-210X.12590.

van Meerkerk, I., Boonstra, B. and Edelenbos, J. (2013) Self-Organization in Urban Regeneration: A Two-Case Comparative Research. *European Planning Studies* **21(10)**: 1630 – 1652. doi: 10.1080/09654313.2012.722963.

Van Noordwijk, A.J., McCleery, R.H. and Perrins, C.M. (1995) Selection for the Timing of Great Tit Breeding in Relation to Caterpillar Growth and Temperature. *Journal of Animal Ecology* **64(4)**: 451 - 458. doi: 10.2307/5648.

Vaugoyeau, M., Adriaensen, F. , Artemyev, A., Bańbura J., Barba, E., Biard, B., Blondel, J., Bouslama, Z., Bouvier, J.C., Camprodon, J., Cecere, F., Charmantier, A., Charter, M., Cichoń, M., Cusimano, C., Czeszczewik, D., Demeyrier, V., Doligez, B., Doutrelant, C., Dubiec, A., Eens, M., Eeva, T., Faivre, B., Ferns, P.N., Forsman, J.T., García-del-Rey, E., Goldshtein, A.,. Goodenough, A.E., Gosler, A.G., Grégoire, A., Gustafsson, L., Harnist, I., Hartley, I.R., Heeb, P., Hinsley, S.A., Isenmann, P., Jacob, S., Juškaitis, R., Korpimäki, E., Krams, I., Laaksonen, T., Lambrechts, M.M., Leclercq, B., Lehikoinen, E., Loukola, O., Lundberg, A., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Merino, S., Mitrus, C., Mönkkönen, M., Morin, X., Nager, R.G., Nilsson, J.A., Nilsson, S.G., Norte, A.C., Orell, M., Perret, P., Perrins, C.M., Pimentel, C. S., Pinxten, R., Richner, H., Robles, H., Rytkönen, S., Senar, J.C., Seppänen, J.T., da Silva, L.P., Slagsvold, T., Solonen, T., Sorace, A., Stenning, M. J., Tryjanowski, P., von Numers, M., Walankiewicz, W. & Møller, A.P. (2016) Interspecific variation in the relationship between clutch size, laying date and intensity of urbanization in four species of hole-nesting birds. *Ecology and Evolution* **6 (16)**: 5907 - 5920. doi: 10.1002/ece3.2335.

Vaugoyeau, M., Meylan, S. & Biard, C. (2017) How does an increase in minimum daily temperatures during incubation influence reproduction in the Great Tit *Parus major*? *Journal of Avian Biology* **48(5):** 714 – 725. doi: 10.1111/jav.01208.

Vedder, O., Bouwhuis, S., and Sheldon, B.C. (2013) Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS biology* **11(7)**: e1001605.

Verboven, N. and Visser, M. E. (1998) Seasonal variation in local recruitment of Great Tits: The Importance of being early. *Oikos*, **81(3**): 511 – 524, https://www.jstor.org/stable/3546771. doi: 10.2307/3546771.

Verhulst, S. and Tinbergen, J.M. (1991) Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit *Parus major. Journal of Animal Ecology* **60(1)**: 269 – 282, https://www.jstor.org/stable/5459. doi: 10.2307/5459.

Verhulst, S., Van Balen J.M. and Tinbergen, J.M. (1995) Seasonal decline in reproductive success of the Great Tit: Variation in time or quality? *Ecology* **76(8)**: 2392 – 2403.

Villarini, G. and Krajewski, W.F. (2010) Review of the different sources of uncertainty in single polarization radar-based estimates of rainfall. *Surveys in Geophysics* **31(1)**: 107 – 129. doi: 10.1007/s10712- 009-9079-x.

Villaseñor, N. R., Driscoll, D.A., Escobar, M.A.H., Gibbons, P., & Lindenmayer, D.B. (2014) Urbanization Impacts on Mammals across Urban-Forest Edges and a Predictive Model of Edge Effects. *PLOS ONE* **9(5)**: e97036. doi: 10.1371/journal.pone.0097036.

Visser, G. H. (1998) *Development of temperature regulation.* In Avian Growth and Development. Evolution Within the Altricial-precocial Spectrum (ed. J. M. Starck and R. E. Ricklefs), pp. 117-156. Oxford: Oxford University Press.

Visser, M.E., Adriaensen, F., Van Balen, J.H., Blondel, J., Dhondt, A.A., Van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D. L. (2003) Variable responses to large-scale climate change in European Parus populations. *Proceedings of the Royal Society of London B: Biological Sciences* **270(1513)**: 367 - 372. doi: 10.1098/rspb.2002.2244.

Visser, M.E. & Both, C. and Lambrechts, M.M. (2004) Global Climate Change Leads to Mistimed Avian Reproduction. Advances in Ecological Research 35: 89 – 110. doi: 10.1016/S0065-2504(04)35005-1.

Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* **272(1581)**: 2561 - 2569. doi: 10.1098/rspb.2005.3356.

Visser, M.E., Noordwijk, A.V., Tinbergen, J.M., & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B: Biological Sciences* **265(1408)**: 1867 - 1870.

Visser, M.E., Holleman, L.J.M. and Gienapp, P. (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147(1)**: 164 - 172. doi: 10.1007/s00442-005-0299-6.

Visser, M.E., Schaper, S.V., Holleman, L.J.M., Dawson, A., Sharp, P., Gienapp, P. & Caro, S.P. (2011) The effects of temperature and genetic background on timing of avian reproduction. *Functional Ecology* **25**:868 – 877. doi: 10.1111/j.1365-2435.2011.01844.x.

Visser, M.E., te Marvelde, L. and Lof, M.E. (2012) Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* **153 (Suppl. 1)**: 75 – 84. doi: 10.1007/s10336-011-0770-6.

Visser, M.E. and Verboven, N. (1999) Long-term fitness effects of fledging date in Great Tits. *Oikos* **85**: 445 – 450.

Walker, W.H., Meléndez-Fernández, O.H., Nelson, R.J. & Reiter, R.J. (2019) Global climate change and invariable photoperiods: A mismatch that jeopardizes animal fitness. Ecology and Evolution **9(17)**: 10044 - 10054. doi: 10.1002/ece3.5537.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J-M., Hoegh-Guldberg, O. &Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416(6879)**: 389 - 395.

Walther, G.R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **365**: 2019 – 2024. doi: 10.1098/rstb.2010.0021.

Watson, H., Videvall, E., Andersson, M.N. & Isaksson, C. (2017) Transcriptome analysis of a wild bird reveals physiological responses to the urban environment. *Scientific Reports* **7(1)**: 1 - 10. doi: 10.1038/srep44180.

Wawrzyniak, J., Kaliński, A., Glądalski, M., Bańbura, M., Markowski, M., Skwarska, J., ZielińSki, P., Cyżewska, I. & Bańbura, J. (2015) Long-Term Variation in Laying Date and Clutch Size of the Great Tit *Parus major* in Central Poland: A Comparison between Urban Parkland and Deciduous Forest. *Ardeola*. **62(2**): 311 – 322. doi: 10.13157/arla.62.2.2015.311.

Wawrzyniak, J., Glądalski, M., Kaliński, A., Bańbura, M., Markowski, M., Skwarska, J., Zieliński, P. & Bańbura, J. (2020) Differences in the breeding performance of Great Tits *Parus major* between a forest and an urban area: a long term study on first clutches. *European Zoological Journal* **87(1)**: 294 – 309. doi: 10.1080/24750263.2020.1766125.

Webb, D.R. (1987) Thermal Tolerance of Avian Embryos: A Review. *The Condor* **89(4)**: 874 - 898. doi: 10.2307/1368537.

Webber, S.L. (2012) The role of food availablity in determining the energetic and life history costs of reproduction in short-lived birds. PhD thesis, University of Birmingham, Birmingham, UK.

Wesolowski, T., Czeszczewik, D., Rowiński, P. and Walankiewicz, W. (2002) Nest soaking in natural holes – a serious cause of breeding failure? *Ornis Fennica* **79**: 132 – 138.

Wesołowski, T., and Rowiński, P. (2006) Timing of bud burst and tree-leaf development in a multispecies temperate forest. *Forest Ecology and Management* **237(1-3)**: 387 - 393. doi: 10.1016/j.foreco.2006.09.061.

Whitehouse, M.J., Harrison, N. M., Mackenzie, J., & Hinsley, S. A. (2013) Preferred habitat of breeding birds may be compromised by climate change: unexpected effects of an exceptionally cold, wet spring. *PLoS One* **8(9)**: e75536. doi: 10.1371/journal.pone.0075536.

Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Review* **49**:207 –264. doi: 10.1111/j.1469-185X.1967.tb01419.x

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75(5)**: 1182 – 1189. doi: 10.1111/j.1365-2656.2006.01141.x.

Wickham, H. (2016) *ggplot2: Elegant graphics for data analysis*. 2nd Edition. Springer-Verlag, New York, NY. [Computer software].

Wilkin, T.A., Garant, D., Gosler, A.G. & Sheldon, B.C. (2006) Density effects on life-history traits in a wild population of the Great Tit *Parus major*: analyses of long-term data with GIS techniques. *Journal of Animal Ecology* **75(2)**: 604 – 615. doi: 10.1111/j.1365-2656.2006.01078.x.

Wilkin, T.A., Perrins, C.M., & Sheldon, B.C. (2007a) The use of GIS in estimating spatial variation in habitat quality: a case study of lay-date in the Great Tit Parus major. *Ibis* **149(s2)**: 110 - 118. doi: 10.1111/j.1474-919X.2007.00757.x.

Wilkin, T.A., Garant, D., Gosler, A.G. & Sheldon, B.C. (2007b) Edge effects in the Great Tit: Analyses of long-term data with GIS techniques. *Conservation Biology* **21(5)**: 1207 - 1217. doi: 10.1111/j.1523-1739.2007.00767.x.

Wilkin, T.A., King, L.E. and Sheldon, B.C. (2009a) Habitat quality, nestling diet, and provisioning behaviour in Great Tits Parus major. Journal of Avian Biology 40(2): 135 – 145. doi: 10.1111/j.1600-048X.2009.04362.x.

Wilkin, T.A., Gosler, A.G., Garant, D., Reynolds, S.J. & Sheldon, B.C. (2009b) Calcium effects on life-history traits in a wild population of the Great Tit (*Parus major*): Analysis of long-term data at several spatial scales. *Oecologia* **159(2)**: 463 - 472. doi: 10.1007/s00442-008-1222-8.

Wingfield, J. C. and Farner, D. S. (1980) Control of seasonal reproduction in temperate-zone birds. *Prog. Reproductive Biology* **5**: 62 - 101.

Woodward, I., Aebischer, N., Burnell, D., Eaton, M., Frost, T., Hall, C., Stroud, D. & Noble, D. (2020) Population estimates of birds in Great Britain and the United Kingdom. *British Birds*

113(2): 69 - 104.

Xie, S., Su, Y., Xu, W., Cai, W., Wang, X., Lu, F. & Ouyang, Z. (2019) The effect of habitat changes along the urbanization gradient for breeding birds: An example from the Xiong'an New Area. *PeerJ*. **7**: e7961, 1 - 22. doi: 10.7717/peerj.7961.

Yang, L.H. and Rudolf, V.H.W. (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology letters* **13(1)**: 1 - 10. doi: 0.1111/j.1461-0248.2009.01402.x.

Yang, L.H., Postema, E.G., Hayes, T.E., Lippey, M.K. and MacArthur-Waltz, D.J. (2021) The complexity of global change and its effects on insects. *Current Opinion in Insect Science* **47**: 90 – 102. doi: 10.1016/j.cois.2021.05.001.

Young, I.R., Zieger, S. and Babanin, A.V. (2011) Global trends in wind speed and wave height. *Science* **332**: 451 – 455.

Zhou, D., & Chu, L. M. (2012) How would size, age, human disturbance, and vegetation structure affect bird communities of urban parks in different seasons? *Journal of Ornithology* **153**: 1101 - 1112.

Zuckerberg, B., Bonter, D. N., Hochachka, W. M., Koenig, W. D., DeGaetano, A. T. & Dickinson, J. L. (2011) Climatic constraints on wintering bird distributions are modified by urbanisation and weather. *Journal of Animal Ecology* **80(2)**: 403 – 413. doi: 10.1111/j.1365-2656.2010.01780.x.

Zurita, G., Pe'er, G., Bellocq, M.I. & Hansbauer, M.M. (2012) Edge effects and their influence on habitat suitability calculations: A continuous approach applied to birds of the Atlantic forest. *Journal of Applied Ecology* **49(2)**: 503 – 512. doi: 10.1111/j.1365-2664.2011.02104.x

Zuur, A.F., Ieno, E.N. and Smith, G.M. (2007) *Analysing ecological data*. Vol. 680. Springer, New York, NY, USA.

Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009) *Mixed effects models and extensions in ecology with R.* Springer, New York, NY, USA.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1(1)**: 3 - 14. doi: 10.1111/j.2041-210X.2009.00001.x.

Zuur, A. F., Hilbe, J. M. and Ieno, E. N. (2013) *A beginner's guide to GLM and GLMM with R: A frequentist and Baysian perspective for ecologists*, *Beginner's Guide Series*. Highland Statistics Ltd, Newburgh, UK.

Appendices

Appendix One

Appendix 1a

Averaged habitat data from four habitat surveys conducted at each site.

For each site (n = 31), data on the percentage of different types of vegetation cover were collected from habitat surveys conducted in 2013 (and 2016 for Holders Woods). Habitat surveys were undertaken within a 10m radius of nestboxes (n = 4). Table A1.1 provides the averaged habitat survey data (% coverage of different habitat cover) calculated from the raw data for each site.

Table A1.1. Averaged habitat survey data for each site. Raw values for each variable were calculated as the percentage of the total vegetation cover type (trees, shrubs, herbaceous and grass cover), as well as bare ground within a 10m radius from the nestbox. Data from four nestboxes at each of the 31 sites were then averaged to estimate the typical habitat cover. Data are also provided on the mean percentage of native, deciduous (native and non-native) and evergreen (coniferous) trees (relative to total tree counts) for each site. Sites are in order of increasing urbanisation and colour coded according to their urban land class classification (based on the percentage of built landcover). **ULC1** (green) = least urbanised (suburban sites); **ULC2** (yellow) = dense-suburban; **ULC3** (orange) = moderately urbanised sites; **ULC4** (purple) = highly urbanised; **ULC5** (red) = most densely urbanised.

Site ID	% Tree cover	% Herbaceous cover	% Shrub cover	% Grass cover	% Bare Ground	% Native Trees	% Deciduous Trees	% Evergreen Trees
HILL	6.25	38.75	26.50	8.50	20	85	83	17
SUTTON	9.25	53.25	0.50	0	37	72	98	2
SAN	5	49.50	21.50	5.00	19	87	100	0
WGVP	9.50	27	8.50	10.50	44.50	91	100	0
PERRY	4.50	32.50	4	24.50	34.50	32	100	0
HOLD	50	2.50	26.25	1.25	20	86	72	28
CANNON	8.75	30	13.25	28.25	19.75	87	98	2

PINES	10	39.50	37.25	4.50	8.75	72	80	20
BAT	7	19.25	29.50	3.50	40.75	97	100	0
OAKW	7	34.75	36.75	0	21.50	78	58	42
POPES	5.50	47.75	6	21.75	19	100	100	0
ROOK	5.25	15.25	11.50	39.50	28.50	80	91	9
SELLY	2.75	2	1.75	89.75	3.75	20	100	0
HAN	3	1.50	1.25	50.75	43.50	52	96	4
SHE	9.50	45	7.25	6.25	32	62	100	0
RAD	9.50	43.50	30.50	0.75	15.75	100	100	0
CALL	7.75	53.75	17	3	18.50	99	100	0
MAN	6.50	25	40.50	16.25	11.75	75	100	0
BUR	9	57.50	8	22	3.50	72	100	0
SOHO	6.50	11.50	7.25	25.75	49	58	100	0
CHAM	3.25	1	1.25	65.25	29.25	45	100	0
PHIL	3.75	0	0	75.5	20.75	29	100	0
MOI	3.75	8.75	7	68.50	11	85	100	0
COW	8	62.75	3.25	8	18	71	100	0
BAR	5.5	2.75	5.25	26.25	60.25	53	99	1
GAR	2.75	0	0	60.25	37.50	0	100	0
WARS	2	0.75	8.25	44.25	44.75	36	93	7
HIGH	2.75	0	1	48.25	48	50	80	29
CITY	3.25	18	13.25	36.25	29.25	48	88	12
GUC	3.75	43	15.25	0	38	75	100	0
PARK	1.50	1	3.75	46.25	47.50	55	100	0

Appendix 1b

Photographic key used to aid age determination and hatching date of Blue Tit nestlings in the field when nest visits occurred ≥72 hours after nestlings hatched.

Whilst the guide illustrates the daily development of Great Tits (*Parus major*) from hatching through to fledging, Blue Tits follow a very similar growth and development trajectory. Hatching dates and age assessments where used were considered approximate since environmental conditions including weather and food availability can affect development. (Source: Boumeester, R. (2008). *Leeftijdenkaart nestjongen mezen* Available at:

https://www.vogelwachtuffelte.nl/wp-content/uploads/2016/03/LEEFTIJDENKAART-NESTJONGEN-KOOLMEES-klein.pdf).

LEEFTIJDENKAART NESTJONGEN MEZEN.

Op deze kaart zijn foto's van de koolmees als voorbeeld gehanteerd, maar deze foto's van de ontwikkeling van de groei in het neststadium is bruikbaar voor alle mezensoorten.

0 dag. Donkerrode huid.
Code N0.

1 dag. Let op verschil met
jong 0 dagen oud. Code N1.

2 dagen. Puntjes op vleugel
zichtbaar. Code N1.

3 dagen. Kleur van veren op
vleugel. Code N1/N2.

4 dagen. Let op begin van
verengroei rug. Code N1/N2.

5 dagen. Begin pinnetjes
slagpennen. Code N1/N2.

6 dagen. Slagpennen in
begin van pin. Code N4.

7 dagen. Slagpennen nog
net in pin. Code N4.

8 dagen. Let op veren op
rug en nek. Veren net uit
bloedspoel komend. Code N5

9 dagen. Soms ogen open.
Code N5.

10 dagen. Veervorm op spoel
herkenbaar. Code N5.

z.o.z. (dag 11t/m19)

11 dagen. Let op lengte veer uit bloedspoel. Code N5.

12 dagen. Let op lengte veer uit bloedspoel. Code N5.

13 dagen. Let op lengte veer uit bloedspoel. Code N5.

14 dagen. Slagpennen half volgroeid. Code N6.

15 dagen. Let op lengte slagpennen. Code N6.

16 dagen. Let op lengte slagpennen. Code N6.

17 dagen. Let op terugtrek mondhoekplooi. Code N6.

18 dagen. Let op terugtrek mondhoekplooi. Code N7.

19 dagen. Uitvliegdag. Code N7.

Let op:

Bepalen leeftijd is **meest betrouwbaar van dag 0 tot dag 9** en te ijken na berekenen geboortedag bij wekelijkse nestkastcontrole (datum 1^{e} ei + legselgrootte + 13 dgn = uitkomstdatum). Hierin staat 13 dgn voor de broedtijd - 1 dag omdat op de dag van laatste eileg het broeden begint.

Neem van dag 16 t/m 19 de vogels niet meer uit het nest, maar schat leeftijd in het nest en ijk dit met schatting van vorige controle. (controleer zeer voorzichtig want jongen zijn springerig, voorkom vroegtijdig uitvliegen).

Leer van onderlinge leeftijdsverschillen binnen 1 nest (veroorzaakt bij aanvang broeden voor completering legselgrootte en 2^{e} broedsels).

Appendix Two

Filtering of six years of Blue Tit breeding data from 31 sites across an urban gradient in the city of Birmingham, UK resulting in the creation of 3 separate dataframes.

Three separate breeding datasets were derived from the raw data (Table A2.1). The first included all breeding attempts in which clutches had reached completion and the female had initiated incubation (n=752 records). The second filtered data to only include nests in which at least one chick successfully hatched, (n = 662 records) and the third filtered data to only include nests in which at least one chick fledged (n=554 records). Breeding analyses for each response variable were then based on the appropriate dataset (Table 3.1) that retained both total and partial failures.

	Dataset		
Response Variable	Clutch Filtered (n=752*)	Brood Filtered (n=662)	Fledged Filtered (n=554)
Clutch Size	✓		
Laying Date	✓		
Hatching Date		✓	
Maximum Brood Size	✓	✓	
Fledgling Numbers		✓	✓
Hatching Success (Binomial)	✓	✓	
Fledging Success (Binomial)		✓	✓
Breeding Success Binomial)	✓	✓	
Hatching Success (Binary)	✓		
Fledging Success (Binary)		✓	
Breeding Success (Binary)	✓		

Table A2.1: Response variables and their associated datasets derived from the raw data and used in the analyses of six years (2013-2018) of Blue Tit breeding data from 28 sites stratified across an urban gradient in the city of Birmingham, UK. ✓ 'Zero-filtered data': datasets (not used for analyses here) which exclude complete breeding failures associated with the response which are commonly used in the analysis of bird breeding data.

Appendix Three

Summaries of the model frameworks for all final global Built (Table A3.1) and ULC (Table A3.2) models used in the analyses of measures of reproductive performance (capturing laying, incubation and brood rearing periods) in Chapter 3.

All global models performed better than nested and null models on the basis of summary outputs, ANOVA tests and comparisons of AIC values (ΔAIC ≥2).

Response	**Specification of Response Variable**	**Conditional Model Fixed Effects**	**Conditional Model Random Effects**	**Model**	**Family / Link**	**Zero Inflation /Truncation Term)**
Clutch Size	Count	**sc.BLC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number)	glmmTMB	Compois (Log Link)	
Brood Size	Count	**sc.BLC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Compois (Log Link)	zi = Site ID
Hatching Success (Proportional)	Vector (Brood size, Number of eggs not hatched)	**sc.BLC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID) + (1|Year)	glmmTMB	Binomial (Logit Link)	
Hatching Success (Binary)	Binary (0=No eggs hatched 1= 1≥ eggs hatched	**sc.BLC + I(sc.BLC ^2) + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID) + (1|Year)	glmmTMB	Binomial (Logit Link)	
Fledgling Numbers	Count	**sc.BLC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.Occ**	(1|Site ID) + (1|Year)	glmmTMB	Compois (Log Link)	zi = Site ID
Fledging Success (Proportional)	Vector (Number of hatchlings fledged, Number of hatchlings died)	**sc.BLC + sc.GLC + sc.MeanNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.AHD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	zi = Site ID

Fledging Success (Binary)	Binary (0=No chicks fledged, 1=≥1 fledglings)	**sc.BLC + I(sc.BLC ^2) + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.AHD + sc.Occ**	(1|Site ID /Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	
Breeding Success (Proportional)	Vector (Number chicks fledged, Total nest failures (inc. addled eggs and dead nestlings)	**sc.BLC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	zi = Site ID
Breeding Success (Binary)	Binary (0=No chicks fledged, 1= ≥1 fledglings)	**sc.BLC + I(sc.BLC ^2) + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	

Table A3.1. Summaries of model frameworks for the **final global built models** used to analyse breeding success outcomes for Blue Tits breeding across an urban gradient in the city of Birmingham over six breeding seasons (2013-2018). The conditional fixed effects, random effects structure, model and family are described for each response variable. Landscape scale variables are highlighted in grey, habitat variables in green and biotic variables in orange. The default random effects structure was Year crossed with Nest Box nested in Site ID. (sc. = scaled and centred covariates; BLC = % built landcover; GLC = % garden landcover; MeNDB = mean density of native, deciduous broadleaved trees; Edge = mean distance of nestboxes within a site to the edge of tree cover; InvSI = inverse Simpson's Diversity Index (native and non-native tree diversity); $_{log}$SiteArea = (log) Site Area; ALD = April laying date; AHD = April Hatching Date; Occ = occupancy). Polynomial terms are specified in parentheses.

Table A3.2. Summaries of the model frameworks for the **final global ULC models** used to analyse breeding success outcomes for Blue Tits breeding across an urban gradient in the city of Birmingham over six consecutive breeding seasons (2013-2018). The conditional fixed effects, random effects structure, model and family are described for each response variable. Landscape scale variables are highlighted in grey, habitat variables in green and biotic variables in orange. The default random effects structure was Year crossed with Nest Box nested in Site ID. (sc. = scaled and centred covariates BLC = % built landcover; GLC = % garden landcover; MeNDB = mean density of native, deciduous broadleaved trees; Edge = mean distance of nestboxes within a site to the edge of tree cover; InvSI = inverse Simpson's Diversity Index (native and non-native tree diversity); $_{log}$SiteArea = (log) Site Area; ALD = April laying date; AHD = April Hatching Date; Occ = occupancy). Polynomial terms are specified in parentheses.

Response	**Specification of Response Variable**	**Conditional Model Fixed Effects**	**Conditional Model Random Effects**	**Model**	**Family / Link**	**Zero Inflation /Truncation Term)**
Clutch Size	Count	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Compois (Log Link)	
Brood Size	Count	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Compois (Log Link)	zi = Site ID
Hatching Success (Proportional)	Vector (Brood Size, Number of eggs not hatched)	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID) + (1|Year)	glmmTMB	Binomial (Logit Link)	
Hatching Success (Binary)	Binary (0=No eggs hatched 1= 1≥ eggs hatched	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	

Fledgling Numbers	Count	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Compois (Log Link)	zi = Site ID
Fledging Success (Proportional)	Vector (Number of hatchlings fledged, Number of hatchlings died)	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.AHD**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	zi = Site ID
Fledging Success (Binary)	Binary (0=No chicks fledged, 1= ≥1 fledglings)	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.AHD + sc.Occ**	(1|Site ID) + (1|Year)	glmmTMB	Binomial (Logit Link)	
Breeding Success (Proportional)	Vector (Number chicks fledged, Total nest failures (inc. addled eggs and dead nestlings)	**ULC + sc.GLC + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	zi = Site ID
Breeding Success (Binary)	Binary (0=No chicks fledged, 1=≥1 fledglings)	**ULC + sc.GLC + I(sc.GLC ^2) + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.ALD + sc.Occ**	(1|Site ID/Box Number) + (1|Year)	glmmTMB	Binomial (Logit Link)	

Appendix Four

Summaries of the model frameworks for all final global built models used to analyse nestling morphometrics (Table A4.1) and measures of survival and brood reduction across two developmental stages (Table A4.2) in Chapter 4.

Nestling morphometric traits (Table A4.1) include mean nestling mass (MNM), mean (brood-level) body condition (MeanRBC) and brood mass asymmetry (ASYM).

Survival/brood breeding outcomes include: the probability of nestling survival (PNS; final breeding outcome (survive/died) for individual nestlings alive at ringing); Early Brood Survival (EBS: the proportion of nestlings surviving to ringing age (≥8 days) relative to brood size at hatching; Late Brood Survival (LBS: the proportion of nestlings fledged relative to brood size at hatching, and proportion of early stage nestling deaths relative to all nestling deaths recorded during brood rearing for each nest (proportional brood reduction; PBR).

Comparisons of AIC values across the *a priori* considered nested and global models using the ANOVA function, implied that simpler models incorporating landscape+biotic predictor blocks provided an equal or more parsimonious fit (i.e. ΔAIC ≤2) for the analysis of meanRBC, PNS and LBS response variables and these models are also presented. For the analysis of EBS, the landscape+habitat predictor block model fitted the dataset equally as well as the global model. In comparison, habitat-only and combined habitat+biotic models provided poor model fits across all response variables, suggesting that variation in the characteristics of the wider urban landscape exert a potentially greater effect on nestling size, body condition and survival to fledging. It should be noted, however, that in the few cases where nested models performed better than global models, there was little difference between model summary outputs of significant covariates and associated inferences and conclusions drawn. Consequently for all response variables the global model was selected and is discussed in the main chapter.

Table A4.1. Summaries of the final global models analysed for mean nestling mass (MNM), brood weight Asymmetry (ASYM), and mean (brood) body condition measured using residuals from a global regression of nestling weight against tarsus length (meanRBC). The conditional fixed effects, random effects structure, model and family are described for each response variable (both built and ULC models). Details of alternative models are also provided where nested models were found to be equally competitive or performed better than global models (ΔAIC ≤2). Landscape scale variables are highlighted in grey, habitat variables in green and biotic variables in orange. The default random effects structure was Year crossed with Nest Box nested in Site ID. (sc. = scaled and centred covariates BLC = % built landcover; GLC = % garden landcover; MeNDB = mean density of native, deciduous broadleaved trees; Edge = mean distance of nestboxes within a site to the edge of tree cover; InvSI = Inverse Simpson's Diversity Index (native and non-native tree diversity); $_{log}$SiteArea = (log) Site Area; ALD = April laying date; AHD = April Hatching Date; Brood = brood size; Occ = occupancy; Ringing Age = ringing age; MeBOSTrees = Mean number of birch, oak and sycamore trees;. Polynomial terms are specified in parentheses.

Response	**Conditional Model Fixed Effects**	**Conditional Model Random Effects**	**Model**	**Family**	**AIC**
MNM (Built)	**Year** + sc.BLC + sc.GLC + **sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.Edge + sc.MeBOSTrees + sc.AHD + sc.Brood + sc.RingingAge + sc.Occ**	(1|Site ID)	lmer	Gaussian (Identity Link)	1540.4
MNM (ULC)	**Year** + ULC + sc.GLC + **sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.$_{log}$SiteArea + sc.Edge + sc.MeBOSTrees + sc.AHD + sc.Brood + sc.RingingAge + sc.Occ**	(1|Site ID)	lmer	Gaussian (Identity Link)	1535.6
ASYM (Built) (log transformed)	**Year** + sc.BLC + sc.GLC + **sc.MeNDB + sc.InvSI + sc.$_{log}$SiteArea + sc.Edge + sc.MeBOSTrees + sc.AHD + sc.Brood + sc.RingingAge + sc.Occ**	(1|Site ID)	lmer	Gaussian (Identity Link)	277.2
ASYM (Built Alternative) (log transformed)	**Year** + sc.BLC + sc.GLC + **sc.AHD+ sc.Brood + sc.RingingAge+sc.Occup**	(1|Site ID)	lmer	Gaussian (Identity Link)	**272.5**

ASYM (ULC) (log transformed)	**Year** + ULC + sc.GLC + **sc.MeNDB + sc.InvSI + sc.**$_{log}$**SiteArea + sc.Edge + sc.MeBOSTrees + sc.AHD + sc.BroodSize + sc.RingingAge + sc.Occ**	N/A	lm	N/A	
MeanRBC (Built)	**Year** + sc.BLC + sc.GLC + **sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.**$_{log}$**SiteArea + sc.Edge + sc.MeBOSTrees + sc.AHD+ sc.Brood + sc.RingingAge + sc.Occ**	(1|Nestbox ID)	lmer	Gaussian (Identity Link)	1036.0
MeanRBC (ULC)	**Year** + sc.BLC + sc.GLC + **sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.**$_{log}$**SiteArea + sc.Edge +sc.MeBOSTrees + sc.AHD + sc.BroodSize + sc.RingingAge + sc.Occ**	(1|Nestbox ID)	lmer	Gaussian (Identity Link)	1036.0

NB a term capturing the total number of preferred native tree species (oak, sycamore and birch) was also included *a priori* in models but not found to be significant or to improve model fit.

Table 4.2. Summaries of the final global models analysed for “Survival” response variables: probability of nestling survival (PNS); Early (EBS) and LBS (Late) Brood Survival and proportion of nestling deaths occurring prior to ringing relative to all nestling deaths throughout brood rearing (PBR). Conditional fixed effects, random effects structure, model and family are described for each response variable (both built and ULC models). Details of alternative models are also provided where nested models were found to be equally competitive or performed better than global models (ΔAIC ≤2). The default random effects structure was Year crossed with Nest Box nested in Site ID. (sc. = scaled and centred covariates BLC = % built landcover; GLC = % garden landcover; MeNDB = mean density of native, deciduous broadleaved trees; Edge = mean distance of nestboxes within a site to the edge of tree cover; InvSI = Inverse Simpson’s Diversity Index (native and non-native tree diversity); $_{log}$SiteArea = (log) Site Area; ALD = April laying date; AHD = April Hatching Date; Brood = brood size; Occ = occupancy; Ringing Age = ringing age; MeBOSTrees = Mean number of birch, oak and sycamore trees;. Polynomial terms are specified in parentheses.

Response	Conditional Model Fixed Effects	Conditional Model Random Effects	Model	Family	Zero Inflation Model	AIC
PNS (Built)	**BINARY FLEDGED (0,1) ~** sc.BLC + sc.GLC **+ sc.MeBOSTrees + sc.MeNDB + sc.Edge + sc.InvSI + I(sc.InvSI^2)+ sc.$_{log}$SiteArea + sc.AHD + sc.BroodSize + sc.Occ**	(1|Site ID/Box Number)+ (1|Year	glmmTMB	Binomial (Logit link)	N/A	1404.1
PNS (Built: Alternative)	**BINARY FLEDGED (0,1) ~** sc.BLC + sc.GLC + **sc.AHD + sc.BroodSize + sc.Occ**	(1|Site ID/Box Number)+ (1|Year)	glmmTMB	Binomial (Logit link)	N/A	**1398.7**
PNS (ULC)	**BINARY FLEDGED (0,1) ~ Year +** ULC + sc.GLC **+ sc.MeBOSTrees + sc.MeNDB + sc.Edge + sc.InvSI + sc.$_{log}$SiteArea + sc.MeTotalBOS + sc.AHD + sc.BroodSize + sc.Occ**	Brood ID	glmmTMB	Binomial (Logit link)	N/A	1096.3
PNS (ULC: Alternative)	**BINARY_FLEDGED (0,1) ~ Year +** ULC + sc.GLC + **sc.AHD + sc.BroodSize + sc.Occ**	Brood ID	glmmTMB	Binomial (Logit link)	N/A	**1175.0**

EBS (Built)	**cbind(Survival Pre-ringing, Deaths pre-ringing) ~** sc.BLC + sc.GLC+ I(sc.GLC^2) + sc.MeNDB +sc.InvSI + I(sc.InvSI^2) + sc.Edge + sc.$_{log}$SiteArea + sc.ALD	(1|Site ID)+ (1|Year)	glmmTMB	Betabinomial (Logit link)	zi= ~1	2263.9
EBS (Built: Alternative)	**cbind(Survival Pre-ringing, Deaths Pre-ringing) ~** sc.BLC + sc.GLC+ I(sc.GLC^2) + sc.MeNDB +sc.InvSI + I(sc.InvSI^2) + sc.Edge + sc.$_{log}$SiteArea	(1|Site ID)+ (1|Year)	glmmTMB	Betabinomial (Logit link)	zi= ~1	2263.8
EBS (ULC)	**(cbind(Survival Pre-ringing, Deaths Pre-ringing) ~** ULC + sc.GLC + I(sc.GLC^2) + sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.Edge + sc.$_{log}$SiteArea + sc.ALD + sc.Occ	(1|Site ID)+ (1|Year)	glmmTMB	Betabinomial (Logit link)	zi= ~1	2269.5
EBS (ULC: Alternative)	**(cbind(Survival Pre-ringing,Deaths_Pre-ringing) ~** ULC + sc.GLC + I(sc.GLC^2) + sc.MeNDB + sc.InvSI + I(sc.InvSI^2) + sc.Edge + sc.$_{log}$SiteArea	(1|Site ID)+ (1|Year	glmmTMB	Betabinomial (Logit link)	zi= ~1	**2268.5**
LBS (Built)	**(cbind(Survival_PostRinging,Deaths_PostRinging) ~** sc.BLC + sc.GLC + sc.MeanBOSTrees + sc.MeNDB +sc.InvSI+ I(sc.InvSI^2) + sc.Edge + sc.$_{log}$SiteArea + sc.ALD + sc.Occ	(1|Site ID/Box Number) +(1|Year)	glmmTMB	Binomial (Logit link)	zi= ~1	1105.2
LBS (Built: Alternative)	**(cbind(Survival Post-ringing, Deaths Post-ringing) ~** sc.BLC + sc.GLC + sc.ALD + sc.Occ	(1|Site ID/Box Number) +(1|Year)	glmmTMB	Binomial (Logit link)	zi= ~1	**1102.9**
LBS (ULC)	**(cbind(Survival Post-ringing, Deaths Post-ringing) ~ Year +** ULC + sc.GLC + sc.MeBOSTrees + sc.MeNDB + sc.InvSI + sc.Edge + sc.$_{log}$SiteArea + sc.ALD + sc.Occ	(1|Site ID)	glmmTMB	Binomial (Logit link)	zi= ~1	1145.8
PBR (Built)	**(cbind(Deaths Early, Deaths Late) ~** sc.BLC + sc.GLC + sc.MeBOSTrees + sc.MeNDB +sc.InvSI + sc.Edge + sc.$_{log}$SiteArea + sc.ALD	(1|Site ID)+ (1|Year	glmmTMB	Betabinomial (Logit link)	N/A	851.4
PBR (Alternative)	**(cbind(Deaths Early,Deaths Late) ~** sc.ALD	(1|Site ID)+ (1|Year	glmmTMB	Betabinomial (Logit link)	N/A	**841.2**
PBR (ULC)	**(cbind(Deaths Early,Deaths Late) ~** ULC + sc.GLC + sc.MeBOSTrees + sc.MeanNDB +sc.InvSI + sc.EdgeDistance + sc.logSiteArea + sc.ALD	(1|Site ID)+ (1|Year	glmmTMB	Betabinomial (Logit link)	N/A	849.2

NB a term capturing the total number of preferred native tree species (oak, sycamore and birch) was also included *a priori* in models but not found to be significant or to improve model fit.

Appendix Five

Explanation of sliding window analyses on which modelling within the *climwin* packages are run.

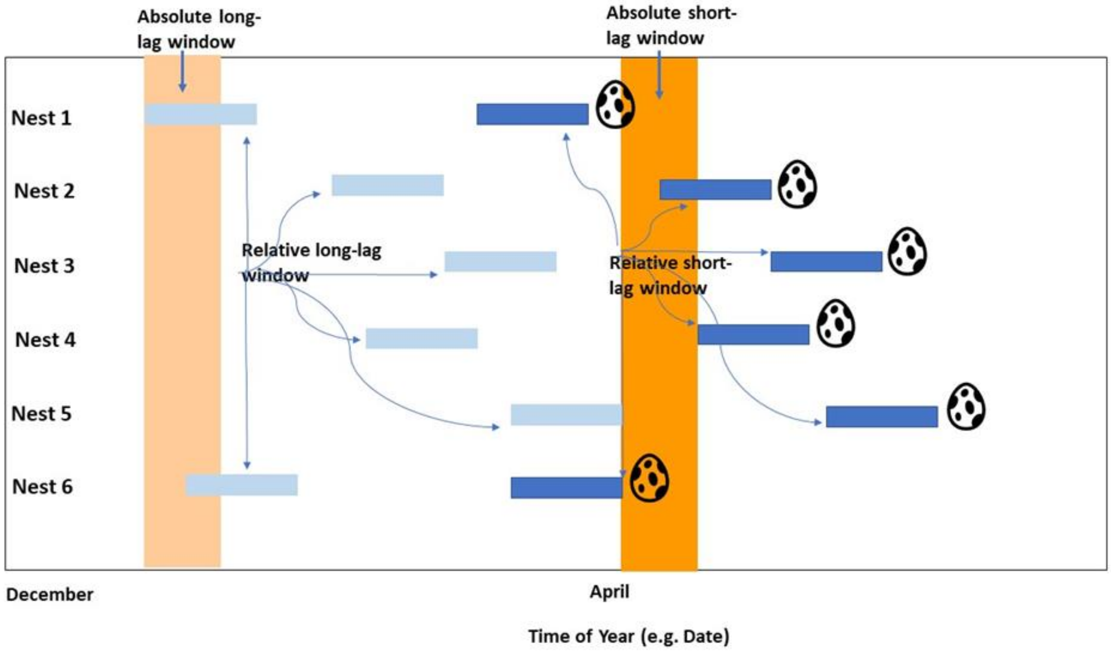


Figure A5.1. The schematic diagram above illustrates the different time windows that can be considered in the analysis of weather effects on biological systems, using the example of first egg date (laying date) as a response variable. The timing of egg laying for each individual nest in this example is represented by the egg symbol. Short- and long-lag periods (represented by dark and light areas respectively) refer to the length of time elapsed between the weather signal (e.g. mean temperature) and the timing of egg laying (i.e. more distant (January) or recent (April)). Absolute time windows (represented by light orange (long-lag) and dark orange (short-lag) areas) assume that laying dates for all nests are affected by a weather signal during a fixed period (i.e. the time window is the same across all nests). However, egg laying dates, like the majority of breeding responses, exhibit wide variation in timings across individual nests, thus meaning that the absolute time window identified in some cases could potentially occur after trait expression (nests 1 and 6 in this example). Relative time windows are an alternative approach to critical climatic time window analysis that takes into consideration each individual reproductive attempt and the associated time when the breeding trait was expressed. As such, in this example, the time window (represented by light blue (long-lag) and dark blue (short-lag) areas) varies relative to the timing of egg laying for each individual nest. Using the short-lag time window to further explain this approach, this might be the average temperature calculated over the 30 days directly preceding the laying date of each individual nest. (Adapted from van de Pol *et al*., 2016).

Appendix Six

Outputs from the initial stages of the *climwin* analysis to determine the best climate signals (comparing temperature and precipitation variables for each breeding response investigated.

Tables A6.1 - A6.3 provide details from steps 1-3 of the *climwin* analysis. For each response variable all of the potential climate signals across all possible sets of time windows were tested (i.e. candidate models) and compared against the baseline model. For each weather variable investigated (mean temperature, maximum temperature, minimum temperature, daily rainfall and dry days) the best aggregate/function weather signal combinations and their associated critical time window were identified from a comparison of candidate models with the baseline model (on the basis of their ΔAICc values, as given in the tables below). The *climwin* critical window is also provided which gives the window open and close days (relative to the biological date of the response variable = day 0). The weather predictor variables of interest were then randomised using the built in *randwin* function (specifying 100 randomisations) to quantify the likelihood of obtaining a similar or better AICc value for the climate signal by chance. The significance values from this step are provided in the table below for each candidate climate signal. Significant climate signals (with values $P_{\Delta AICc} \leq 0.05$) were then considered for further exploratory analysis as described in Chapter 5.

Table A6.1							
Response Variable/Biological Date	**Climate Signal**			***Climwin* and randomisation modelling output**			
Probability of Hatching Success / Hatching Date	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**ΔAICc (of Climate models relative to Baseline)**	**Model selected for further analysis**	**PΔAICc**
					Baseline AICc = 4752.0		
	Daily Mean Temp	Mean	Linear	0	-71.34		0.06•
	Daily Mean Temp	Mean	Quadratic	0	-71.34		0.28
	Daily Max Temp	Max	Linear	10 – 9	-56.21		0.26
	Daily Max Temp	Max	Quadratic	10 - 9	-54.19		0.64
	Daily Min Temp	Min	Linear	0	-81.76		**0.04**
	Daily Min Temp	Min	Quadratic	0	-91.93		0.24
	Daily Rainfall	Mean/Sum	Linear	14 – 0	-62.54		0.25
	Daily Rainfall	Mean/Sum	Quadratic	16 -10	-83.62		0.32
	Dry Days	NA	NA	NA	NA	NA	NA
Proportional Hatching Success/Hatching Date	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**ΔAICc (of Climate models relative to Baseline)**	**Model selected for further analysis**	**PΔAICc**
					Baseline AICc = 1720.8		
	Daily Mean Temp	Mean/Sum	Linear	1 - 0	-37.96		**0.01** (Mean)
	Daily Mean Temp	Mean/Sum	Quadratic	2 – 1	-46.60		**0.01** (Mean)
	Daily Max Temp	Mean/Sum	Linear	3 – 1	**-42.22**	✓	**<0.01** (Mean)
	Daily Max Temp	Mean/Sum	Quadratic	2 - 1	**-47.96**	✓	**0.01** (Mean)
	Daily Min Temp	Min/Mean	Linear	1 -1	-12.79		0.41
	Daily Min Temp	Min	Quadratic	26 – 9	-33.68		0.12
	Daily Rainfall	Mean/Sum	Linear	31 – 22	**-41.92**	✓	**<0.001** (Mean)
	Daily Rainfall	Mean/Sum	Quadratic	31 – 22	**-40.96**	✓	**<0.001** (Mean)
	Dry Days	Mean	Linear	4 – 3	-13.92		0.38

Table A6.2							
Response Variable/Biological Date	Climate Signal			*Climwin* and randomisation modelling output			
Probability of Fledging Success/Fledging Date	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**ΔAICc (of Climate models relative to Baseline)**	**Model selected for further analysis**	**PΔAICc**
					Baseline AICc = 4723.7		
	Daily Mean Temp	Mean/Sum	Linear	3 – 1	-67.50		NA
	Daily Mean Temp	Mean/Sum	Quadratic	2 - 1	-68.62		NA
	Daily Max Temp	Max	Linear	3 - 1	-106.04	✓	**<0.001**
	Daily Max Temp	Max	Quadratic	3 – 3	-113.78		0.07
	Daily Min Temp	Min/Mean	Linear	13 – 13	-42.35		0.44
	Daily Min Temp	Min/Mean	Quadratic	19 – 19	-130.12		0.07
	Daily Rainfall	Max	Linear	11 – 3	-68.49		0.26
	Daily Rainfall	Mean/Sum	Quadratic	13 – 9	-70.51		0.57/ 0.51
	Dry Days	Mean/Sum	Linear	4 - 3	-96.33		0.06
Proportional Fledging Success/Fledging Date	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**ΔAICc (of Climate models relative to Baseline)**	**Model selected for further analysis**	**PΔAICc**
					Baseline AICc = 2646.2		
	Daily Mean Temp	Mean/Sum	Linear	11 – 8	-19.13		NA
	Daily Mean Temp	Mean/Sum	Quadratic	9 – 9	-28.50		NA
	Daily Max Temp	Max	Linear	12 -1	-7.83		NA
	Daily Max Temp	Max	Quadratic	16 – 7	-40.95	✓	**0.05**
	Daily Min Temp	Min	Linear	20 – 0	-26.35		0.07
	Daily Min Temp	Min	Quadratic	20 - 0	-35.29		0.19
	Daily Rainfall	Mean/Sum/Max	Linear	10 - 10	-18.33		0.57
	Daily Rainfall	Max	Quadratic	9 - 4	-33.63		0.20
	Dry Days	Max	Linear	19 – 4	-32.23		0.09

Table A6.3							
Response Variable/Biological Date	**Climate Signal**			***Climwin* and randomisation modelling output**			
Nestling body mass / Date of weighing (Data = 2017-2018)	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**AICc (Baseline Model)** **ΔAICc (Climate models)**	**Selected model for further analysis**	**PΔAICc**
					Baseline AICc = 3951.2		
	Daily Mean Temp	Mean	Linear	20 - 13	-102.36		**<0.001**
	Daily Mean Temp	Sum	Linear	20 – 13	-98.20		NA
	Daily Mean Temp	Mean	Quadratic	16 – 4	-155.02	✓	**<0.001**
	Daily Mean Temp	Sum	Quadratic	16 – 4	-139.63		NA
	Daily Max Temp	Mean	Linear	20 – 4	-106.80		**<0.001**
	Daily Max Temp	Max	Linear	20 – 14	-99.05		NA
	Daily Max Temp	Sum	Linear	20 – 4	-101.14		NA
	Daily Max Temp	Mean	Quadratic	16 – 4	-125.08	✓	**<0.001**
	Daily Max Temp	Max	Quadratic	20 – 4	-117.17		NA
	Daily Max Temp	Sum	Quadratic	16 – 13	-112.44		NA
	Daily Min Temp	Mean	Linear	12 – 3	-133.65		**<0.001**
	Daily Min Temp	Min	Linear	11 – 2	-91.12		NA
	Daily Min Temp	Mean	Quadratic	12 – 6	-158.41	✓	**<0.001**
	Daily Min Temp	Min	Quadratic	10 – 9	-137.42		NA
	Daily Rainfall	Mean	Linear	19 - 5	-126.66		**<0.001**
	Daily Rainfall	Sum	Linear	19 - 5	-121.24		NA
	Daily Rainfall	Mean	Quadratic	19 – 5	-202.16	✓	**<0.001**
	Daily Rainfall	Sum	Quadratic	19 – 5	-185.91		NA
Nestling body mass / Date of weighing (Data = 2013-2018)	**Climate Variable**	**Aggregate Statistic**	**Effect (Function)**	**Window Range (days relative to biological date)**	**AICc (Baseline Model)** **ΔAICc (Climate models)**	**Selected model for further analysis**	**PΔAICc**

	Daily Mean Temp	Mean/Sum	Linear	5 - 0	-105.5		NA
	Daily Mean Temp	Mean/Sum	Quadratic	5 – 0	-122.40		NA
	Daily Max Temp	Mean/Sum	Linear	6 – 0	-155.84	✓	**<0.001**
	Daily Max Temp	Max	Linear	6 – 4	-115.42		NA
	Daily Max Temp	Mean/Sum	Quadratic	6 – 1	-162.74	✓	**<0.001**
	Daily Max Temp	Max	Quadratic	6 – 0	-132.32		**<0.001**
	Daily Min Temp	Min	Linear	2 - 0	-114.42		**<0.001**
	Daily Min Temp	Min	Quadratic	2 - 0	-156.28		**<0.001**
	Daily Rainfall	Mean/Sum	Linear	1 – 0	-67.44		**<0.001**
	Daily Rainfall	Max	Linear	4 - 0	-76.36		**<0.001**
	Daily Rainfall	Mean	Quad	7 – 0	-90.72		**<0.001**
	Daily Rainfall	Sum	Quad	19 – 7	-118.82	✓	**<0.001**
	Dry Days	Mean/Sum	Linear	8 – 2	-86.08	✓	**<0.001**

Tick marks indicate the climate signals and critical windows considered for further analysis.