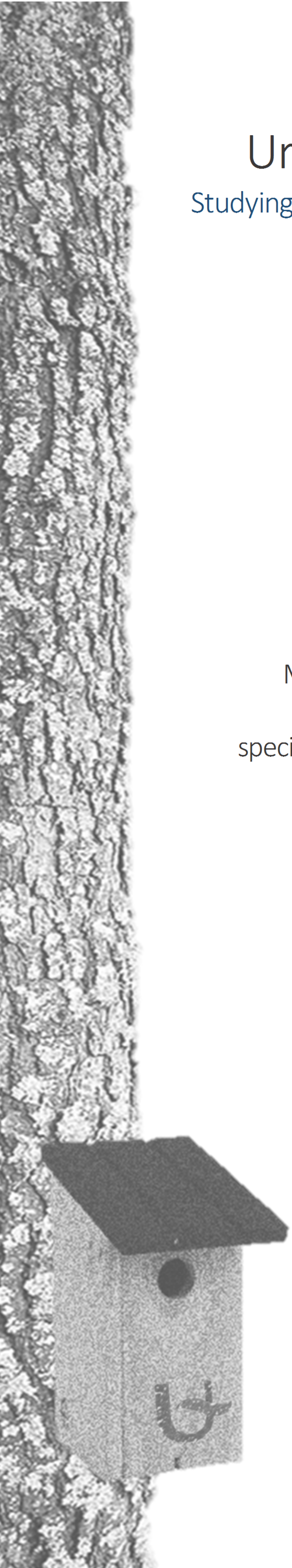


Urban areas as ecological traps

Studying great tits *Parus major* along an urbanisation gradient

Thesis by
Jacques de Satgé

Master Project submitted to obtain the degree of
Master of Biology
specialisation ‘Biodiversity: Conservation and Restoration’

Supervisor: Erik Matthysen

University of Antwerp
Faculty of Science
Department of Biology
Submitted: August 2016

Contents

Summary

Many studies have reported negative effects of urbanisation on bird breeding success, with the role of food thought to play a particularly significant role. The negative effects of city environments on birds have lead researchers to suggest that urban areas may represent ecological traps, whereby individuals settle preferentially in urban habitats but show poor reproductive success relative to other available rural habitats. In this context, this thesis sought to test the effects of urbanisation measured at two spatial scales on both the breeding success of great tits *Parus major*, and its food during the breeding season. A nested design was used in study sites in northern Belgium with *a priori* quantified degrees of urbanisation at both local and regional scales. Results found breeding success to vary at one or both spatial scales of urbanisation for all measured parameters: in urban areas great tits displayed advanced laying dates and breeding success was lower than in rural areas, with smaller clutch sizes, lower nestling masses and fewer fledglings per egg. Results regarding food showed that the proportion of caterpillars provisioned to nestlings varied with local scale urbanisation, with significantly lower proportions of caterpillars provisioned to nestlings in urban areas. Moreover, the proportion of caterpillars provisioned was found to have a significant positive effect on nestling mass. Provisioning rates and caterpillar lengths were not found to vary with urbanisation. Results of this study suggest that food quality plays a key role in breeding success in cities, highlight the importance of utilising multiple spatial scales in analysing urbanisation effects, and ultimately provide support to the ecological trap hypothesis.

Layman's summary

Urban areas are often viewed as attractive to birds, as they can offer additional sources of food and more opportunities for nesting sites. Despite this, urbanisation has been found to have negative effects on birds' reproductive success with differences in food quality and quantity between rural and urban environments suggested as a key reason for these differences. This thesis attempted to understand the role of urbanisation on the breeding success of a ubiquitous bird, the great tit *Parus major*, as well as on the quantity and quality of its food during the breeding season. To investigate this, this study used a nested design whereby nestboxes were placed in subplots (200m x 200m) located within larger plots (3km x 3km), and both plot and subplots were selected according to their urbanisation degree - low, medium or high. The results showed that the birds' reproductive success tended to decline with increasing urbanisation; birds in more urban areas laid fewer eggs, had nestlings of lower masses, and produced fewer fledglings. Food brought by parents to their nestlings was also found to vary with the degree of urbanisation. In urban areas, nestling were provisioned with lower proportions of caterpillars when compared with those in rural areas. However, food was provisioned with the same frequency, and caterpillar sizes did not differ between sites of different urbanisation. The results also showed that nestlings were heavier if their diet consisted of a larger proportion of caterpillars. These results support the idea that birds in urban areas have lower reproductive success despite the apparent advantages cities may offer, and that differences in food quality have a key role to play in determining breeding success. Furthermore, this study highlights that the scale of urbanisation is an important factor in affecting bird breeding success.

Introduction

Urbanisation and ecological trap theory

The urbanisation of natural landscapes is accelerating worldwide, changing the physical structure, local climates and ecological processes of once natural habitats while irreversibly altering patterns of biodiversity (Marzluff 2001; McKinney 2002; Seto et al. 2011). Today, more than half of the world's population lives in cities, while in Belgium this figure stands at 98 percent (United Nations 2014). The expansion of urban landscapes comes into direct conflict with nature, with factors such as increasing household density being strongly correlated with negative effects on wildlife (Peterson et al. 2007). Urban impacts on wildlife are wide-ranging: urban-driven shifts in land use result in the decline and local extinction of numerous taxonomic groups (Ree and McCarthy 2005) and drives biotic homogenisation (McKinney 2006). Roughly one-third of the world's known amphibian species are threatened by urbanisation (Hamer and McDonnell 2008), many mammals are 'urban-avoiders' (McKinney 2002) whose habitat requirements are directly at odds with the fragmented urban landscape (Miller and Hobbs 2002; Ree and McCarthy 2005), and bird communities have been shown to lose diversity and structural complexity with increasing urbanisation (Clergeau et al. 2006a; Liker et al. 2008).

While urban landscapes are markedly different from natural surroundings (Marzluff 2001) they still encompass substantially variable habitats ranging from green spaces in city parks to low-density suburban areas (Chamberlain et al. 2009). The tendency for urban spread and the consequent envelopment of natural habitat fragments represents a complex conservation problem (Miller and Hobbs 2002). Urban environments likely represent a continuum of selective novelty (Clergeau et al. 2006b) ranging from remnant natural areas exposed to urban pressures, to wholly novel environments such as newly created urban green spaces like city parks and gardens (Goddard et al. 2010). A combination of urban spread and the colonisation of these new urban environments has seen several species occurring in higher densities in urban areas than more natural habitats (termed 'urban-positive species' - Stracey 2011). This phenomenon is well documented for several bird species (Hedblom and Söderström 2012; Stracey and Robinson 2012).

Cities represent potentially attractive areas to avian populations for several reasons; they offer additional concentrated sources of food such as birds feeders, urban waste and fruit-bearing exotic shrubs and trees (Mennechez and Clergeau 2001; Robb et al. 2008a; Chamberlain et al. 2009), as well as readily available water, vegetation that is permanently disturbed due to pruning and mowing (Stracey and Robinson 2012), and convenient shelters and nesting sites in the form of nestboxes and city infrastructure (Hedblom and Söderström 2012). These factors can all act as positive cues in informing habitat choice, particularly for birds selecting habitats on the basis of food availability and vegetation. However, despite these positive cues, urban areas often act as an 'ecological trap', whereby a poor habitat becomes relatively more attractive, thus "baiting" an individual to settle (Dwernychuk and Boag 1972; Gates and Gysel 1978; Robertson and Hutto 2006). For birds in an urban context, this occurs when individuals settle in cities and built-up areas despite artificially high levels of disturbance and novel sources of mortality (Stracey 2011; Stracey and Robinson 2012). This mismatch between cue and reality arises when rapid environmental change (urbanisation) uncouples the cues that individuals use to assess habitat quality from the true quality of the environment (Robertson and Hutto 2006). Given that these cues have developed through evolutionary selection, such a trap arises when an organism is constrained by its evolutionary past to make a mistake, despite the fact that more suitable conditions occur elsewhere (Schlaepfer et al. 2002). In simpler terms, the positive outcome normally associated with a species' fixed preference (and its given cue) becomes a negative outcome (Misenhelter and Rotenberry 2000).

Urbanisation effects

Given their potential as ecological traps and drivers of behavioural change (Liker et al. 2008), urban areas and their effects on bird populations have been closely scrutinised in literature. Chamberlain et al. (2009) performed a meta-analysis of studies comparing rural and urban passerine birds in a pair-wise fashion to determine differences in key breeding success parameters. Evaluating 19 species, they found profound effects of urban areas on avian communities, primarily in the form of earlier laying dates (16 of 19 studies), smaller clutch sizes (33 of 46 studies) and lower nestling weights (10 of 11 studies). Similar findings regarding earlier lay dates in urban bird populations were found in a meta-analysis by Deviche and Davies (2014). This disparity between rural and urban bird populations highlights the importance of determining the drivers of this difference.

In disentangling the causal factors responsible for urban-rural bird population disparities, an understanding and comparison of rural and urban habitats is required. Several factors are critical to avian breeding success and phenology (Table 1), and the majority of these factors differ strongly between rural and urban areas (McKinney 2002; Chamberlain et al. 2009). Of these factors, the role of food, environmental conditions (light and temperature) and urban habitat structure are discussed in further detail.

Table 1: A literature summary regarding key parameters that may shape avian breeding success and laying date across urban and rural habitats

	Urban	Rural	Sources
Food quantity	Higher abundances of food and food types due to anthropogenic food sources such as bird feeders and refuse. Potentially lower natural food abundances (e.g. caterpillars) than rural areas.	Tendency (case-specific) for lower overall quantity of food than urban areas – lacking supplementary food sources. But caterpillar abundances are often observed to be higher.	Cowie and Hinsley 1988; Chace and Walsh 2006; Leston and Rodewald 2006; Isaksson and Andersson 2007; Robb et al. 2008; Chamberlain et al. 2009; Mackenzie et al. 2014
Food quality	Lower overall food quality – often energy rich but protein poor. Supplementary foods contain fewer amino acids required for egg formation and nestling growth. Arthropods observed to be of lower carotenoid quality.	Higher quality food available to nestlings, as measured by the proportion of caterpillars provisioned as well as their carotenoid quality.	Perrins 1991; Solonen 2001; Isaksson and Andersson 2007; Harrison et al. 2010; Hedblom and Söderström 2012
Temperature	Warmer – urban 'heat island' effect maintains higher urban temperatures relative to rural surrounds.	Cooler – average ambient temperatures are lower than urban zones.	McKinney 2002; Shochat et al. 2006; Seto et al. 2011; Deviche and Davies 2014
Light	City lights artificially lengthen daily photoperiod.	Fewer or no lights, photoperiod therefore defined by actual day length.	Partecke et al. 2004; Kempenaers et al. 2010; Deviche and Davies 2014; Solonen and Hilden 2014
Predation	Higher abundance of predators (e.g. pet cats) but predator activity does not necessarily increase accordingly (given supplementary food for predators). Predation may not cause additive mortality.	Lower abundance of predators, and increased variability in predation rates in accordance with natural population fluctuations.	Marzluff 2001; Baker et al. 2008; Chamberlain et al. 2009; Stracey 2011
Habitat structure	Natural vegetation largely replaced with built habitat and managed vegetation consisting of fragmented tree cover. Typically highly fragmented; lack of interconnectivity increases isolation of breeding sites.	Greater degree of natural vegetation. Typically comprises larger patch sizes exhibiting better interconnectivity and fewer edge effects.	Friesen et al. 1995; Mörtberg 2001; McKinney 2002; Chace and Walsh 2006; Chamberlain et al. 2009; Banbura and Banbura 2012

Food availability and type

Numerous bird-related studies have focused on diet and the importance of food type, prey provisioning, prey availability and predator-prey timing in determining breeding success (e.g. Perrins 1991; Verboven et al. 2001; Rytkönen and Krams 2003; Chamberlain et al. 2009; Wilkin et al. 2009). Placed within the context of the urban landscape, the subject of food availability and suitability becomes ever more relevant (Chamberlain et al. 2009). Food plays a critical role in adult bird condition and is highly important during the breeding season, with ramifications for reproductive phenology and breeding success (Amrhein 2014). The manner in which food varies with urbanisation therefore has strong potential to at least partially explain population differences between rural and urban environments.

Both the quality and quantity of urban food have a key role to play in affecting clutch sizes, nestling condition, fledgling success and laying dates (Chamberlain et al. 2009; Harrison et al. 2010; Deviche and Davies 2014). In the UK and USA more than 43% and 75% of households regularly feed birds respectively (Amrhein 2014). This supplementary food, along with refuse-sourced foods, provides easily accessible energy-rich resources to urban populations (Chamberlain et al. 2009). Harrison et al. (2010) showed experimentally that food provisioning significantly advanced clutch initiation date in both great and blue tits. The advancement in laying is in-part attributable to several food-related factors. Supplementary food is likely to produce better pre-laying feeding conditions, allowing females to reach nutritional thresholds at an earlier stage (Chamberlain et al. 2009; Harrison et al. 2010). Moreover, the availability of earlier food in the breeding season may cue earlier reproductive phenology in the expectation of richer foraging conditions during the time of peak nestling demand (the cue/anticipation hypothesis: Lack 1954; Perrins 1965). Anthropogenic food sources therefore have the potential to trigger a ‘false-start’ in egg laying; a phenomenon with significant repercussions: mistimed breeding which misses peak caterpillar abundance can result in higher starvation rates of urban chicks and thus poorer nestling condition (Perrins 1991; Chamberlain et al. 2009).

The relationship between supplementary food and clutch size of wild birds has often been shown to be positive (Amrhein 2014). A review by Robb et al. (2008b) reported that 28 studies found that clutch sizes of wild birds were increased by supplementary feeding, 34 studies found no effect and just one study found a negative effect. It must be noted that the vast majority of these studies took place in non-urban habitats. In urban areas clutch sizes are observably smaller relative to non-urban areas (e.g. Bailly et al. 2016) despite the fact that food availability is likely higher. This suggests that the food-clutch size relationship may not be straightforward in urban environments. This is typified in Harrison et al.’s (2010) finding that great tits exhibited smaller clutch sizes when continuously provisioned with supplementary food. This may be the a result of protein-poor supplementary food sources, whereby a lack of amino acids limits egg formation (Williams 1996, but see Nager et al. 1997). Alternatively, additional food may boost population densities which can in turn reduce clutch sizes on a per brood basis (Wilkin et al. 2006). However, density effects may hinge on the heterogeneity of local environments; at high densities some birds may be forced into nearby sites of poorer quality (e.g. lower food quantity and/or quality) and subsequently lay smaller clutches (Dhondt et al. 1992; Wilkin et al. 2006). However, variation in clutch size also has a strong genetic element (Postma and van Noordwijk 2005), which may influence the way in which clutch size and the local environment interact. Clutch sizes are more likely to be adaptive to local conditions where immigration between habitats of varying quality is low, as an influx of genes from outside areas is prevented (Postma and van Noordwijk 2005; Chamberlain et al. 2009). In this case clutch size can be expected to be fixed at the optimum for the local environment (Perrins 1965; Leston and Rodewald 2006). If gene flow between heterogeneous habitats is sufficiently high to prevent genetic differentiation, two possibilities exist. Firstly, clutch size may represent the average optimum across all habitat types, i.e. it is non-adaptive (Dhondt et al. 1990; Postma and van Noordwijk 2005). Or secondly, the genotype underlying clutch sizes illustrates plasticity (Husby et al. 2010) which enables clutches of different sizes in accordance with environment (rural or urban). In a city context, the degree to which clutch sizes are adaptive is further blurred by the fact that the urban areas can result in poorer quality adult birds (Liker et al. 2008), a finding potentially linked with food quality (further discussed below). Smaller clutches in urban areas may therefore simply be the result of poorer quality breeders (Riddington and Gosler 1995) and not necessarily an adaptive response.

Food quality has been shown to be poorer in urban areas than neighbouring rural areas. Anthropogenic food sources may be energy rich, but are often lacking in protein content (Chamberlain et al. 2009), and important nestling foods such as caterpillars have been shown to be of lower quality with lower carotenoid concentrations (Isaksson and Andersson 2007). Food quality can influence adult condition and have knock-on effects for breeding success (Chamberlain et al. 2009). Female tits cannot synthesise egg-building nutrients such as carotenoids and must source them from their local environments (Bailly et al. 2016), and urban eggs have been shown to be of poorer quality than rural counterparts (Isaksson et al. 2008; Bańbura et al. 2010). Urban nestlings hatched from lower quality eggs may therefore be placed at a prior disadvantage; nestling growth and survival are strongly linked to egg quality with effects extending beyond rearing (Krist 2011; Marri and Richner 2014). This effect may be compounded during nestling development if nestlings receive a lower quantity or poorer quality of caterpillars (Isaksson and Andersson 2007; Wawrzyniak et al. 2015), as caterpillars are regarded as high-quality dietary items (Wilkin et al. 2009a). Many forms of urban supplementary foods do not constitute good nestling-food substitutes (Chamberlain et al. 2009; Harrison et al. 2010) as they fail to meet high protein requirements of the nestling diet (Gosler 1993; Harrison et al. 2010). As such, where high quality foods are lacking in urban areas, poorer quality replacement foods (e.g. other arthropods of lower nutritional value - Hargitai et al. 2016) may lead to poorer nestling condition and lower fledgling success rates (Chamberlain et al. 2009). Some studies have observed parental compensation for food of lower quality, whereby provisioning rates increased in poorer quality habitats (Isaksson and Andersson 2007; Mägi et al. 2009). Similar compensation has been observed when prey items delivered to nestlings are smaller in size (Van Balen 1973).

Environmental conditions

Temperature and light are both factors which are seen to increase as one moves from rural areas towards the urban core (McKinney 2002). These conditions play key roles in dictating laying dates of birds and can have knock-on effects on breeding success (Deviche and Davies 2014). Increase in day length (photoperiod) is a primary driver of reproductive behaviours (e.g. singing, courtship, nesting) in birds, but between-year variation means that temperature, rainfall and food abundance act as secondary cues (Deviche and Davies 2014). Thus the combination of artificial light sources and the 'heat island' effect in cities has been shown to trigger earlier laying in many city-dwelling birds (Kempenaers et al. 2010; Deviche and Davies 2014; Wawrzyniak et al. 2015). While earlier laying dates in the wild are often viewed as advantageous and an indicator of good winter feeding (Robb et al. 2008a), in urban areas the advancement of laying dates can have significant repercussions for food availability and thus breeding success. City breeding pairs who breed earlier may exhibit a maladaptive laying date leading to a mismatch between the time of peak nestling food demand and the peak in food availability itself (Lambrechts et al. 1997; Kempenaers et al. 2010). This issue is further complicated by urban-driven changes in arthropod lifecycles. Urban environmental conditions can extend the plant growing season and plant peak growth, which in turn changes the peak in arthropod abundance as these populations seek to exploit new green vegetation (Visser et al. 2006). This represents another novel condition generated by urban environmental conditions that urban populations have to adapt to, and may be in part responsible for earlier reproductive phenology (Deviche and Davies 2014).

Urbanisation: habitat structure and scale

Built-up landscapes comprise a host of infrastructures, from roads and railways to industrial complexes and suburban sprawl. The process of urbanisation transforms landscapes, as land-cover changes see a rise in built-up areas and a subsequent loss of natural habitat (Seto et al. 2011). While habitat loss is conceptually distinct from fragmentation (Fahrig 2003), urban driven land-use change also fragments the landscape (McKinney 2002). While primarily studied in non-urban habitats (Crooks et al. 2004), fragmentation has often been shown to have negative effects on birds (Paton 1994; Chamberlain et al. 2009). Fragmentation in urban areas is argued to have the same deleterious effects on urban birds as in other fragmented landscapes (Fernández-Juricic and Jokimäki 2001; Evans et al. 2009). Moreover, urban habitats are often more highly fragmented than natural landscapes (Chamberlain et al. 2009) and can have strong ramifications for breeding success. For example, a high degree of patch isolation in the urban environments of Florida has been shown to reduce the breeding success of scrub jays, whereby longer dispersal distances reduced breeder survival and isolated patch clusters meant that males (not as likely as females to undertake long-distance dispersion) became the limiting sex (Breininger 1999).

As habitats are lost to urban development, remaining natural areas often become increasingly fragmented into smaller but potentially more numerous remnant patches (Collins et al. 2000; Mörtberg 2001; McKinney 2002). Well-described aspects of fragmentation such as edge effects, patch size and patch isolation (Fahrig 2003) are also relevant in urban environments. Within an urban context, these mechanisms of fragmentation can be linked with proximate effects that affect bird breeding success. Factors such as the urban heat island (Deviche and Davies 2014), artificial sources of light (Kempenaers et al. 2010) or increased human disturbance are arguably the manifestations of patch edge effects. In rural areas, edge effects have been shown to negatively influence breeding success (e.g. tit breeding success improves with increasing distance away from forest edges (Deng and Gao 2005; Wilkin et al. 2007a), while edge effects have also been described in urban areas. For example, breeding densities of most birds studied by Evan et al. (2009) were observably higher in the centre of city parks than at their edges. Moreover, elements such food availability may also be affected by fragmentation. Passerine provisioning rates have been shown to be higher in smaller forest fragments (as studied in blue and great tits - Nour et al. 1998) and important bird prey groups such as insects are highly susceptible to the adverse effects of fragmentation (Didham et al. 1996). Fragmentation can negatively influence important great tit food sources such as the winter moth (Van Dongen et al. 1994), and aspects such as patch size have been investigated in relation to the proportion of food types available in fragmented forest habitats (Nour et al. 1998). Oaks and other native trees carry high caterpillar biomass (Perrins 1991) relative to exotic trees (Mackenzie et al. 2014), and therefore the effects of urbanisation on vegetation (e.g. the loss of native species - McKinney 2002; Mackenzie et al. 2014) have consequences for avian food availability and quality in cities.

A key question regarding urban fragmentation is determining whether the edge, size and isolation effects are driven at local or larger scales. Different scales can imply different ecological processes or pattern. Clergeau et al. (2006b) highlight the diversity of these scales in the urban environment, ranging through the habitat level (local scale), the landscape level (e.g. city district), the sub-regional level (e.g. whole town) and up to the bio-climate level (continental). They argue that each scale is driven by unique processes, and to account for scale dependencies in many taxa urban research should therefore attempt to include multiple spatial scales (Hostetler 2001; Goddard et al. 2010). At a local scale, fragmented tree cover in urban parks, streets or gardens has been found to increase direct sunlight on nestboxes, thereby raising nest temperatures in already warm urban micro-climates (Banbura and Banbura 2012). Moreover, fine-scale tree density has also been shown to affect passerine phenology (Wilkin et al. 2007b). At larger scales, factors like patch isolation become important. Some birds show a negative response to isolation of habitat patches in the urban matrix and are unwilling to cross urban barriers (Evans et al. 2009). This could have important knock-on effects; birds restricted to the city may exhibit poorer adult condition (Liker et al. 2008) and ultimately lower breeding success than their rural counterparts (Chamberlain et al. 2009).

Given the important role urbanisation may have in affecting the breeding success of birds, as mediated by food, environmental and habitat-structuring effects, this thesis aims to understand the variation of both breeding success and the food of great tits *Parus major* along an urbanisation gradient measured at two spatial scales.

Study species

A vast collection of literature has been accrued on the great tit *Parus major*. Aspects of great tit biology most pertinent to this study are highlighted here, namely the great tit breeding cycle and behaviour, phenology and diet.

Distribution

Great tits are widely distributed across Eurasia and are versatile in their habitat preferences. Great tits primarily breed in deciduous and mixed forests (showing a preference for oak trees in Europe) but are also found widely in a range of anthropogenic landscapes from plantations and orchards to city parks and gardens (Gosler et al. 2013).

Breeding patterns and phenology

Great tit egg-laying in much of Europe typically begins in April, with nests having been prior built by females in tree cavities and nestboxes. The date of clutch laying is closely linked to spring temperature as this provides an indicator for optimal timing with peak caterpillar populations (Gosler 1993) – tits tend to lay earlier in warm springs because caterpillars emerge earlier (Perrins 1991). Clutches tend to be between six and twelve eggs and are incubated for approximately 13 days before hatching. It takes a further 18-20 days for nestlings to fledge (Perrins 1991).

Diet and provisioning

Gosler (1993) attributes the great tit's broad geographical range to the diversity of its diet. Great tits are omnivorous passerines, primarily opting for a combination of invertebrates and seeds. The demand for these food types is dictated both by season and phenology. The specific targeting of invertebrates is linked to a high protein demand during the breeding season as nestlings require the protein for growth and development. This need for protein is not limited to the breeding season; great tits are regarded as principally insectivorous. This is reflected in their diet; great tits have been shown to target more than 135 invertebrate families including 32 families of moths and butterflies (especially larvae), 21 of beetles, 18 of bugs, 15 of flies, 14 of wasps and allies, and 14 of spiders. However, when these prey are not abundant (during the winter season) the tits primarily forage for seeds. Great tits have been shown to take advantage of a wide range of seeds representing more than 40 plant families.

The quality of early nutrition in tit nestlings can have strong repercussions for offspring size, morphology and survival (Wilkin et al. 2009a). During the breeding season great tits are almost completely insectivorous and broods require a steady supply of food. Caterpillars (e.g. the Winter Moth *Operophtera brumata* or the Green Tortrix *viridana*) make up a majority of dietary items as their role as high-quality prey items for nestlings is of fundamental importance to tit breeding success (Perrins 1991; Verboven et al. 2001; Rytkönen and Krams 2003; Isaksson and Andersson 2007; Wilkin et al. 2009a). At peak food demand (nestlings aged 9-10 days) great tits in Britain have been observed bringing caterpillars to the nest at almost one per minute, with over 700 feeding visits per day (Perrins 1991). To provision at such rates tits synchronise their breeding cycles with the life cycles of caterpillars, aiming for periods of peak caterpillar abundance (Van Noordwijk et al. 1995; Isaksson and Andersson 2007). As aforementioned, this synchronisation is related to temperature and photoperiod, but is also reliant on further cues such as the caterpillar population itself (Gosler 1993). Such is the importance of this food source that the mean clutch-size of the great tit has been significantly correlated with the numbers of caterpillars in a season (Perrins 1991; Verboven et al. 2001), and the proportion of caterpillars provisioned has been used as an index for food quality and has been show to improve fledgling condition and success (Verboven et al. 2001; Wilkin et al. 2009a).

Addressing knowledge gaps

Comparative research on birds in urban and rural settings is a well-explored field, and a series of meta-analyses has explored urban effects on avian populations (e.g. Marzluff 2001; Chace and Walsh 2006; Chamberlain et al. 2009; Deviche and Davies 2014). Great tits have also been studied within an urban-rural framework (e.g. Horak and Lebreton 1998; Isaksson and Andersson 2007; Banbura and Banbura 2012), sometimes with the specific aim of observing differences in breeding success and phenology (e.g. Solonen 2001; Hedblom and Söderström 2012; Solonen and Hilden 2014). Great tits represent an excellent model species for such studies given their readiness to take to nestboxes along a range of urbanisation levels. However, many studies lack quantified levels of urban environmental variation and large enough sample sizes needed to make substantive claims (Marzluff 2001; Fahrig 2003;

Chamberlain et al. 2009). Furthermore, little is known about the role of urban scale in affecting great tit demography (but see Wilkin et al. 2007) or about the effects of the interaction between nest sites (local environment) and the broader environment. Moreover, the influence of food availability and quality on breeding success within the urban context remains a key question (Amrhein 2014).

To address these issues this study utilised a nested design involving study sites with *a priori* quantified degrees of urbanisation at both local scale and regional scales. Data were collected from twenty nestbox plots (and an additional 61 single-box locations) strategically placed across northern Belgium. Major Belgian cities such as Antwerp, Brussels and Ghent were used as reference points to set up independent replicates, ensuring that plots adequately covered urban, sub-urban and rural areas along a quantified rural-urban gradient. The intricacies of this study design and the data collection are further clarified in the methodology section. This design provides a framework for answering key questions about the relationship between urbanisation, food and great tit breeding success.

Aims and objectives

The overall aim of this thesis is to study the variation in great tit breeding success along an urbanisation gradient and the factors driving this variation:

Aims

i. To analyse variation in reproductive parameters (laying date, clutch size, nestling weight and fledgling success) collected from nestbox plots in 2014 and 2015, and to correlate these data with relevant biological and temporal variables
ii. To ascertain the role of urbanisation at differing spatial scales in driving variation in breeding success
iii. To analyse variation in food data collected from a subset of filmed nestboxes in 2015 and 2016, and to correlate these data with relevant biological, environmental and temporal variables
iv. To ascertain the role of urbanisation at differing spatial scales in driving variation in food provisioned to nestlings during the breeding season
v. To determine if and how variation in food quantity and quality may explain urbanisation effects on breeding success

Predictions and hypotheses

Regarding the effects of urbanisation on breeding success of great tits:

i. Earlier laying dates are predicted with increasing levels of urbanisation at one or both measured spatial scales
ii. Declines are expected in all measured breeding parameters (clutch size, nestling weights, fledgling success) with increasing levels of urbanisation at one or both measured spatial scales
iii. The effects of subplot and plot spatial scales are expected to be dependent on one another (i.e. a significant interaction is expected)

Regarding the role of food in explaining breeding success variation:

i. Breeding success is hypothesised to correlate positively with the proportion of caterpillars in nestling diet and with the proportion of larger prey items, and negatively with higher provisioning rates
ii. The proportion of caterpillars provisioned to nestlings and the size of caterpillars is expected to decline with increasing urbanisation

Methodology

Study area and design

The study area and design utilised by this thesis were developed as part of an inter-university project entitled 'Spatial and environmental determinants of Eco-Evolutionary Dynamics (SPEEDY)*:* anthropogenic environments as a model', as a framework to study several target organisms (aquatic as well as terrestrial) over strong gradients of urbanisation. This required a spatially explicit design with detailed characterisation of landscape structure. The set-up described here is that which pertains to this thesis, and its target organism, the great tit.

In the general SPEEDY design, a total of 27 plots were selected (each 3km x 3km) across three regions: Antwerp, Gent and Brussels/Leuven (Figure 1). Plots were classified in ArcGIS into three urban categories according to percentage built-up area. The cut-off points for percentage of built-up area were defined as 0-3% for 'low' urbanisation, 5-10% for 'moderate' urbanisation and >15% for 'high' urbanisation. To ensure that 'low' urbanisation areas had high natural value, these plots had to meet the additional criterion that they also consisted of >20% of ecologically valuable areas (as defined by the 'Biologische Waarderingskaart' - Vriens et al. 2011). For simplicity, the three degrees of urbanisation (low, moderate, high) are referred to in this thesis as colours: low = *green*, moderate = *yellow* and high = *red*.

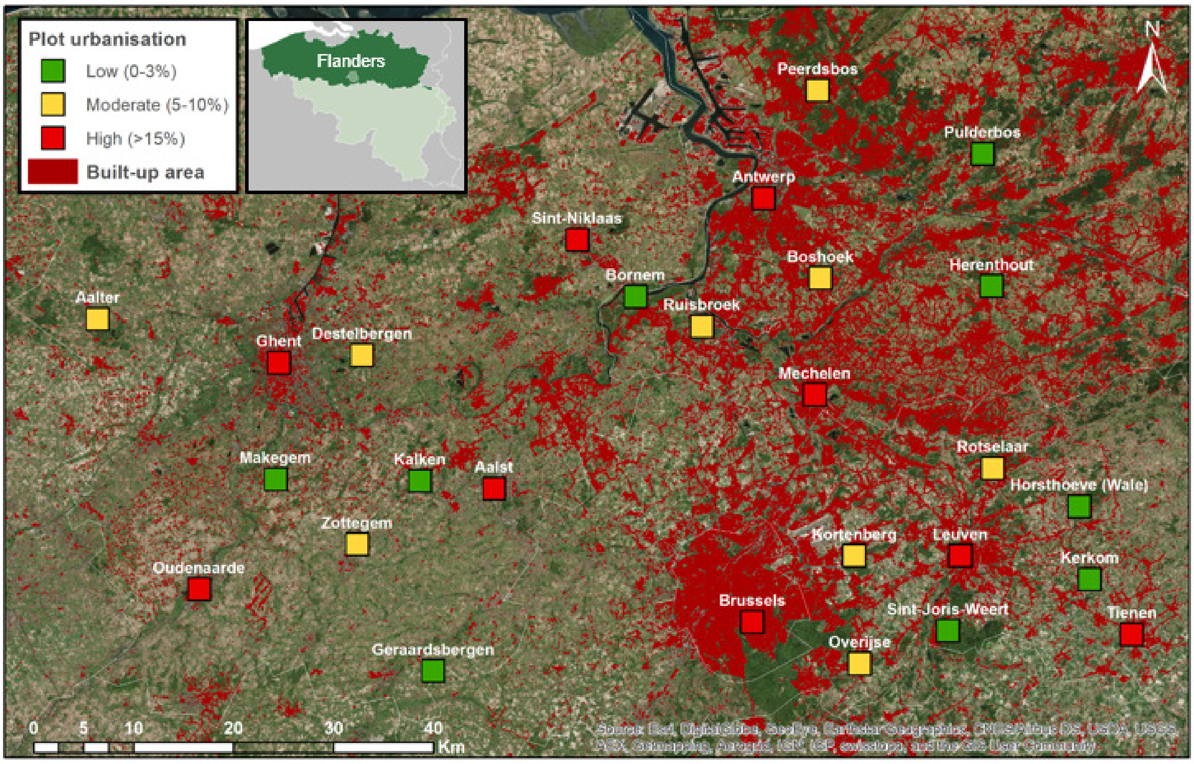


Figure 1: Map of northern Belgium showing the 27 study area plots (3km x 3km – boxes not to scale) in the context of urban spread (builit up areas - Agency for Geographical Information Flanders 2016).

Red plots (high urbanisation) were characteristically dominated by cities or towns, yellow plots (moderate urbanisation) were typically a mixture of farmland or wooded areas and small villages or residential areas, while green plots (low urbanisation) were dominated by larger wooded areas and/or farmland.

Each city region (Antwerp, Ghent, and Brussels) contained 3 replicates of green, yellow and red plots. One red plot was placed within the main city itself and two others in neighbouring smaller cities to ensure spatial independence and to improve statistical power. Each plot was further divided into 200m by 200m subplots which were also classified into the three degrees of urbanisation (green, yellow, red) using the same criteria as above. Within each plot, nestboxes were installed (or in some cases, existing boxes were used) in one subplot of each urbanisation level, resulting in a total of 81 locations (3 subplots in each of 27 plots). For reasons of logistical feasibility and statistical power, 20 subplots were chosen to hold a larger number of nestboxes (typically 15-20 boxes). These contained two replicates of each plot/subplot "colour" combination (e.g. two "red in green" combinations, meaning a "red" subplot within a "green" plot) plus two additional replicates of the most extreme combinations ("red in red", and "green in green"). In the remaining 61 subplots three or four nestboxes were installed with the aim of obtaining data from at least one great tit nest.

Thus, the plot-subplot nested structure of the study design was intended to enable the study of great tits at two urban spatial scales: their immediate environment (200m x 200m) and the broader regional context (3km by 3km); as well as to inform how the two urban spatial scales interact in affecting great tits and their food. A supplementary measure of urbanisation at a local scale – the nestbox urbanisation ratio (NUR) – was also calculated. This measured the percentage of built up area within a 200m buffer of each nestbox.

NUR values were calculated to describe fine-scale variation in urbanisation at a local scale. Despite the fact that subplot colours were defined *a priori*, the exact locations of nestboxes within a subplot sometimes represented deviations from the expected urbanisation level of that subplot (e.g. a nestbox located at the edge of green subplot may be exposed to higher urbanisation from the neighbouring area). However, subplot colours were defined based on the assumption that biodiversity effects operate mainly at low to modest levels of built up area (i.e. urbanisation thresholds of 0-3%; 5-10%; >15%), meaning that NUR values (calculated post-hoc) illustrated a strongly right-skewed distribution. NUR values were therefore log transformed to improve their normality and their representation of the intended urbanisation gradient.

Fieldwork

Fieldwork took place over three successive breeding seasons from 2014-2016. Fieldwork consisted of nestbox checks to gather information relating to breeding success, and the filming of nestboxes to collect data on nestling food (Figure 2).

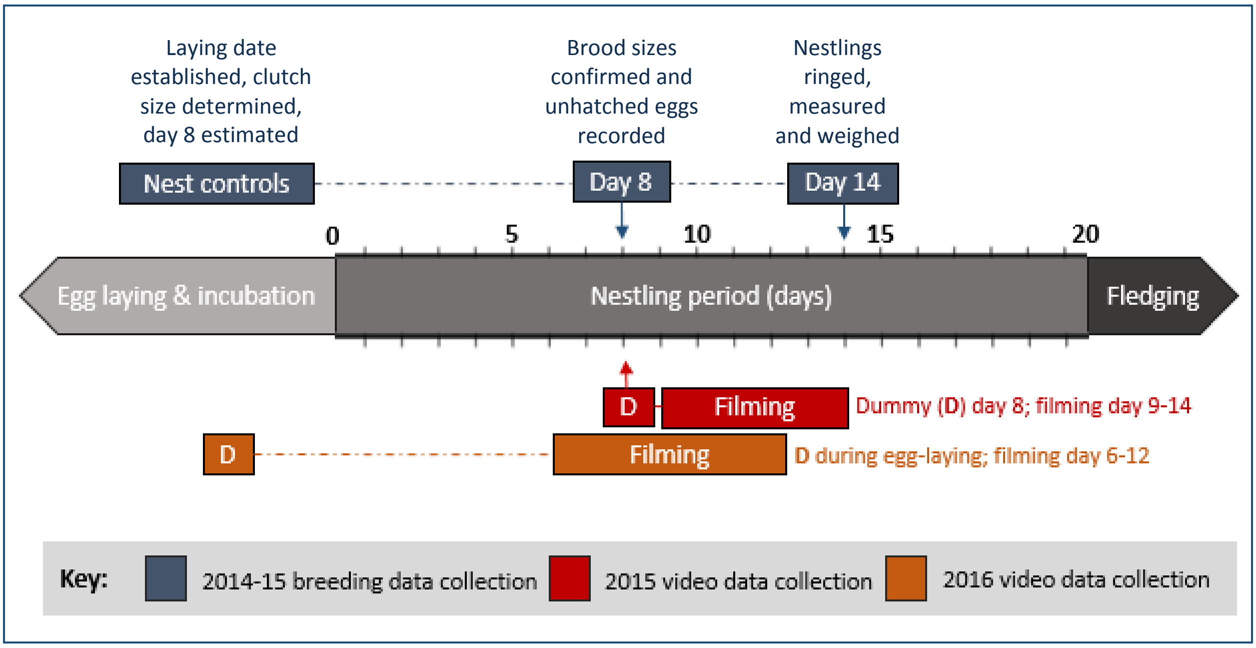


Figure 2: An overview of fieldwork activities and protocols for data collection of great tit breeding and food-related parameters (videos) over the 2014-2016 field seasons in relation to a typical great tit breeding timeline

Breeding data collection

Breeding data were collected over three consecutive breeding seasons from 2014 to 2016. Nestboxes were visited approximately weekly before egg laying (typically in mid-April). First-egg dates ('laying date') were estimated after the first observation of a partially laid clutch, under the assumption that one egg is laid per day (Perrins 1965; Matthysen et al. 2011). Nests were checked when chicks were 8 days old (henceforth referred to as 'day 8'); brood details were confirmed: nestlings alive and dead were recorded and the number of unhatched eggs noted. On day 14, nestlings were ringed and weighed to the nearest 0.01g and any further unhatched eggs were noted. Because of constraints in processing the breeding data (requiring multiple data manipulations and quality checks on data collected by different researchers), only the fully processed 2014 and 2015 breeding data were analysed in this thesis.

Video data collection

Video data were successfully collected from 56 nestboxes over both the 2015 (n = 22) and 2016 (n = 34) breeding seasons. Nestboxes were selected to cover variation in urbanisation at both plot and subplot level. The video protocol comprised two sets of equipment: the dummy setup and the recording setup. The dummy setup consisted of a within-nestbox dummy camera, a camera mount (attached to the underside of the nestbox lid) and an external cabling box. The recording setup consisted of a within-nestbox camera (“Mini spy-camera with Infrared Leds 85nm” - www.spywebshop.nl), and an HD digital recorder and 12V battery pack (stored in the external cabling box).

Filming protocol for both seasons was near identical but slight changes were made in 2016 to improve video success rates. Dummy cameras were installed in nestboxes in advance of filming to allow breeding pairs a period of habituation (Stuber et al. 2014). In 2015, the dummy setup was installed on day 8. In 2016 dummy setup installation took place during the egg-laying/ brooding period to allow for a longer habituation time. The recording setup was installed at a mean (± SD) nestling age of 11.0 ± 1.4 days (range: 9-14 days) in 2015 and a mean nestling age of 7.7 ± 1.3 days (range: 6-12 days) in 2016. Recordings were performed earlier in 2016 to increase the number of recordings at younger nestling ages. This was done as 2015 data revealed higher levels of starvation prior to filming thereby potentially biasing filming toward better-fed nests in this year. Cameras were set at 30fps and motion sequences captured during filming were automatically written to an HD digital recorder. Nestboxes were filmed for a minimum of two hours (Pagani-Núñez and Senar 2013). Filming generally took place between 09:00 and 13:00, with dry periods (no or very little rain) targeted to best capture provisioning behaviour (Radford et al. 2001; Oberg et al. 2014).

Filming targeted as many different boxes and areas as were feasible, requiring shorter filming events and small and transportable cameras. Other studies often utilise cameras built in to nestbox lids (e.g. Stuber et al. 2014) which improves video resolution (often at a much higher expense) but limits mobility and sample sizes. The approach of this study thus optimised sample sizes and costs, but at the expense of higher image quality.

Video data capture

Videos were processed using Matlab (version 1.10.0; 2010) to limit footage to key action sequences; namely the arrival and departure events of adult birds. An algorithm developed by Swinnen et al. (2014) was used to measure the amount of pixel variation (i.e. changes in motion in the footage) to cut the film into individual action events. Each event consisted of the 3 seconds of footage leading up to a point of maximum motion detection, and the 3 seconds following. This ensured enough time to view a provisioning event in full. Algorithm validation determined that there was a tendency towards false-positives (e.g. an event triggered by passing pedestrians) meaning that such events had to be manually excluded from footage. Processed videos from each nestbox were strung together chronologically using Windows Movie Maker (2012) and viewed frame by frame to allow for extraction and calculation of relevant data (Table 2).

Table 2: Data recorded and calculated from video footage of nestboxes during 2015-2016 field seasons

Measure	Definition
Filming time	Time between installation and removal of camera
Disturbance time	The elapsed time between the camera set-up time and the first recorded provisioning event: (*1st entry time*) – (*Set-up time*)
Visit duration	The amount of time a provision event takes; i.e. The time elapsed between a parent entering the nestbox and then leaving again
Parent gender	'Male', 'female' or 'unidentifiable' genders recorded – determined by the sexually dimorphic trait of the length and width of the breast stripe (Gosler 1993)
Prey type	Three classes recorded: 'caterpillar', 'other' or 'unidentifiable'
Prey length	Prey items provisioned were sized relative to the beak length of the great tit, sized to the nearest half-beak length (e.g. a caterpillar length of 2.5 beak lengths)
No. provisions	The number of prey items delivered during a single filming period of a nestbox
Provisioning time	The time elapsed between the camera take-down time and the fourth recorded provisioning event. First three provisioning events excluded to account for any initial abnormal provisioning behaviour (e.g. hesitation, camera examination, etc.)
Provisioning rate	(*No. of provisions – first 3 provisions*) / (*Provisioning time*). First three provisions excluded from the total provision count to retain consistency with provisioning time calculation

Prey length was defined relative to beak length of the provisioning parent. Gosler (1987) found the average beak length in an Oxford population of great tits to be 13.34 ± 0.47 mm (n = 1626), a measure used to approximate the true length of prey items. The proportion of caterpillars provisioned to nests was calculated as a proxy for quality of nestling diet (Wilkin et al. 2009a).

Statistical analyses

Statistical analyses were performed to ascertain the role of urbanisation in affecting both the breeding success of great tits and aspects relating to their food during the nestling period. Several generalised linear mixed-effects models (GLMMs) were built to explore data from the breeding and food data sets using RStudio (R Core Team 2015) and package lme4 (Bates et al. 2015).

Three model types were built for the analyses of both data sets, to provide insight into how and where urbanisation has an effect:

I. **Urbanisation models** were built by defining a response variable (e.g. clutch size) and regressing it against the urban factor variables 'plot' (urbanisation level at a 3km x 3km scale; three levels: green, yellow, red) and 'subplot' (urbanisation at a 200m by 200m scale; three levels: green, yellow, red), an interaction term of the two urban levels, the ‘year’ (accounting for inter-annual variation between field seasons) and ‘area’ as a random effect.

II. **Full models** contained explanatory terms as defined for urbanisation models as well as supplementary explanatory variables (e.g. clutch size) deemed important to explaining variation in the relevant response variable.

III. **Final models** were derived from full models by the step-wise reduction of non-significant terms via repeated ANOVA (Analysis of Variance) tests; Type II Wald Chi-square tests for models with binomial or Poisson distributions and Type III ANOVA tests for normally-distributed models.

Model validation was undertaken using a series of standard model validation graphs and checks for normality of model residuals (Zuur et al. 2009). Quantile-Quantile plots and histograms of the model residual plots were used to assess normality, while residuals versus fitted values plots were used to determine the degree of heteroscedasticity in residual variance.

In addition to standard model interpretation techniques using model intercepts and predictor estimates, the R package “effects” (Fox 2003) was used to interpret GLMM model terms. This generated data frames and plots (“effect displays”) of model terms by computing model-fitted values for each term. The values of other predictors were fixed at typical values (e.g. a covariate fixed at its mean) to allow for term-by-term interpretation.

Breeding data analyses

Four response variables were explored in the breeding data analysis on how breeding success varies with urbanisation on differing spatial scales, namely: laying date (LD), clutch size (CS), fledglings per egg (FPE) and mean nestling mass (MNM). These are variables which have been frequently measured in assessing breeding success of great tits (e.g. Solonen 2001; Chamberlain et al. 2009; Hedblom and Söderström 2012; Mackenzie et al. 2014; Bailly et al. 2016). Mean nestling mass is both a strong predictor of survival chance (Garnett 1981; Tinbergen and Boerlijst 1990) and has been shown to be strongly linked with food (both quantity and timing) (Naef-Daenzer et al. 2000; Matthysen et al. 2011). The breeding parameter ‘fledglings per nest’ (e.g. in Nager et al. 1997) was not formally analysed given its components are encompassed by the combination of ‘fledglings per egg’ and ‘clutch size’ variables and given the non-normal nature of its distribution (zero-inflated counts).

Breeding data were cleaned prior to analyses to separate out unwanted effects and optimise model performance. In order to separate out effects of clutch abandonment, data were limited to nests where incubation had started (>1 one young hatched). To reduce variation associated with different clutch types, the data set was further reduced to first-clutch nests only, thereby excluding any second and replacement clutches. First clutches were defined during fieldwork as the first known clutch of a breeding pair. A stricter definition was applied to the laying date model (described below). Laying dates were converted to ordinal dates (Julian day = days elapsed since January 1st). In models which incorporated clutch size (either as a response or explanatory variable), the data set was trimmed to include only nests where the exact number of eggs in a clutch had been confirmed during fieldwork.

LD and MNM models comprised continuous response variables (Julian day and mass respectively), and both models were fitted with a normal distribution. The CS model modelled count data (number of eggs) and was fitted with a Poisson distribution. The FPE model was based on a proportional response variable and was subsequently fitted with a binomial distribution.

The full LD model was identical to the urbanisation model as no additional explanatory variables were included. Model validation of the LD model highlighted a distorted effect of outlier data values on the model residuals, as reflected by a skewed distribution of the residuals. A fitted vs Pearson residuals plot revealed that the outliers consisted of nests initiated substantially later in the season than mean yearly laying dates. This was considered a result of the broad definition of first clutches (the first known clutch of breeding pair) whereby outliers may have represented second breeding attempts or replacement clutches. As such, data were subset by a stricter definition: first clutches were defined as all clutches laid within six weeks of the first clutch of the season (2014: day 76-118, 2015: day 78-120; n = 421). First clutches have been defined as clutches laid within the first four weeks of the season (Visser et al. 2003), but this study used six weeks to account for potential between-area differences and urban-level variation. Both the normality and homogeneity of model residuals was improved by the data sub-setting.

The full CS model included laying date (Julian day) as an additional explanatory variable given its potential importance in explaining variation in clutch sizes (Boyce and Perrins 1987; Kempenaers et al. 2010).

Both the FPE and MNM models were fitted with several additional explanatory variables. Laying date and laying date squared (a second order polynomial term) were included in the full models because breeding success is often shown to correlate with a temporal peak in food availability, first increasing but then levelling off or even decreasing as the season progresses (Visser et al. 2006; Matthysen et al. 2011).

The MNM full model included two further explanatory variables. Weighing age was included to reflect the differences in the age at which nestlings were weighed (range: 12-16, mean ± SD: 14.88 ± 0.76), and brood size (number of nestlings in the nest at the time of weighing) to incorporate effects of within-nest competition between chicks for food.

The full FPE GLMM failed to converge and model residuals failed to show a normal distribution despite several transformation attempts of response and explanatory variables. A plot of fitted vs Pearson residual values revealed heteroscedasticity of variance in model residuals, while the model summary illustrated a negligible contribution of the model's random effects structure in explaining additional variance (i.e. between area variation was nearly zero). To allow for model convergence and improve the normality of model residuals, the model was simplified to a GLM (Generalised Linear Model), thereby excluding the random effect 'area'.

Alternate versions of each breeding model were built, whereby the categorical fixed effect 'subplot' was replaced with the continuous log-transformed variable 'NUR' (Nestbox Urbanisation Ratio). NUR models were built for comparative purposes, to provide insight into whether urbanisation classified into three classes (at a subplot level) adequately represented variation in urbanisation.

Food data analyses

The smaller sample size of the food data set meant that red areas were underrepresented at both plot and subplot level. Filming of nests in red areas could not be carried out at times due to poor nestling condition or failed nests. Of 56 nests recorded in 13 areas, at the plot level 20 were green, 24 were yellow areas and 14 were red, while the subplots consisted of 26 green areas, 20 yellow areas and 12 red areas. To account for fewer red areas, food-based full and urbanisation models did not include interaction terms so as to maintain statistical power and allow for model convergence.

Three models were built to analyse data regarding food and its provisioning during the nestling period and how this varied with urbanisation degree and scale. These tested the response variables 'provisioning rate' (PR), 'proportion of caterpillars provisioned' (PCP), and 'mean caterpillar length' (MCL).

PR and MCL models were fitted to a normal distribution, while the PCP model was fitted with a Poisson distribution. All models contained 'year' (2015 or 2016) as a fixed effect to account for inter-annual variation, 'calendar day' (an ordinal measure of date included to account for changes in prey abundance over time), and 'area' (n = 12) as a random effect to account for random variation between areas. The full models for PR, MCL and PCP contained the remaining 'urbanisation model' explanatory variables (plot and subplot), as well as 'brood size' (number of nestlings in the nest at time of filming), 'nestling age' (average age of nestlings at time of filming) and 'average temperature' (the regional temperature on the day of filming – www.wunderground.com). Models for PR and PCP also included the covariate 'calendar day squared', a second order polynomial term for calendar day to reflect a potential peak in prey abundance (Matthysen et al. 2011).

A further model was built to test the relationship between mean nestling mass and the aforementioned food variables. The MNMf model (mean nestling mass: food variables) was fitted with a normal distribution. MNM was regressed against year as fixed effect, calendar day, and calendar day squared, with area as a random effect. In addition, the variables 'proportion of caterpillars provisioned' (caterpillars can be considered as an index for diet quality - Wilkin et al. 2009), 'mean length of caterpillars provisioned' (a proxy for prey size or biomass of prey delivered to the nest), 'provisioning rate' and 'weighing age' (the age at which nestlings were weighed) were incorporated as explanatory variables.

NUR-based versions of food models were not built as NUR values were not quantifiable for all boxes in the food data set.

Results

Breeding analyses

Breeding analyses were based on a data set of 458 first-clutch nests where incubation could be confirmed (≥ 1 young hatched): 197 nests in 2014 and 261 nests in 2015. Breeding pairs typically laid their first eggs in April: mean (± SD) ordinal laying dates were 93.3 ± 5.9 days in 2014 (approx. 4 April) and 104.5 ± 6.4 days in 2015 (approx. 15 April). Urbanisation at a plot scale was found to explain a significant part of the variance in laying dates (LD) (Table 3). LD model estimates showed that laying dates were earliest in red plots, followed by yellow plots and lastly green plots (Figure 3). Variation explained by inter-annual differences was also significant for the LD model (Table 3), with model estimates highlighting later laying dates in 2015 than 2014. (Figure 4). Subplot-level urbanisation was near-significant in explaining LD variation in both the final and urbanisation models (Table 3).

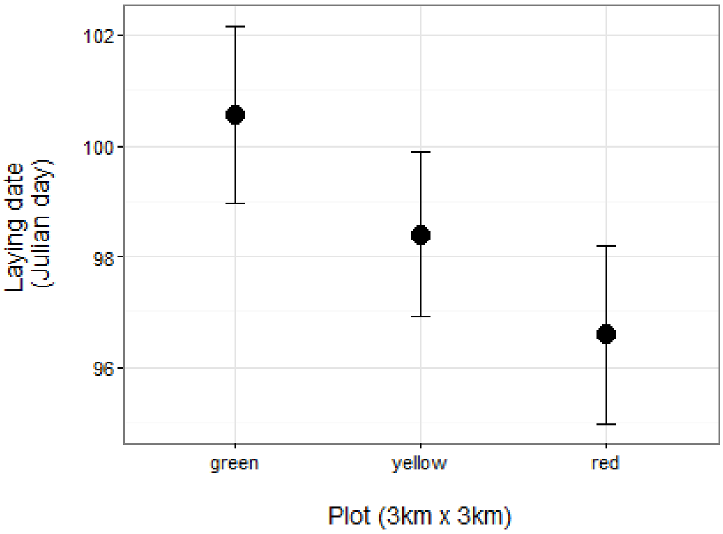


Figure 3: GLMM model-fitted estimates for laying dates at three levels of plot urbanisation: green, yellow and red. Bars indicate 95% confidence intervals.

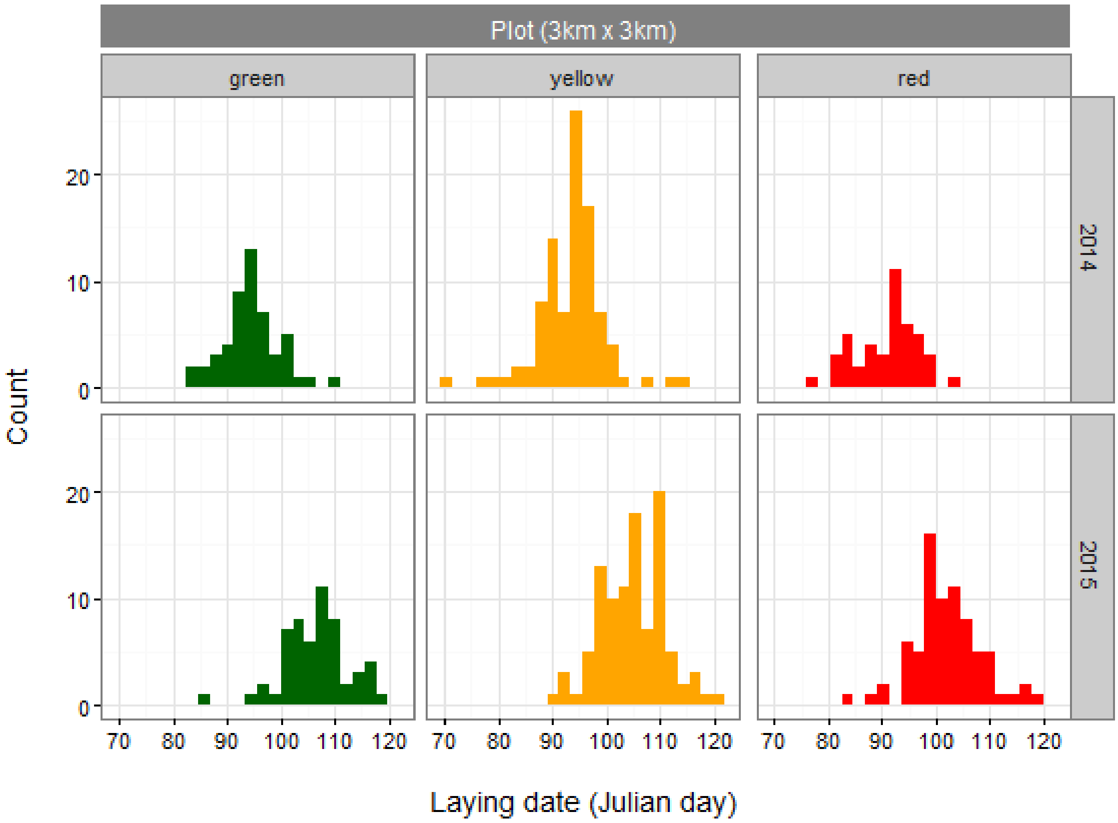


Figure 4: Inter-annual variation in ordinal laying dates for breeding pairs over the 2014 and 2015 breeding seasons, grouped by plot-level urbanisation classes (green, yellow and red).

The average clutch size (CS) across the two years was 8.4 ± 1.9 eggs (9.0 ± 1.8 eggs in 2014; 7.9 ± 1.9 eggs in 2015) with a range of 3-14 eggs. Urbanisation at both plot and subplot levels (but not their interaction) was significant in explaining clutch size variance (Table 4). CS model estimates suggested progressively smaller clutches along an increasing urban gradient (green-yellow-red) at both urban scales (Figure 5). When comparing extremes, the additive effects of both scales amounted to a marked difference with CS estimates of 9.34 (95% CI: 8.54-10.22) in ‘green in green’ sites (green subplot nested in a green plot) to 7.34 (95% CI: 6.65-8.09) in ‘red in red’ sites. Laying date was also found to significantly explain part of CS variation and the model estimated decreasing clutch sizes with later laying dates (Table 4). Inter-annual variation in clutch sizes was deemed insignificant by ANOVA tests (Table 4). Analysis of variance tests on the CS urbanisation model (Table 4), which excluded the covariate laying date, found plot and year to be significant but saw subplot lose significance in its explanatory power of clutch sizes.

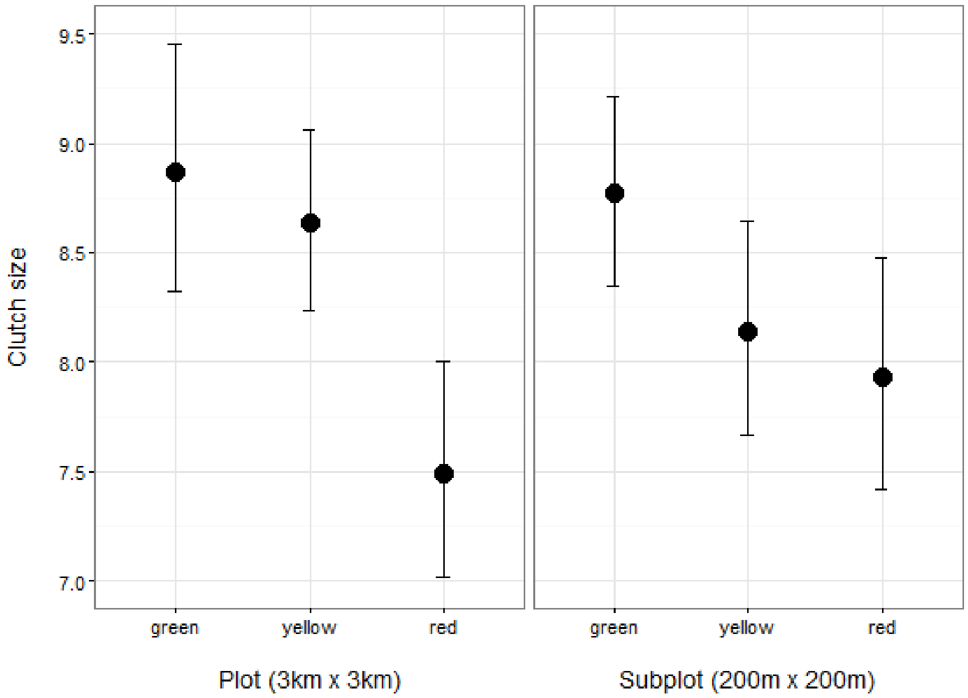


Figure 5: GLMM model-fitted estimates for great tit clutch sizes in relation to urbanisation degree (green, yellow, red) at both plot and subplot scales. Bars indicate 95% confidence intervals.

The mean nestling mass (MNM, measured at day 14) was highly similar over the two breeding seasons: 16.3 ± 1.6 grams in 2014 and 16.1 ± 1.8 grams in 2015. Analysis of variance tests on MNM GLMM variables revealed several terms significant in explaining variance in nestling mass (Table 5). Urbanisation at both plot and subplot scales explained significant variation in nestling mass and MNM model estimates calculated lower mean nestling masses with increasing urbanisation at both spatial scales. The covariates brood size, laying date and weighing age were all found to explain significant variation in nestling masses. The MNM model estimated that mean nestling masses were likely to increase in smaller broods, that masses decreased with later laying dates and that nestling masses increased with increasing weighing age. Subplot urbanisation and weighing age were the only explanatory variables which remained significant in explaining MNM in the urbanisation model. The MNM model had a near-significant term for the interaction variable 'Plot: Subplot' (Table 5). 'Green in green' areas saw nestlings with the highest mean masses and with the smallest range, while 'red in red' plots had the lowest mean masses (Figure 6). Data suggested that stronger subplot urbanisation effects were observed in green and yellow plots in comparison with red plots (Figure 6).

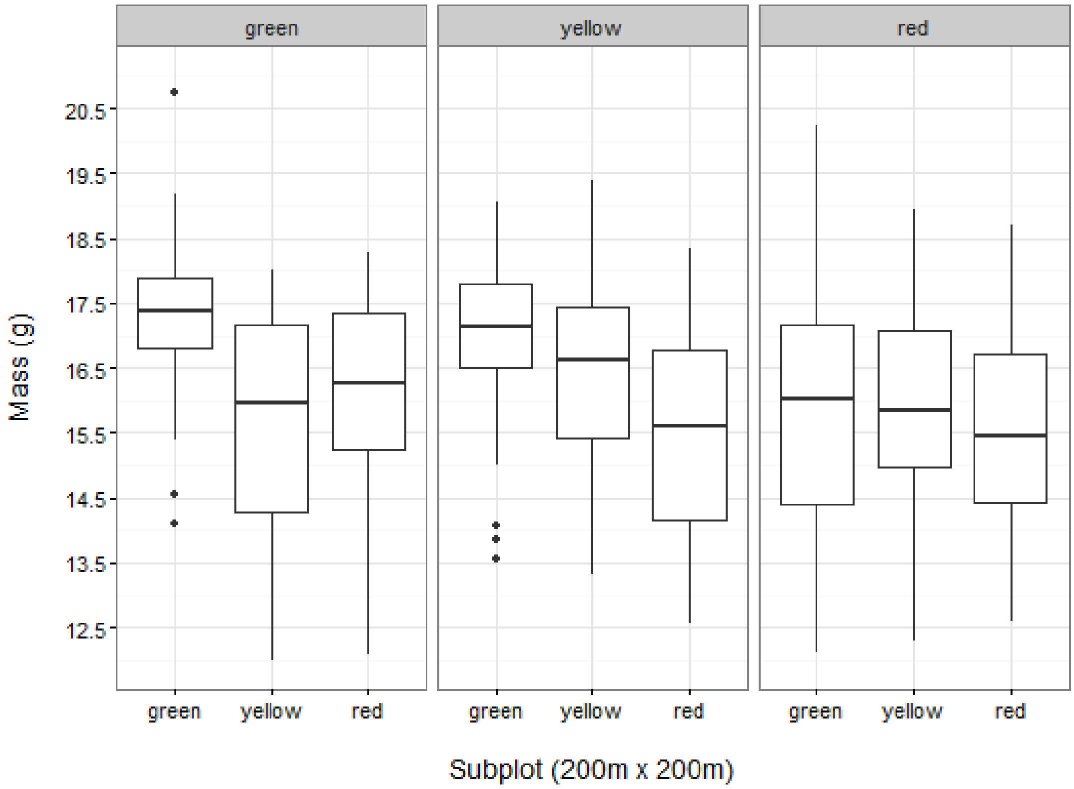


Figure 6: Boxplot summaries of raw data for nestling masses at different subplot urbanisation levels (green, yellow, red) grouped by plot scale.

Nests over the two seasons produced an average of 6.2 ± 3.0 fledglings, corresponding on average to 0.74 ± 0.31 fledglings per egg. More fledglings were produced per attempt in 2014 than 2015; 7.0 ± 3.2 fledglings and 5.6 ± 2.7 fledglings respectively, and raw data suggested a decline in the mean number of fledglings produced per nest with increased levels of urbanisation at both scales (Figure 7). Formal GLM analyses of the number of fledglings per egg found the interaction term comprising the two urban scales to be significant (Table 6). Model estimates predicted the highest number of fledglings per egg in 'green in green' areas and the lowest number in 'yellow in red' areas (Figure 8). Red plots showed the smallest range of subplot differences in FPE, while yellow plots illustrated the largest range (Figure 8). Laying date and inter-annual differences (year) also explained a significant part of FPE variation (Table 6). Model estimates indicated lower FPE ratios in nests initiated later in the season (Table 6). Laying date squared was not found to explain significant additional variation in the number of fledglings per egg (Table 6).

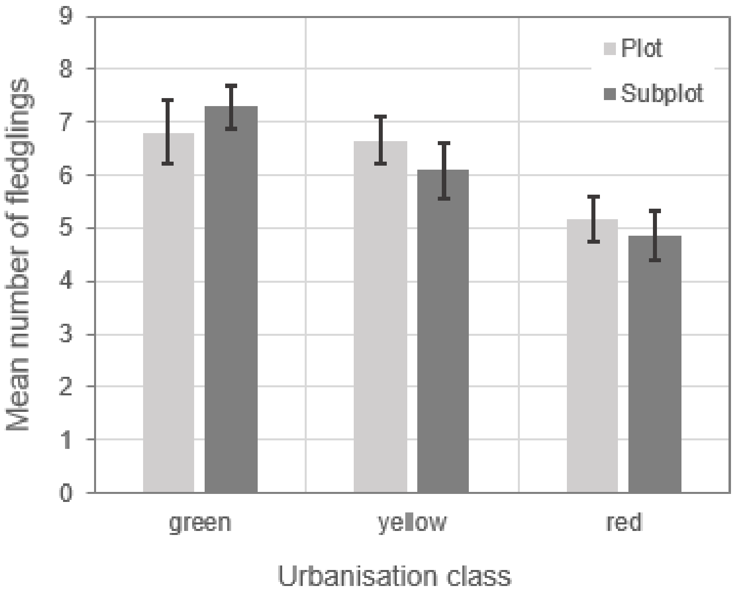


Figure 7: The mean number of fledglings produced per nest in relation to three urbanisation classes (green, yellow, red) in both plots (3km x 3km) and subplots (200m x 200m). Bars indicate 95% confidence intervals.

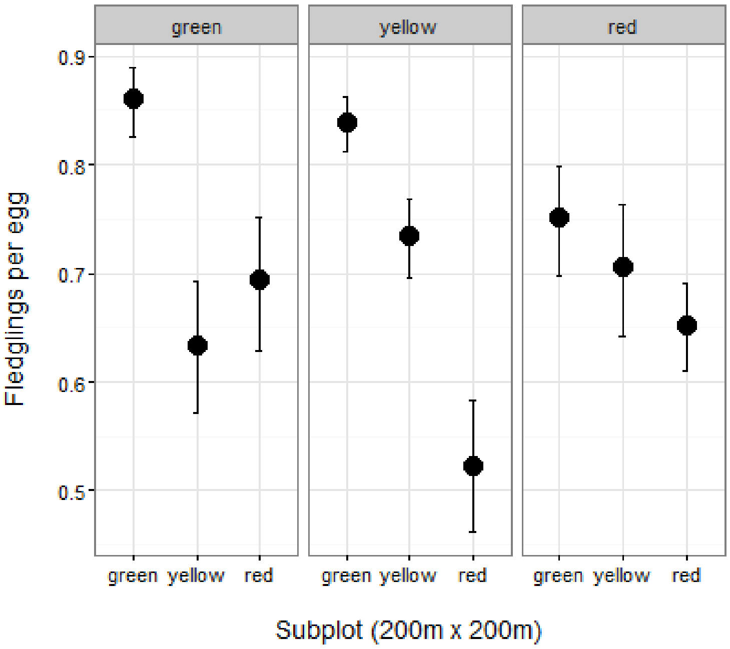


Figure 8: GLM model-fitted estimates for the number of fledglings per egg in great tit nests in relation to subplot urbanisation degree (green, yellow, red) as modified by a significant interaction with plot urbanisation degree (green, yellow, red). Bars indicate 95% confidence intervals.

Breeding model coefficients of determination and estimates of variance determined by random effect 'area' are summarised in Table 7. The random effect of variable 'area' was found to explain considerable variation in MNM and LD models, while explaining very little variation in the CS model (Table 7). Model summaries for alternate breeding models utilising the NUR covariate are found in Appendix I. Breeding models of CS and MNM produced the same final models regardless of whether NUR (continuous) or subplot (categorical) was used (Table 14 & Table 15, Appendix I). As in the original full MNM model, the MNM alternate model contained a near-significant interaction term for the urban scales, whereby green plots showed the strongest effect on the relationship between mass and NUR (Figure 9). The final LD model changed with the inclusion of NUR; 'plot' was no longer found to be significant, while NUR was found to be strongly significant in explaining laying date variation. (Table 13, Appendix I). The FPE model also produced a slightly different result with the inclusion of NUR; the 'year' term changed from significant in the original model (with subplot) to near significant in the alternate model (with NUR) (Table 16, Appendix I), but otherwise remained the same.

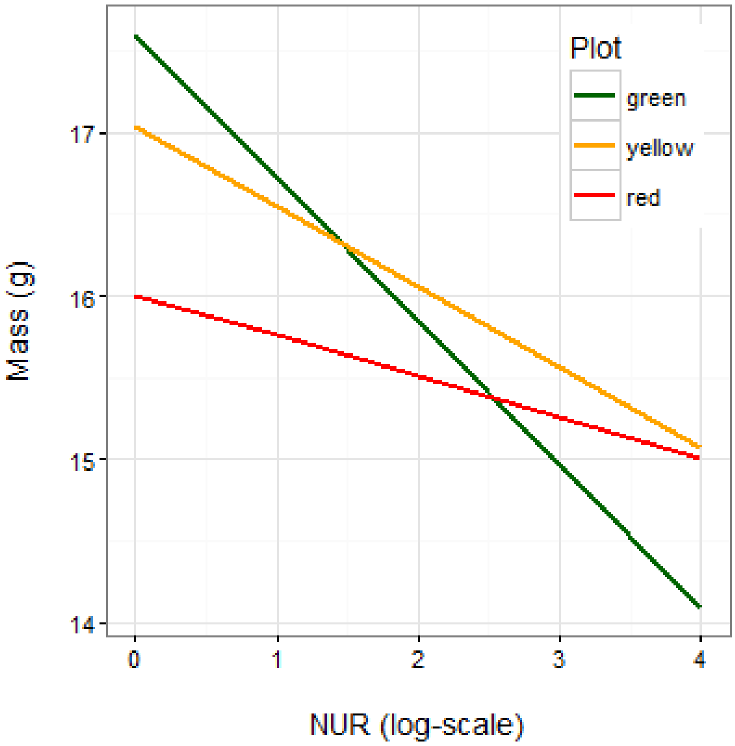
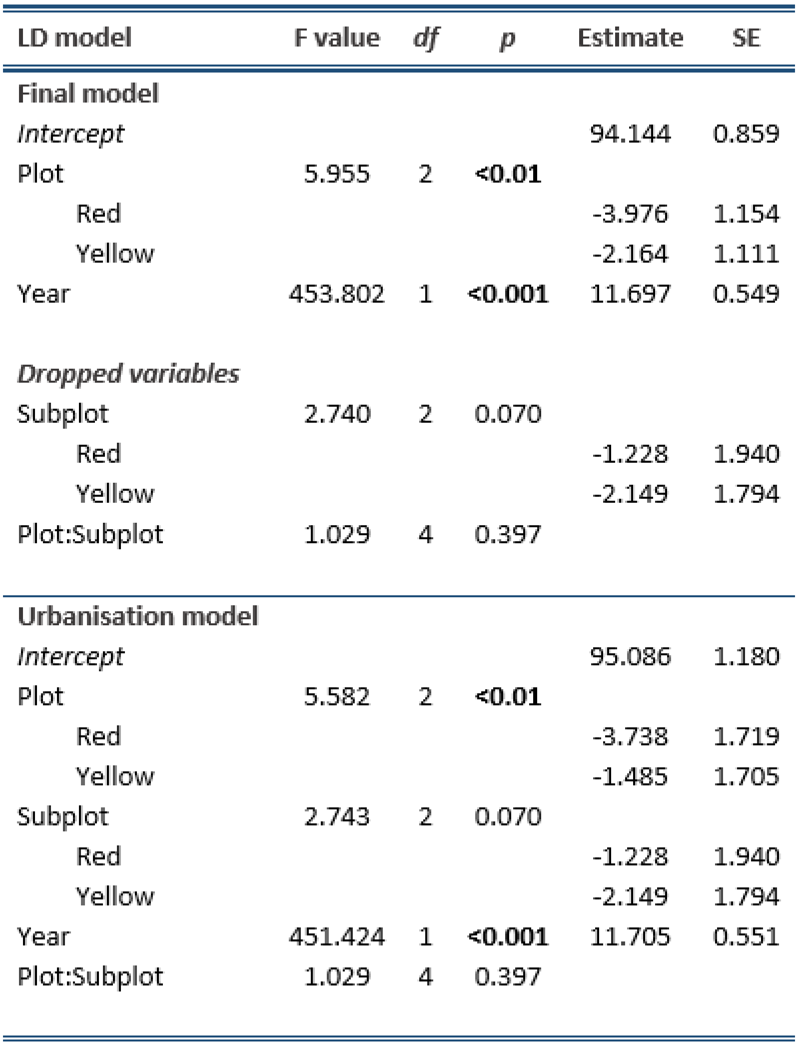


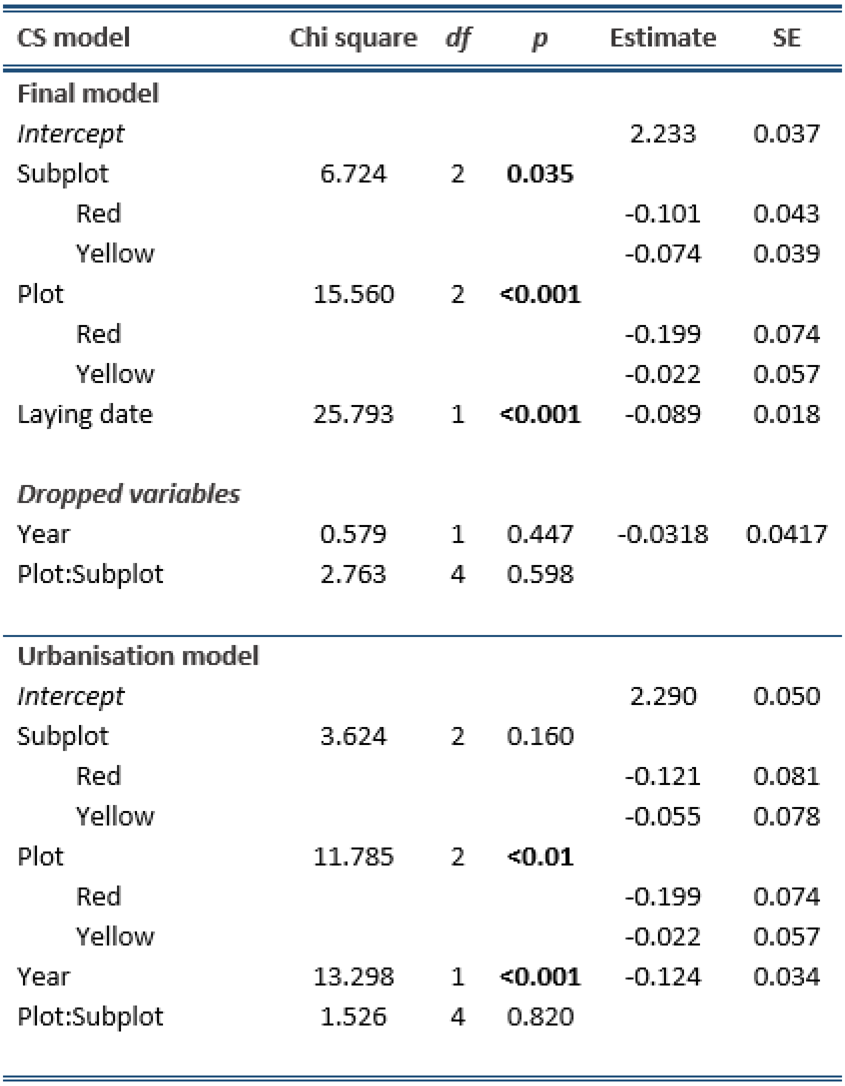
Figure 9: The relationship between NUR (Nestbox Urbanisation Ratio, plotted at log scale) and nestling mass within each plot type, as estimated by the MNM alternate GLMM (Table 15, Appendix I).

Table 3: GLMM summaries and analyses of variation for the effects of urbanisation on great tit laying dates (LD; n=421) observed during the 2014 and 2015 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales, their interaction, and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).



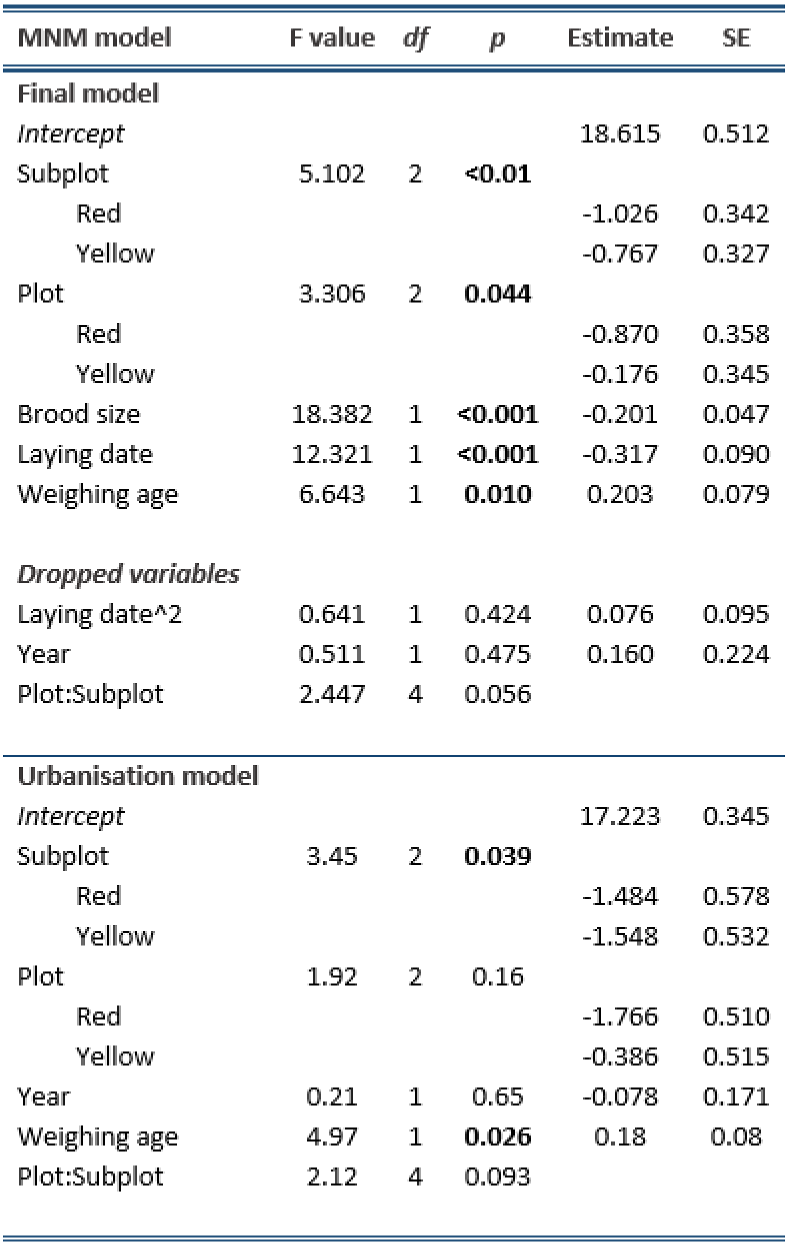
LD model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				94.144	0.859
Plot	5.955	2	**<0.01**		
Red				-3.976	1.154
Yellow				-2.164	1.111
Year	453.802	1	**<0.001**	11.697	0.549
Dropped variables					
Subplot	2.740	2	0.070		
Red				-1.228	1.940
Yellow				-2.149	1.794
Plot:Subplot	1.029	4	0.397		
Urbanisation model					
Intercept				95.086	1.180
Plot	5.582	2	**<0.01**		
Red				-3.738	1.719
Yellow				-1.485	1.705
Subplot	2.743	2	0.070		
Red				-1.228	1.940
Yellow				-2.149	1.794
Year	451.424	1	**<0.001**	11.705	0.551
Plot:Subplot	1.029	4	0.397		

Table 4: GLMM summaries and analyses of variation for the effects of urbanisation and laying date on great tit clutch sizes (CS; n=434) recorded during the 2014 and 2015 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales, their interaction, and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).



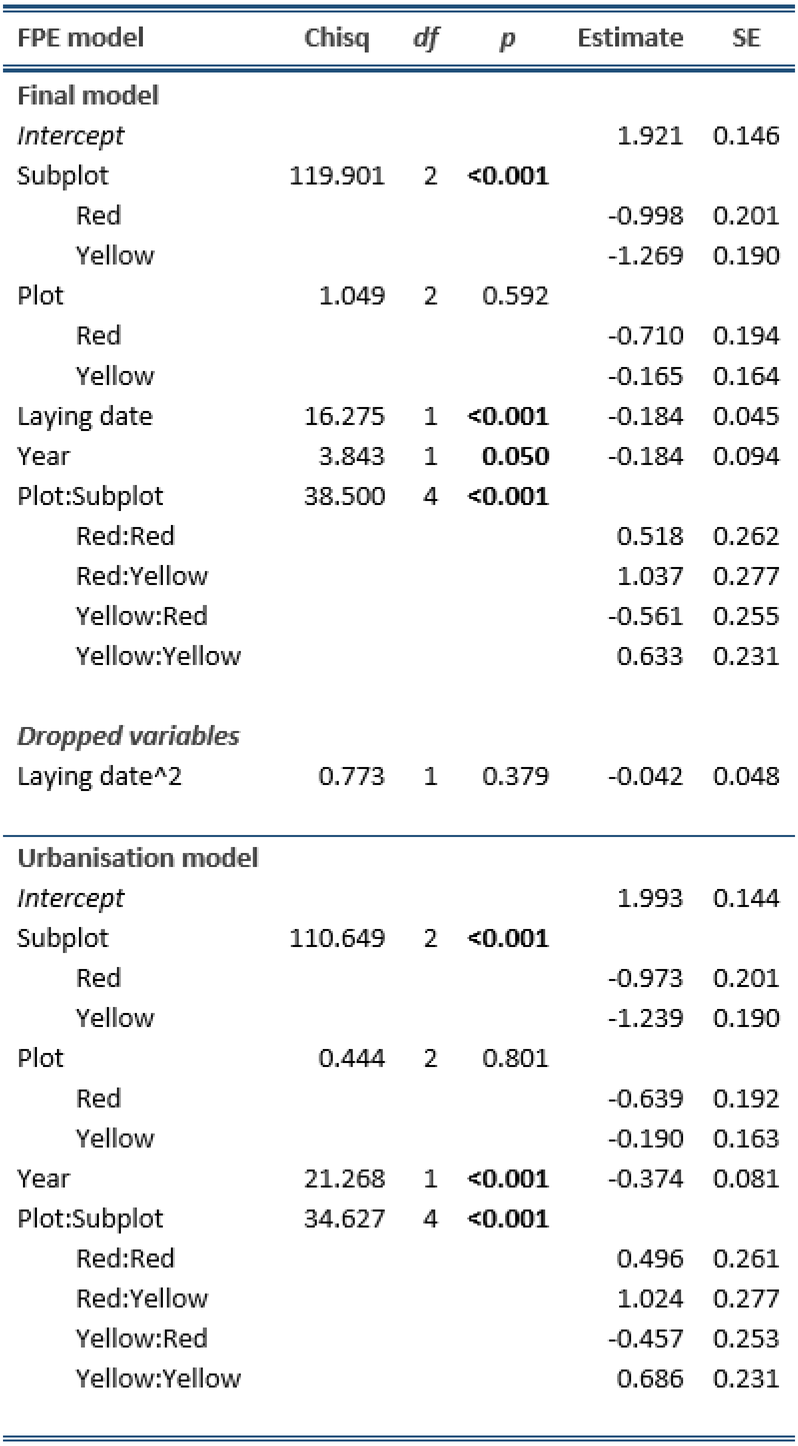
CS model	Chi square	*df*	*p*	Estimate	SE
Final model					
Intercept				2.233	0.037
Subplot	6.724	2	**0.035**		
Red				-0.101	0.043
Yellow				-0.074	0.039
Plot	15.560	2	**<0.001**		
Red				-0.199	0.074
Yellow				-0.022	0.057
Laying date	25.793	1	**<0.001**	-0.089	0.018
Dropped variables					
Year	0.579	1	0.447	-0.0318	0.0417
Plot:Subplot	2.763	4	0.598		
Urbanisation model					
Intercept				2.290	0.050
Subplot	3.624	2	0.160		
Red				-0.121	0.081
Yellow				-0.055	0.078
Plot	11.785	2	**<0.01**		
Red				-0.199	0.074
Yellow				-0.022	0.057
Year	13.298	1	**<0.001**	-0.124	0.034
Plot:Subplot	1.526	4	0.820		

Table 5: GLMM summaries and analyses of variation for the effects of urbanisation and relevant breeding and measurement parameters on great tit mean nestling masses (MNM; n=369) recorded during the 2014 and 2015 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales, their interaction, and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).



MNM model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				18.615	0.512
Subplot	5.102	2	**<0.01**		
Red				-1.026	0.342
Yellow				-0.767	0.327
Plot	3.306	2	**0.044**		
Red				-0.870	0.358
Yellow				-0.176	0.345
Brood size	18.382	1	**<0.001**	-0.201	0.047
Laying date	12.321	1	**<0.001**	-0.317	0.090
Weighing age	6.643	1	**0.010**	0.203	0.079
Dropped variables					
Laying date^2	0.641	1	0.424	0.076	0.095
Year	0.511	1	0.475	0.160	0.224
Plot:Subplot	2.447	4	0.056		
Urbanisation model					
Intercept				17.223	0.345
Subplot	3.45	2	**0.039**		
Red				-1.484	0.578
Yellow				-1.548	0.532
Plot	1.92	2	0.16		
Red				-1.766	0.510
Yellow				-0.386	0.515
Year	0.21	1	0.65	-0.078	0.171
Weighing age	4.97	1	**0.026**	0.18	0.08
Plot:Subplot	2.12	4	0.093		

Table 6: GLM summaries and analyses of variation for the effects of urbanisation and relevant breeding parameters on the number of great tit fledglings per egg (FPE; n=442) recorded during the 2014 and 2015 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales, their interaction, and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).



FPE model	**Chisq**	***df***	***p***	**Estimate**	**SE**
Final model					
Intercept				1.921	0.146
Subplot	119.901	2	**<0.001**		
Red				-0.998	0.201
Yellow				-1.269	0.190
Plot	1.049	2	0.592		
Red				-0.710	0.194
Yellow				-0.165	0.164
Laying date	16.275	1	**<0.001**	-0.184	0.045
Year	3.843	1	**0.050**	-0.184	0.094
Plot:Subplot	38.500	4	**<0.001**		
Red:Red				0.518	0.262
Red:Yellow				1.037	0.277
Yellow:Red				-0.561	0.255
Yellow:Yellow				0.633	0.231
Dropped variables					
Laying date^2	0.773	1	0.379	-0.042	0.048
Urbanisation model					
Intercept				1.993	0.144
Subplot	110.649	2	**<0.001**		
Red				-0.973	0.201
Yellow				-1.239	0.190
Plot	0.444	2	0.801		
Red				-0.639	0.192
Yellow				-0.190	0.163
Year	21.268	1	**<0.001**	-0.374	0.081
Plot:Subplot	34.627	4	**<0.001**		
Red:Red				0.496	0.261
Red:Yellow				1.024	0.277
Yellow:Red				-0.457	0.253
Yellow:Yellow				0.686	0.231

Table 7: Degree of variance explained by random effect ‘area’ for each full breeding model. Marginal (fixed effects) and conditional (fixed and random effects) coefficients of determination (R^2) for breeding models reported

Model	Random effect variance (±SD)	Marginal R^2	Conditional R^2
LD	8.391 ± 2.897	0.51	0.63
CS	$4.674e^{-18} \pm 2.162e^{-09}$	0.12	0.12
MNM	0.664 ± 0.815	0.16	0.37
FPE	NA	0.14	NA

Food analyses

A total of 133.5 hours of footage was captured for the 56 nests recorded in 2015 and 2016; with a mean (± SD) video length of 143.1 ± 20.4 minutes per nest (range: 120.9 – 193.2 minutes). At the plot level a total of 19 green, 12 red and 21 yellow areas were filmed, while at subplot level 24 green, 10 red and 18 yellow areas were filmed. The mean disturbance time was 12.3 ± 10.2 minutes, and the average provisioning time recorded was 118.7 ± 22.5 minutes for filmed nests over both seasons. Brood sizes of recorded nests ranged from 2 – 13 nestlings, with a mean brood size of 6.9 ± 2.3 nestlings. The sex of the provisioning parent was largely unidentifiable; parental sex was successfully determined in just 33.2% of provisioning events. In identifiable cases, males and females were found to provision 59.9% and 40.1% of prey items respectively.

Prey items were provisioned to nestlings at an average rate of 0.52 ± 0.27 items per minute, with a marked difference in provisioning rates (PR) over the two years: 0.70 ± 0.27 items per minute in 2015 compared to 0.41 ± 0.21 items per minute in 2016. Neither urbanisation at a plot or subplot scale was determined to have a significant effect in explaining provisioning rate variation, as determined by analysis of variance tests on PR GLMM variables (Table 8). Of the eight explanatory variables in the full PR model, only two variables – year and brood size – were significant in explaining PR variance. Model estimates showed that PR increased with brood size and was significantly lower in 2016 (Table 8).

A total of 3760 provisioning events was recorded, of which 2136 (59.5%) were caterpillars, 611 (17.0%) were classified as ‘other’ (e.g. spiders, winged insects, etc.), and 959 (26.7%) were unidentifiable. The average proportion of caterpillars (of identifiable prey) (PCP) provisioned to nestlings in non-urban subplots was 0.90 ± 0.068 compared to 0.67 ± 0.23 in urban plots. GLMM analysis saw the terms calendar day, calendar day squared (second order polynomial term), nestling age and temperature significantly explain variance in PCP to nestlings (Table 9). The association between PCP and calendar day was non-linear, determined by the model to be a negative quadratic relationship (a concave function) (Table 9). The model estimated an increase in PCP with an increase in nestling age, and a decrease in PCP with higher temperatures (Table 9). Both urbanisation scales were near-significant in explaining part of PCP variance, and subplot was found to be significant in the urbanisation model (Table 9). The urbanisation model estimated highest PCP proportions in green subplots (0.87), and highly similar lower values in yellow (0.67) and red subplots (0.68) (Figure 10).

The average length of prey delivered to nestlings was approximately 24 ± 4 mm, whereby caterpillars were 26 ± 5 mm on average and prey classified as other was generally shorter with an average length of 17 ± 4 mm. Other than inter-annual variation represented by the 'year' term, no model terms fitted to the mean caterpillar length were significant (Table 10).

Analysis of variance of MNMf (mean nestling mass in relation to food variables) model terms found PCP and year to explain significant variance in nestling masses of filmed nests (Table 11). Nestling masses were estimated to increase with PCP (Figure 11). Both 'mean caterpillar length' and 'provisioning rate' model terms were determined as 'near significant' by ANOVA tests in the full MNMf model (Table 11).

Coefficients of determination and estimates of variance determined by random effect 'area' for all food models are summarised in Table 12. The random effect of variable 'area' was found to explain substantial additional variation in PCP, MCL and MNMf models, while explaining a more limited amount of additional variation in the PR model (Table 12).

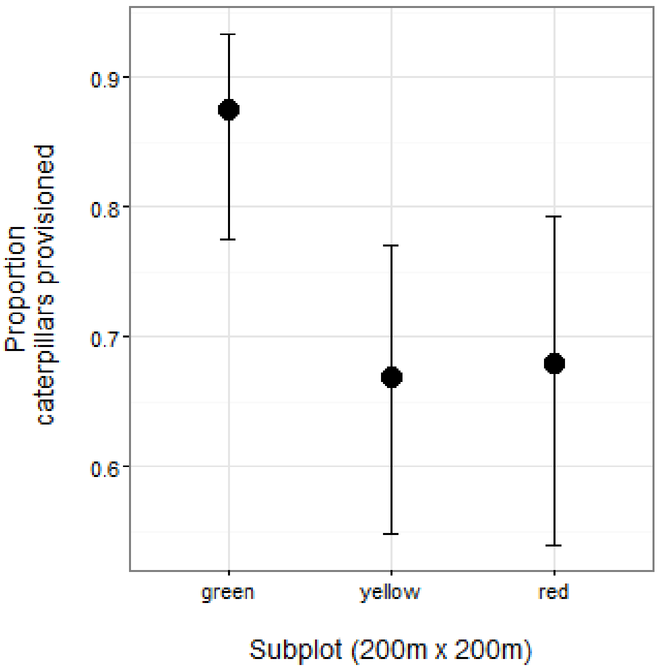


Figure 10: PCP urbanisation model estimates of proportion of caterpillars provisioned to nestlings in relation to urbanisation degree (green, yellow, red) at a subplot scale. Bars indicate 95% confidence intervals.

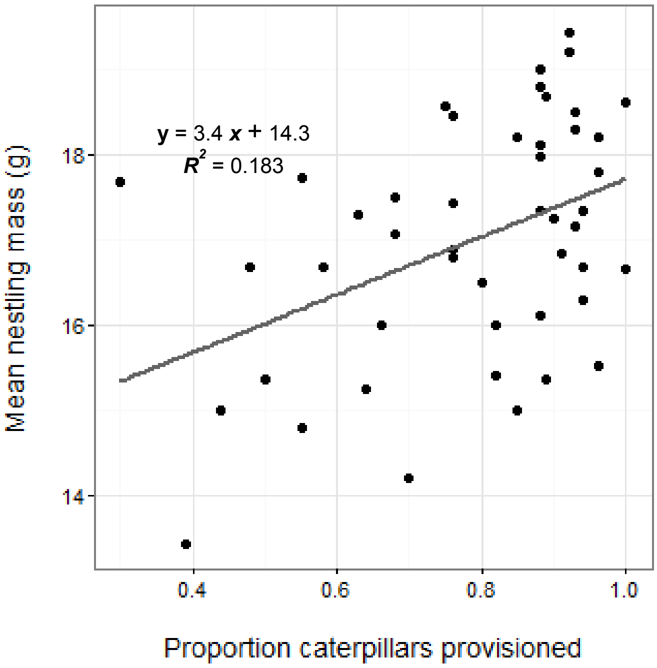
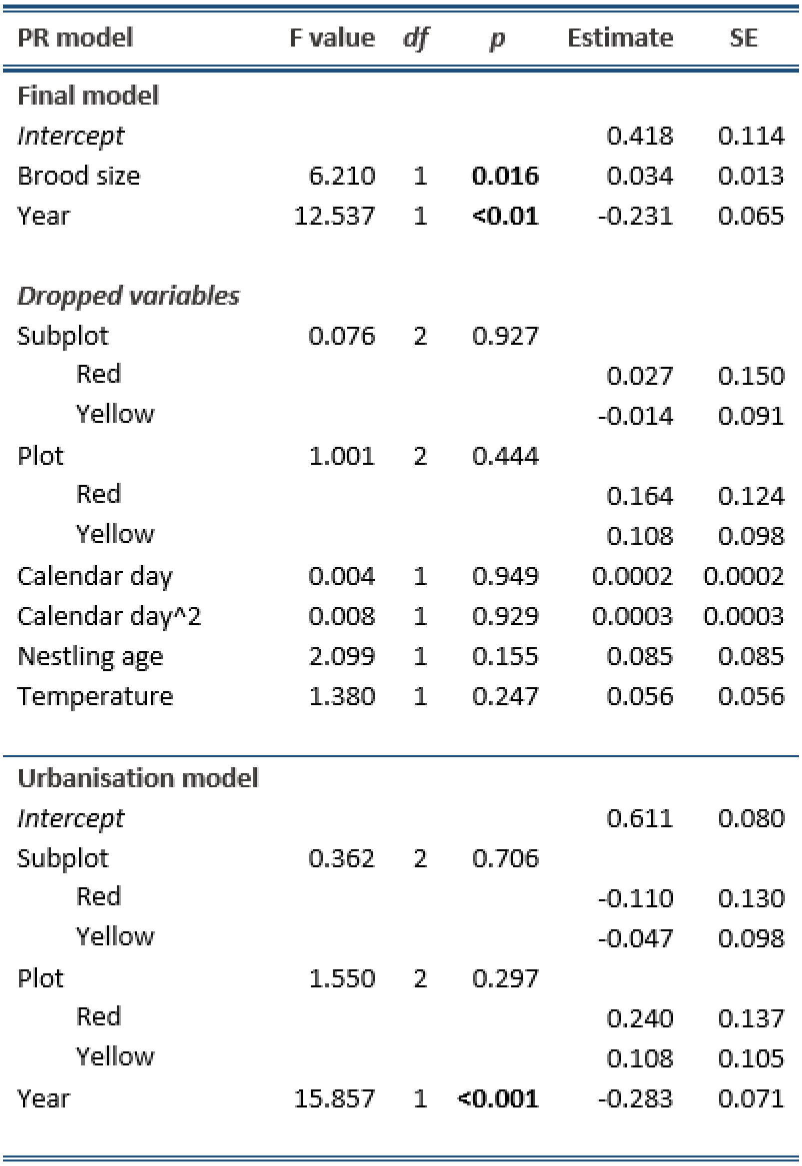


Figure 11: The relationship between nestling mass and the proportion of caterpillars they are provisioned as modelled by a linear model through the raw data (n=48).

Table 8: GLMM model summaries and analyses of variation for the effects of urbanisation and brood parameters on provisioning rates (PR; n=51) determined during the 2015 and 2016 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models, as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).



PR model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				0.418	0.114
Brood size	6.210	1	**0.016**	0.034	0.013
Year	12.537	1	**<0.01**	-0.231	0.065
Dropped variables					
Subplot	0.076	2	0.927		
Red				0.027	0.150
Yellow				-0.014	0.091
Plot	1.001	2	0.444		
Red				0.164	0.124
Yellow				0.108	0.098
Calendar day	0.004	1	0.949	0.0002	0.0002
Calendar day^2	0.008	1	0.929	0.0003	0.0003
Nestling age	2.099	1	0.155	0.085	0.085
Temperature	1.380	1	0.247	0.056	0.056
Urbanisation model					
Intercept				0.611	0.080
Subplot	0.362	2	0.706		
Red				-0.110	0.130
Yellow				-0.047	0.098
Plot	1.550	2	0.297		
Red				0.240	0.137
Yellow				0.108	0.105
Year	15.857	1	**<0.001**	-0.283	0.071

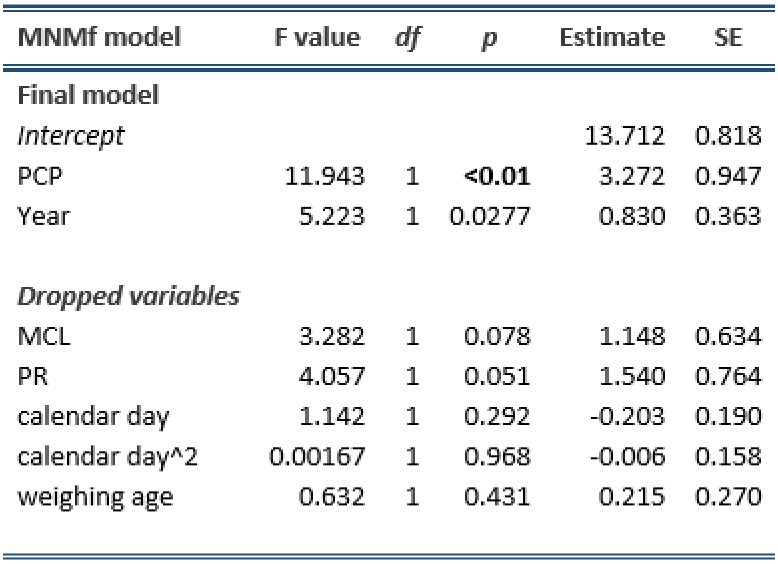
Table 9: GLMM model summaries and analyses of variation for the effects of urbanisation and brood parameters on the proportion of caterpillars provisioned (PCP; n=52) to great tit nestlings in the 2015 and 2016 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models, as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).

PCP model	Chi square	*df*	*p*	Estimate	SE
Final model					
Intercept				0.924	0.572
Calendar day	4.341	1	**0.037**	0.167	0.080
Calendar day^2	13.162	1	**<0.001**	-0.207	0.057
Nestling age	23.840	1	**<0.001**	0.179	0.037
Temperature	13.693	1	**<0.001**	-0.072	0.019
Dropped variables					
Subplot	5.901	2	0.052		
Red				-1.091	0.502
Yellow				-1.109	0.457
Plot	5.704	2	0.058		
Red				0.042	0.684
Yellow				1.138	0.600
Brood size	0.936	1	0.333	-0.032	0.033
Year	0.248	1	0.619	-0.146	0.293
Urbanisation model					
Intercept				2.277	0.415
Subplot	7.744	2	**0.021**		
Red				-1.191	0.492
Yellow				-1.240	0.449
Plot	3.332	2	0.189		
Red				-0.171	0.624
Yellow				0.646	0.534
Year	23.916	1	**<0.001**	-0.902	0.184

Table 10: GLMM model summaries and analyses of variation for the effects of urbanisation and brood parameters on the mean caterpillar length (MCL; n=52) provisioned to great tit nestlings in the 2015 and 2016 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models, as determined by step-wise ANOVA testing. Urbanisation models include only the two urban scales and inter-annual variation represented by year. Bold values indicate statistically significant terms ($p < 0.05$).

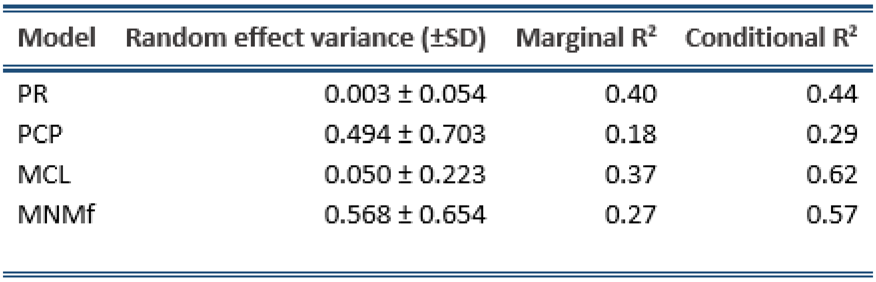
MCL model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				1.722	0.105
Year	14.450	1	**<0.001**	0.404	0.106
Dropped variables					
Subplot	3.068	2	0.072		
Red				-0.516	0.251
Yellow				-0.096	0.191
Plot	0.311	2	0.741		
Red				0.207	0.266
Yellow				0.079	0.221
Calendar day	1.087	1	0.303	0.058	0.056
Brood size	1.848	1	0.182	-0.029	0.021
Nestling age	3.498	1	0.069	0.058	0.031
Temperature	2.521	1	0.120	0.020	0.013
Urbanisation model					
Intercept				1.817	0.174
Subplot	3.040	2	0.073		
Red				-0.486	0.244
Yellow				-0.093	0.200
Plot	0.146	2	0.867		
Red				0.128	0.278
Yellow				0.014	0.225
Year	16.367	1	**<0.001**	0.437	0.108

Table 11: GLMM model summaries and analyses of variation for the effects of food and breeding parameters on mean nestling mass (MNM; n=48) measured in the 2015 and 2016 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models, as determined by step-wise ANOVA testing. Bold values indicate statistically significant terms ($p < 0.05$).



MNMf model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				13.712	0.818
PCP	11.943	1	**<0.01**	3.272	0.947
Year	5.223	1	0.0277	0.830	0.363
Dropped variables					
MCL	3.282	1	0.078	1.148	0.634
PR	4.057	1	0.051	1.540	0.764
calendar day	1.142	1	0.292	-0.203	0.190
calendar day^2	0.00167	1	0.968	-0.006	0.158
weighing age	0.632	1	0.431	0.215	0.270

Table 12: Degree of variance explained by random effect 'area' for each full food model. Marginal (fixed effects) and conditional (fixed and random effects) coefficients of determination (R^2) for food models reported.



Model	Random effect variance (±SD)	Marginal R^2	Conditional R^2
PR	0.003 ± 0.054	0.40	0.44
PCP	0.494 ± 0.703	0.18	0.29
MCL	0.050 ± 0.223	0.37	0.62
MNMf	0.568 ± 0.654	0.27	0.57

Discussion

The results of this thesis provide insight into how great tit breeding success and food provisioning during the breeding season vary with urbanisation at two spatial scales. Breeding results suggested a clear relationship between breeding parameters and urbanisation with overall lower success rates in more urbanized areas at both scales, thereby supporting the ecological trap hypothesis (Schlaepfer et al. 2002; Robertson and Hutto 2006). These findings conform to previous studies evaluating avian breeding success in urban-rural contexts (Chamberlain et al. 2009; Deviche and Davies 2014; Bailly et al. 2016). All breeding-related predictions were confirmed, barring the prediction of a significant interaction between spatial scales for all breeding models - only the fledgling per egg (FPE) model contained a significant urban interaction. Laying dates were found to be more advanced in urban areas than rural ones, a well-studied phenomenon with several implications (Deviche and Davies 2014). Breeding success was determined to be lower with increasing urbanisation at one or both urban spatial scales, as measured by clutch size, nestling masses and the number of fledglings per egg. On the other hand, the role of urbanisation in determining the distribution and availability of food was not consistent across measured food parameters. As hypothesised, the proportion of caterpillars provisioned to nestlings was seen to increase in non-urban areas relative to urban ones at the subplot scale, as modelled by the PCP urbanisation model. This reflects findings of higher caterpillar abundances in natural habitats than urban habitats (Wawrzyniak et al. 2015). Contrary to predictions, provisioning rates and caterpillar lengths did not vary with urbanisation degree, regardless of the spatial scale defined. Results also revealed that the proportion of caterpillars provisioned had a significant positive effect on nestling weight – a finding with interesting implications given PCP model results. Results therefore suggest important connections between breeding success and food during the breeding season, the nuances of which are further explored below.

Laying date

Results of laying date models suggested a strong effect of plot-scale urbanisation on the timing of great tit breeding, whereby laying dates were found to be earlier in more urbanised areas (Figure 3). Advanced laying dates in urban areas is a finding reflected in much of the literature comparing urban and rural bird populations (Chamberlain et al. 2009; Deviche and Davies 2014). This relationship can be tied to several factors thought to influence passerine phenology. Advanced laying dates have been correlated with increased temperature and light (Dhondt and Eyckerman 1979; Ahola et al. 2009; Kempenaers et al. 2010; Matthysen et al. 2011), both environmental conditions known to be higher in cities than surrounding rural areas (Haggard 1990; McKinney 2002). Red plots were positioned in and around major towns and cities in Belgium; Brussels, Antwerp and Ghent being the largest examples. It follows that these plots were among the hottest and well-lit of the 27 studied (although this was not measured), thereby triggering earlier laying dates. Differences in urban and rural micro-climates have been shown to affect birds during the breeding season (Møller et al. 2010; Banbura and Banbura 2012; Wawrzyniak et al. 2015) However, laying dates did not vary significantly among subplot types (although it must be noted that the alternate LD model (Appendix I, Table 13) found local-scale urbanisation to explain significant variation in laying dates). A likely explanation for this finding is that temperature is related to urbanisation at a scale far greater than that of the subplot level (just 200m x 200m). Urban heat islands can significantly increase temperatures in and around cities over spatial areas of several kilometres (Deviche and Davies 2014; McDonnell and Hahs 2015), an extent certainly large enough to influence temperatures in large city parks (i.e. 'green in red' areas in this study).

Beyond the role of temperature and light, food availability is an additional factor shown to affect breeding timing and success. Aspects of quantity, temporal availability and quality of food represent important elements in understanding how food may affect laying date, as well as other breeding parameters still to be discussed. Several studies have reported higher quantities of food in urban environments than rural counterparts. Anthropogenic sources foods, such as food from bird feeders, waste, and exotic plant species (Mennechez and Clergeau 2001; Robb et al. 2008b; Chamberlain et al. 2009) may contribute to increased year-round food availability. Adult great tits exploit a wide range of foods (Gosler 1993) and it follows that they exploit additional anthropogenic sources of food in cities (Chamberlain et al. 2009). While data collected on food in this study found no differences in provisioning rates along an urbanisation gradient, this does not necessarily account for additional foods available to adult birds given the differences in adult and nestling diets and the strong change in food conditions from early to late spring (Gosler 1993). While anthropogenic foods may increase overall food abundance, they are suggested to be of lower quality, being energy-rich but protein-poor (Chamberlain et al. 2009) and lacking in important nutrients (e.g. carotenoids and calcium) needed for egg formation (Bailly et al. 2016).

The abundance of natural food sources (e.g. caterpillars) in rural and urban areas directly before and during the breeding season is somewhat more contested in literature. Isaksson and Andersson (2007) found caterpillars to be more abundant in urban areas than rural areas, and provisioning rates to nestlings twice as high in urban areas. Conversely, Wawrzyniak et al. (2015) recorded caterpillars as being 2-5 times more abundant in natural habitats than urban ones, a finding indirectly reflected by this study in that the proportion of caterpillars provisioned (PCP) to nestlings was highest in green subplots (Figure 10). Given that caterpillars are regarded as a proxy for a high nestling diet (Wilkin et al. 2009a), their abundance in rural and urban areas has important implications for breeding success (as will be later discussed). An important additional finding in Isaksson and Andersson's (2007) study was that caterpillars in urban areas were of lower nutritional quality (as measured by carotenoid content) than their rural counterparts. This suggests that in addition to poor quality anthropogenic food sources, natural food sources may also be of lower quality in urban areas.

Supplementary feeding experiments have been shown to advance laying date in several bird species (Robb et al. 2008a; Robb et al. 2008b) and this phenomenon has been explicitly shown in both blue tits and great tits (Harrison et al. 2010). It is here that the relative importance of winter feeding and feeding pre-laying become important, especially in interpreting the findings of this study that significantly earlier laying dates were found at a plot scale but not a subplot scale (Table 3). Female great tits feeding directly before laying are much more likely to do so within a relatively small area around their nestbox (although potentially larger than the subplot scale - Wilkin et al. 2009b), given that they roost there during laying and even a week or two in advance of laying (Gosler 1993). By contrast, in winter, great tits utilise ranges of several hectares to forage for food (Gosler 1993). A study by Robb et al. (2008a) may shed light on the relative importance of these feeding periods and the increased abundance of food in urban areas. In their study, they artificially provisioned several species of nest-box breeders (their target species being blue tits) with peanuts during winter (a typical bird feeder food source), but stopped the supplementary feeding six weeks in advance of the breeding season. They found significantly advanced laying dates across the nestbox breeding species in the subsequent breeding season, highlighting the high relative importance of winter feeding (which occurs at a large scale). In the urban context, this suggests tits may take advantage of supplementary anthropogenic food sources in winter, which in turn may influence earlier laying in the subsequent season. This line of reasoning links with the findings of this study, whereby the larger scale of urbanisation (plot) was found to explain variation in laying date. Literature therefore suggests that a combination of higher temperatures, light and winter food availability at a large scale in urban areas may influence laying dates in great tits.

Earlier laying in urban areas, as demonstrated by this study, is also likely to feed back into the dynamics of food in urban environments. Great tits time their breeding cycles so as to have young in the nest when caterpillar populations are at their peak (Perrins 1991), meaning that nests initiated too early (or too late) in the season are likely to miss this peak with significant negative repercussions for nestlings (see nestling mass discussion).

Clutch size

Clutch sizes were smaller with increasing levels of urbanisation at both modelled spatial scales (Figure 5). This complements previous findings; Chamberlain et al.'s (2009) meta-analysis highlighted similar urban effects on great tits, whereby urban clutch sizes were smaller than non-urban clutch sizes in six comparative studies. While results conform to other studies, they are also novel in that they explain clutch size variation across a large set of areas with quantified levels of urbanisation at different scales. Other studies tend to lack information regarding spatial scale, and often rely on very strong urban/rural contrasts between few areas (e.g. Solonen 2001; Isaksson and Andersson 2007; Hedblom and Söderström 2012; Bailly et al. 2016).

Explaining why avian clutch sizes are smaller in urban areas is a challenging undertaking, with literature providing evidence for a multitude of factors. Clutch size is influenced by female condition, habitat and pre-laying conditions (Chamberlain et al. 2009; Bailly et al. 2016), as well as genetic flows and genetic inheritance (Dhondt et al. 1990; Postma and van Noordwijk 2005). The role of food in determining clutch sizes is therefore complex as it is involved with each of these factors in nuanced ways.

Clutch size is thought to have a strong genetic link (Postma and van Noordwijk 2005), which suggests smaller clutch sizes in urban areas could be adaptive to poorer urban conditions (e.g. lower quality foods), thus potentially mitigating the effects of an ecological trap (Schlaepfer et al. 2002). While cities are novel environments on an evolutionary time scale, they may represent sufficiently strong selection pressures to enable the micro-evolutionary change associated with an adaptive response (McDonnell and Hahs 2015), especially if they are of a larger spatial scale (McDonnell and Hahs 2015). However, such an adaptive response is likely only possible where gene flow between rural and urban areas is highly limited (Dhondt et al. 1990). Studies on gene flow between great tit populations in rural and urban areas are scarce (Chamberlain et al. 2009), but findings by Björklund et al. (2010) showed that in their study system (urban parks and an adjacent forest population in Barcelona) gene flow between the city and neighbouring rural areas was relatively high. In the presence of inter-area gene flow, clutch sizes may therefore represent an average of the optimum clutch sizes across habitat types (Dhondt et al. 1990). However, this issue is further convoluted by the fact clutch sizes may be relatively plastic (Husby et al. 2010), a factor which could allow for variance in clutch sizes in accordance with environmental conditions (e.g. poor food quality or quantity). In addition, clutch sizes may also reflect poorer quality breeders in urban environments (Liker et al. 2008).

Tit food abundance is generally higher in urban areas (as discussed in the laying date section), which should in theory result in larger clutch sizes given improved female condition (Chamberlain et al. 2009), and is a relationship which has been experimentally shown (Nager et al. 1997). However this is a pattern not often observed in literature comparing clutch sizes between rural and urban environments (Chamberlain et al. 2009). Contrasting evidence has found adult birds in cities to be in poorer condition than their rural counterparts, as has been demonstrated in house sparrows (Liker et al. 2008). Furthermore, while food abundance may be better in city habitats, food quality is often lower (as discussed in the laying date section), and important nutrients needed for egg and yolk formation are likely in shorter supply (Bailly et al. 2016). In fact, the quality of supplementary food may be more important than its abundance. Harrison et al. (2010) found that food supplementation for several weeks (pre-laying to hatching) reduced brood sizes in great and blue tits. These findings have remarkable parallels with patterns in urban environments, and suggest that supplementary food may not always improve breeding productivity. Harrison et al. (2010) argued that the fat-rich protein-poor peanut cake they used as supplementary food may have limited clutch sizes due to a lack of essential amino acids. They further argued that low protein intake at the point of laying may act as predictive cue for lower protein later in the season (Drent and Daan 1980 in Harrison et al. 2010). Given that a substantial amount of protein is required to rear nestlings (Gosler 1993), they suggest this could limit clutch sizes. However, Nager et al. (1997) experimentally found that food quality (tested by two food types of different protein content) provisioning during pre-laying and laying did not influence variation in clutch size in great tits. But this may not reflect the urban environment as food types in urban areas are far more variable than those used by Nager et al. (1997), and the study did not test the effects of provisioning over the preceding winter. Given the frequency and consistency with which clutch sizes are found to be smaller in urban areas than rural counterparts (Chamberlain et al. 2009), this is undoubtedly an area which needs further research to better understand how and if food is a causal mechanism in driving clutch sizes.

The results of this thesis also found smaller clutch sizes with the progress of the breeding season, an observation reflected by several authors (Cowie and Hinsley 1987; Goodenough et al. 2009; Wawrzyniak et al. 2015). This decline is considered to be a response to changing environmental conditions as the season progresses (Perrins 1970), specifically the decrease in available nestling food as the number of caterpillars decline (Naef-Daenzer and Keller 1999; Goodenough et al. 2009).

Nestling mass

The average weight of nestlings was found to be lower with increasing urbanisation degree at both modelled spatial scales (Table 5). Similar findings have been found for a number of other bird species; Chamberlain et al. (2009) cite 10 cases (of 11 examined) whereby urban bird populations showed lower mean nestling weights than rural counterparts, including a study on great tits (Solonen 2001). This thesis provides a novel interpretation of these results given that two spatial scales of quantified urbanisation are accounted for across numerous replicate sites.

Several factors can impact nestling mass, and the results of this study clearly indicate a role for food. Nestling masses were found to increase as nestlings were provisioned with greater proportions of caterpillars (PCP) during the 2015-2016 breeding seasons (Table 11). Other variables such as provisioning rate and mean caterpillar length were found to have near-significant effects on nestling weight (Table 11), and understanding their role would likely be improved by a larger data set. Moreover, the PCP urbanisation model (Table 9) estimated that caterpillars were found in significantly lower proportions in red and yellow subplots compared to green subplots (Figure 10). Subplot was found to have a near significant effect in the full PCP model. PCP was found to have a quadratic relationship with calendar day (Table 9), a relationship described in literature as the peak in caterpillar abundance during the breeding season (Perrins 1991). Additionally, as temperature increased PCP was predicted to decrease by the PCP model (Table 9), alluding to the notion that caterpillar abundances are often higher earlier in the breeding season and decline in the second half of the season as spring progresses (Perrins 1991).

PCP is often used as a proxy for food quality and has been shown to improve fledgling condition and success (Verboven et al. 2001; Wilkin et al. 2009a). This is increasingly relevant in the urban context, given the quantity and quality of caterpillars in the urban environment (see discussion in laying date section). Results of this thesis clearly highlight a link between food quality (PCP) along an urbanisation gradient (Figure 10) and the importance of food quality on bird breeding success (Figure 11). The apparent lack of caterpillars in more urbanised subplots could be attributed to lower densities of trees such as oak (Naef-Daenzer and Keller 1999; Wilkin et al. 2007b), and a lower proportion of indigenous trees relative to exotic ornamental trees (McIntyre 2000; Helden et al. 2012), and in part could explain the observed decline in nestling weights with increasing subplot urbanisation. Given that urban areas exhibited earlier laying dates, the urban effect on nestling weights is compounded by the fact that earlier laying dates were significantly correlated with lower average nestlings masses (Table 5). Again, this has a potential link with food, as early urban nests are possibly poorly timed to exploit peak caterpillar abundances (Verboven et al. 2001).

Interestingly, variation in provisioning rate and mean caterpillar length among areas was not explained by urbanisation at either tested spatial scale (Table 8; Table 10). This suggests that irrespective of similar provisioning efforts and caterpillars of similar size, nestlings in urban areas were still found to weigh less than rural counterparts. This phenomenon has several potential explanations, none of which are mutually exclusive. The first explanation has already been explored; urban nestlings received a lower proportion of caterpillars and this poorer quality diet could drive weight differences. Compounding this diet quality effect, is the finding that caterpillars in rural areas and urban areas may be different in their nutritional content (Isaksson and Andersson (2007) – see laying date discussion). Secondly, some important differences in overall prey size might explain part of the urban-rural differences in observed nestling masses. Urban areas in this study were generally provisioned with a lower proportion of caterpillars, and therefore a higher proportion of other food items (typically spiders, beetles and winged insects). Not only is this ‘other’ food deemed of lower nutritional value (Wilkin et al. 2009a; Hargitai et al. 2016) nor as profitable as caterpillars (Naef-Daenzer et al. 2000), but was also observed to be substantially smaller: caterpillars provisioned were approximated to be 26 ± 5 mm on average, while ‘other’ prey was approximated at 17 ± 4 mm on average. It must however be noted that sizing prey in footage was particularly challenging and some measurement error is expected. Lastly, this difference may be tied to differences in egg quality along the urbanisation gradient. While not explicitly measured in this study, several authors have shown urban-laid eggs to be of poorer quality than eggs laid in neighbouring rural populations (Isaksson et al. 2008; Bańbura et al. 2010). This puts urban nestlings at a prior disadvantage, as nestling growth and survival are strongly linked to egg quality with effects even extending beyond rearing (Krist 2011; Marri and Richner 2014).

This final explanation potentially ties in with the observed result that nestling mass models (original – Table 5, alternate – Table 15, Appendix I) contained near-significant interactions terms for the urban scale interaction term (Figure 6, Figure 9). This relationship could hint at the potential modification of the subplot-level urbanisation effect by the plot-level urbanisation effect. While breeding females are relatively restricted to the nestbox and its immediate surrounds prior to and during laying (Gosler 1993), they may travel larger distances to source higher quality foods (e.g. calcium rich) for egg formation during this period (Wilkin et al. 2009a). If the broader environment consists of relatively poorer food sources this may negatively influence the quality of the eggs, and in turn result in poorer nestlings (Bailly et al. 2016). It therefore stands to reason that broader conditions may play a role in determining how subplot-scale urbanisation influences nestling mass. As illustrated by the results, highest average nestling masses where found in 'green in green' areas, and progressively declined when nested in yellow and red plots (Figure 6). The decline is nestling mass with increasing NUR-scale urbanisation was estimated to be steepest in green plots (Figure 9), an indicator of the particularly high nestling masses from nestboxes located where NUR was zero (i.e. no built up urbanisation with 200m of the nestbox) and nested in a green plot. However, interpretation of the interaction term should be cautionary given it was only near-significant in explaining nestling mass variation.

Nest productivity: fledgling per egg

The number of fledglings per egg declined with urbanisation at the subplot scale, and the effect of subplot urbanisation was dependent on plot-level urbanisation (Table 6). The highest number of fledglings per egg were found in 'green in green' areas while the lowest number was found in 'red in yellow' areas (Figure 8). Findings on the influence of urbanisation on avian nest productivity are mixed, and often species-specific. Nevertheless, Chamberlain et al.'s (2009) meta-analysis found stronger evidence for reduced nest productivity in urban areas compared to rural ones, including two cases for great tits. The findings of this study are therefore in accordance with these results, while the evidence of a response to different spatial scales and their interaction is both a novel and important finding (as will be later discussed).

The productivity of a nest, measured by fledglings per egg, is intrinsically linked to the other breeding parameters measured by this study, which in turn have all been shown to be negatively affected by urbanisation. This has direct consequences for the likelihood of fledgling success. For example, lower nestling masses (as found in more urban areas) have been linked with poorer survival in great tits (Both et al. 1999; Naef-Daenzer and Keller 1999), especially between time of weighing and fledging (Tinbergen and Boerlijst 1990). Moreover, as discussed in the clutch size and laying date sections, poor food quality may negatively influence the quality of eggs females can produce, and in turn result in smaller nestlings with a lower chance of fledgling (Marri and Richner 2014). As is the case for mean nestling masses, the urbanisation effects on FPE are likely compounded by earlier laying dates in urban areas and subsequent mistiming with caterpillar abundance peaks. Nests laid later in the season were also found to have fewer fledglings per egg (Table 6); a relationship also attributed in literature to mistiming peak nestling food demand and peak caterpillar abundances (Perrins 1991; Verboven et al. 2001).

The influence of parameters laying date, clutch size and mean nestling mass on the overall nest productivity (FPE) may also explain the interaction found between the two urban spatial scales. Factors such as laying date (advanced by increasing urbanisation at a plot scale) may lay the foundations for breeding success later in the season. As fully discussed in the laying date section, light, temperature and food supply may trigger earlier breeding and subsequent mismatch between prey and nestling demand. If this is the case, subplots nested in yellow and red plots are potentially more likely to show lower productivity than those nested in green plots – a finding reflected by this study for every subplot colour, barring in ‘yellow in green’ (Figure 8). Interesting model predictions included the very strong effect of yellow plots on red subplots (FPE values lowest for ‘red in yellow’ areas), and the fact that ‘yellow in green’ and ‘red in green’ FPE numbers were highly similar and far lower than ‘green in green’ values. This suggests that yellow areas, representative of 5-10% built-up areas, have effects that are comparable to red areas (>15% built-up areas) and that the threshold at which urbanisation starts to significantly negatively influence nest productivity is relatively low (>5% built-up area).

A combination of literature and the results of this study have shown that food is likely to play a role in driving breeding success along an urbanisation gradient. It has the potential to influence all stages of the breeding cycle, from laying date to nest productivity, as is summarised by Figure 12.

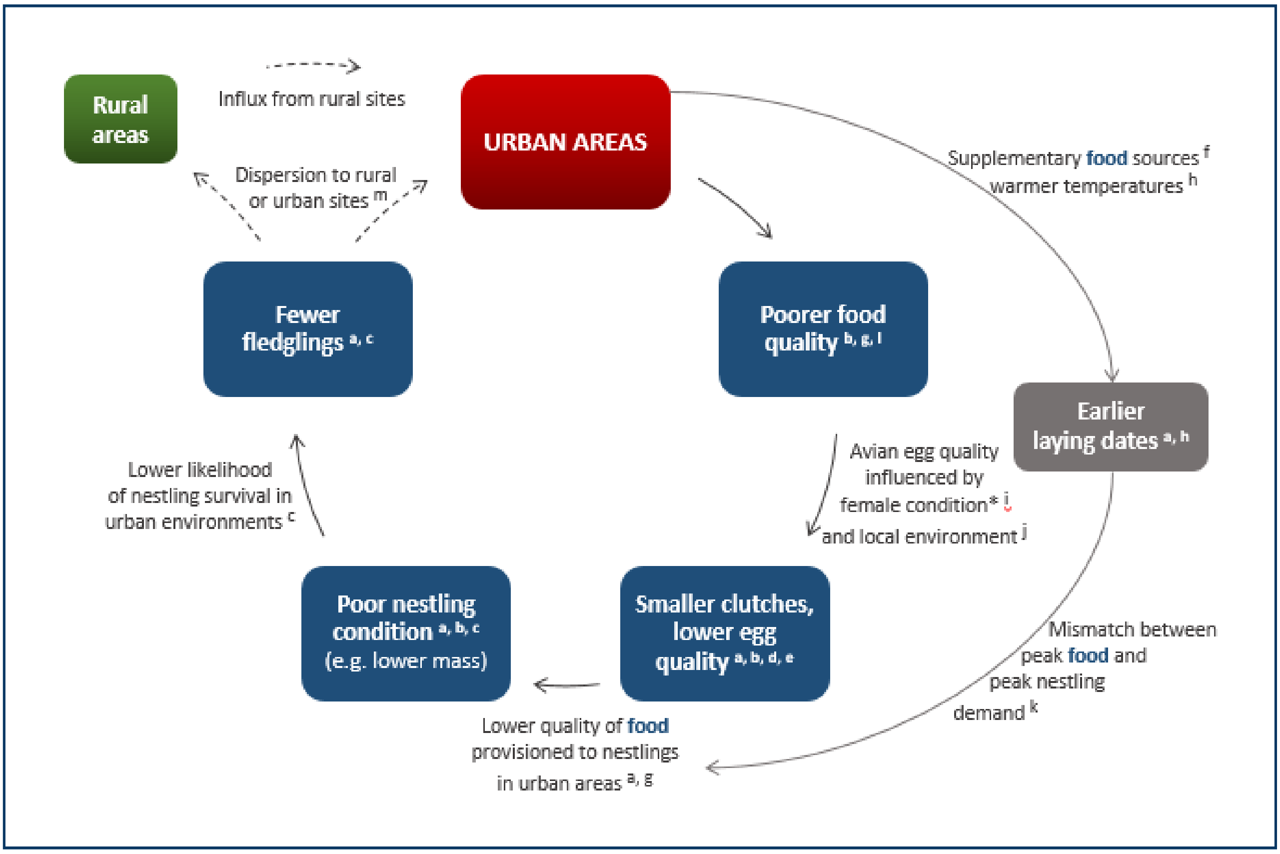


Figure 12: The urban breeding cycle – a food perspective: Examining the potential role of urban food quality and quantity in influencing bird breeding cycles in cities, as derived from literature and the results of this study. *Conflicting evidence – supplementary food in cities thought to improve adult body condition leading to earlier laying dates (Chamberlain et al. 2009), but urban adult birds have been shown to be in poorer condition than their rural counterparts (Liker et al. 2008), a potential knock-on effect of poor nestling development due to poorer diet. Literature cited: [a]this study; [b]Chamberlain et al. 2009; [c]Bailly et al. 2016; [d]Isaksson et al. 2016; [e]Banbura et al. 2010; [f]Harrison et al. 2010; [g]Issakson and Andersson 2007; [h]Deviche and Davies 2014; [i]Blount et al. 2000; [j]Biard et al. 2005; [k]Kempenaers et al. 2010; [l]Wawrzyniak et al. 2015; [m]Björklund et al. 2010

The importance of urbanisation and its scale

Urbanisation at either plot or subplot scale was found to explain variation in every urbanisation model of breeding parameters (Tables 3-6). In other words, in the absence of important covariates (e.g. brood size or laying date) urbanisation was still important in explaining variation in breeding success. It must be noted that the clutch size model was relatively poor in explaining variance, and only the laying date model explained more than half of the response variable variance (Table 7). Additionally, a large proportion of variance in many models (both breeding and food related) was explained by the random effect of area (Table 7, Table 12). However, given that models were built for hypothesis testing and not predictive capabilities, the impacts on urbanisation are still noteworthy.

Urbanisation models of food found relatively strong effects of urbanisation on food. The PCP urbanisation model found subplot was significant in explaining variation in caterpillars provisioned to nestlings (Table 9), an important finding given that caterpillars are regarded as high quality food items (Wilkin et al. 2009a). PCP was also shown to be significant in driving lower breeding success, even when PR and MCL were not correlated (Table 11). PR rate did not vary with urbanisation degree, but it is important to note that it is not a direct measure of food availability and may simply also reflect the limit at which parents are able to forage (Perrins 1991). Similarly, MCL did not vary with urbanisation, although this could be the result of coarse size classes (a result of relatively low video quality) and a relatively small data set.

Model findings highlighted the importance of analysing effects at multiple scales (Goddard et al. 2010). Urbanisation at both measured scales (plot and subplot) was represented in final breeding models, while a significant interaction was observed between urban spatial scales for the FPE model (Table 6). Clergeau et al. (2006) suggest that different scales represent different levels of ecological functioning, each defined by specific processes. In the context of this study, scales effects are likely to influence several proximate factors which in turn affect breeding success.

Urbanisation measured at a large scale was found to have important ramifications for breeding success. As discussed in the laying date section, factors such as temperature and light are likely to operate on a larger scale in influencing the onset of breeding. Moreover, the influence of food on laying date may also operate at a larger scale, and winter foraging (widest in winter - Gosler 1993) has been shown to advance tit laying dates in the subsequent breeding season (Robb et al. 2008a). Important landscape features such as the isolation of habitat patches, barriers, greenways and corridors are arguably more pertinent when viewed at larger scales (Clergeau et al. 2006b). Such features may influence aspects of the breeding cycle such as clutch size. Given the role of gene flow in potential determining adaptive clutch sizes these landscape-scale features become relevant, especially if they play a role in inhibiting or promoting gene flow. This represents a distinct possibility, research has found that the distribution of great tits can be attributed to factors like patch isolation (Evans et al. 2009).

The effects of urbanisation at a large-scale can also determine important aspects of food quality and quantity. Insect assemblages are influenced by fragmentation in the urban matrix, with marked changes in abundance, diversity and community composition (Gibb and Hochuli 2002; Kutschbach-Brohl et al. 2010; Carpintero and Reyes-López 2014). This can have potential knock-on effects for bird breeding success. Pollution both locally and at a city scale may affect bird breeding success and condition in urban environments, either directly or through their food supply (Eeva et al. 2005; Eeva et al. 2008; Hargitai et al. 2016). Eeva et al. (2005) described a shift in provisioning items brought to great tit nestlings in polluted environments (air pollution from a copper smelter), with an increase in lower quality prey items (beetles, winged insects and spiders) as compared with non-polluted areas.

Moreover, detrimental effects pollution on breeding success and changes to provisioning were observable 3-4km away from the smelter, again highlighting a role for larger-scale effects.

While large scale factors clearly need be accounted for, local scale elements such as green space or built-up areas can represent contrasting ecological opportunities and have an important role to play (Clergeau et al. 2006b). In the context of this study, local scales can have key influences on parameters affecting breeding success. Local-scale urbanisation may affect the presence of vegetation and habitats with suitable foods. Oak trees can be viewed as surrogates for local caterpillar availability (Wilkin et al. 2007b), and Wilkin et al. (2007) found oak densities at highly-localised scales (25-70m around nestboxes) to have significant effects on great tit breeding phenology. Caterpillars represent a high-quality food source for nestlings, and their distribution at a small scale has important implications for nestling condition and fledgling success, especially as provisioning parents forage for prey at highly localised scales during the peak of the breeding season (Gosler 1993). A decrease in oaks or other native vegetation (given they carry high caterpillar biomass - Perrins 1991; Mackenzie et al. 2014) is therefore likely to have negative consequences on breeding success. Such local scale factors may even influence clutch sizes, as females are known to reduce their clutch sizes in accordance with local constraints (Bailly et al. 2016) and the local availability of food in urban environments during and pre-laying may have a role to play in influencing clutch sizes (Chamberlain et al. 2009).

Importantly, this thesis has shown that the effects of scale may not always operate independently in influencing breeding success. Findings of the FPE model suggest that the various effects of small-scale urbanisation (subplot) on breeding success are likely dependent on large-scale urbanisation effects, i.e. mechanisms which operate at a larger scale may influence those which operate at smaller scales (Clergeau et al. 2006b; Goddard et al. 2010). A theoretical example illustrates how this may play out in the urban context: higher levels of pollution at a city-scale (Liker et al. 2008) may put oak trees under oxidative stress and thereby lower the carotenoid quality of their leaves (Isaksson and Andersson 2007). This can in turn result in poorer quality caterpillars on these oaks, as they derive their carotenoid content from the leaves (Isaksson and Andersson 2007). Great tit parents foraging at a local scale in urban areas may therefore provision lower quality food, which is likely to result in lower nestling masses and fledgling success (Tinbergen and Boerlijst 1990; Gosler 1993). Without an understanding of the effect of scale, this result may be misinterpreted and incorrectly attributed to a localised factor (diet) without an understanding of a role for the broader scale (urban pollution).

The novel findings of this thesis regarding the effects of urbanisation at different spatial scales have important implications for research. Several studies have compared great tit success between rural and urban areas (e.g. Solonen 2001; Isaksson and Andersson 2007; Bailly et al. 2016). However, many studies lack information regarding spatial scale and tend to examine a limited part of the urban gradient, often relying on very strong urban-rural contrasts between few areas. For example, Solonen (2001) compared four urban sites (ranging 0.14– 0.30 km^2 in size) with just one rural area (2.5 km^2), without providing a quantifiable measure of urbanisation. In so doing, Solonen (2001) effectively compares urban areas measured 'subplot' scale with a rural area defined at a 'plot' scale. This assumes that important parameters (such as laying date) are influenced in the same way at both of these scales, an assumption that this study has found to be invalid. Another example derives from Isaksson and Andersson (2007). They compared two city plots within the limits of Goeteborg Sweden (population size ca 600, 000) with two forest sites approximately 50km south of Goeteborg. A near-identical spatial allocation of plots was performed by Bailly et al. (2016), with two city areas and two forest areas in eastern France. Roughly converted into the terms used by this thesis, these two studies likely compare two 'yellow in red' areas with two 'green in green' areas. This illustrates (not dissimilarly to Solonen 2001) that only a small portion of the rural urban gradient is actually utilised in examining urbanisation effects (by comparison, this thesis utilised nine "colour" combinations), and tends towards comparing extreme situations.

When assessing the results of this study from a conservation perspective, several important elements become apparent. Firstly, the breeding success of great tits (and potentially many other birds along a rural urban gradient) is likelier improved when green areas extend well beyond the subplot scale. Large scale urbanisation (here 3km x 3km) represented a negative effect on success across all breeding parameters. Notably, results suggested that nest productivity is adversely affected by relatively low levels of urbanisation, and that yellow plot effects are comparable to those of red plot effects (as observed for FPE numbers). In light of this, existing green areas which cover larger areas need to be protected, as their larger size is more likely to buffer the effects of neighbouring urbanisation. Secondly, where green fragments already exist within an urban matrix, changes to small-scale landscape elements can potentially improve breeding success. For example, improving caterpillar abundances (e.g. through higher densities of oak tress) in city parks would likely improve nestling masses and subsequent survival. However, smaller-scale solutions are still subject to large-scale urbanisation effects. Thirdly, the type and temporal availability of supplementary food in cities can have knock on effects for breeding success. While supplementation experiments referred to in this study (e.g. Nager et al. 1997; Robb et al. 2008a; Harrison et al. 2010) paint a complex picture, an argument can be made for the notion that supplementary urban food advances laying date (with potentially detrimental consequences) and can reduce clutch sizes, likely as a result of its lower quality (Perrins 1991; Robb et al. 2008a; Harrison et al. 2010). This has important implications for controllable sources of additional food in cities (e.g. bird feeders). While food supplementation typically has pronounced fitness benefits (e.g. Schoech et al.

2008), the role of food (both quality and quantity) may play out differently in urban environments. Evidently further research is needed on this topic (but see Nager et al. 1997) and small-scale food supplementation experiments in different urban areas could represent a good starting point.

Study limitations and future research

Many comparative studies have been critiqued for small sample sizes, a lack of replication and study sites that are qualitatively defined (Fahrig 2003; Robertson and Hutto 2006). This study sought to address these critiques: spatially independent replicates of sites were established and urban levels were quantified into classes as defined by percentage built-up area. However, a few study limitations are apparent. Firstly, the use of urban classes (green, yellow, red) by the SPEEDY study design may limit the amount of variation captured. But, based on a comparison with NUR-based alternate models, the extent of variation lost by the SPEEDY study design seems minimal. Alternate models utilising the 'NUR' continuous variable (Appendix I) were found to be highly similar to original breeding models which utilised the 'subplot' categorical variable. Urbanisation was consistently found to explain variation in breeding parameters across both model sets, the only exception being a switch in the significance of urban scale for the laying date model ('plot' in the original model, 'NUR' in the alternate model). While this exception demonstrates that there may be value in utilising a study design which incorporates sites at the subplot level with a broader range of urbanisation values, model comparisons largely confirm that the SPEEDY study design captured sufficient variation in urbanisation using three classes.

Secondly, a larger food data set would improve modelling capabilities and potentially reveal patterns not present in a smaller data set. The collection of videos during fieldwork was hampered by poor video success rates in the first season, primarily due to technical issues. Success rates were improved in the second season of filming with a few modifications to camera installation procedures.

It also is important to note that several other aspects, beyond the scope of this study, contribute to the dynamics of city environments and potentially the degree to which they act as ecological traps. Factors such as predation, light, temperature and fragmentation have important roles to play and need to be accounted for in developing a more complete urban picture. Moreover, in fully assessing ecological traps, Robertson and Hutto (2006, p.1077) argue that research needs to demonstrate three distinct aspects: first, that settling individuals exhibit a preference for one habitat over another or at least an equal preference for both; second, that a measure of fitness should differ among habitats; and third, that fitness of individuals settling in the (equally) preferred habitat should be lower than fitness in other available habitats. This thesis incorporates the second two aspects of this definition, but did not formally assess habitat preference. As such, the evidence from this thesis supports but does not demonstrate the ecological trap hypothesis. Many studies evaluating urban-rural differences lack robust measures for habitat preference (Robertson and Hutto 2006), and instead use weaker indicators of preference such as population densities in urban and rural sites (e.g. Hedblom and Söderström 2012; Stracey and Robinson 2012).

Nevertheless, this study has added clarity to the role of urban areas as ecological traps, and to the role of food in driving urban-induced changes in great tit breeding success. This provides a platform for further research. While food supplementation experiments have been performed in birds (Robb et al. 2008a; Robb et al. 2008b; Harrison et al. 2010), they have tended to address food quantity not quality (but see Nager et al. 1997). Given the importance of diet quality suggested by the findings of this study, it would be of interest to experimentally determine the role of food quality in driving breeding success. Another interesting aspect of further study would be to quantify the abundance and quality of prey types along an urban gradient, both during and outside of the breeding season. While this has been investigated (Isaksson and Andersson 2007; Wawrzyniak et al. 2015), studies tend to compare a low number of sites and lack replication. Given the potentially key role of food quality in dictating avian breeding success in urban areas, this could add signficant understanding to the field.

Urban areas as ecological traps

Urban areas can act as ecological traps when they 'bait' individuals to settle using attractive environmental cues but in reality have negative effects on fitness when compared with alternative habitats (i.e. rural habitats) (Dwernychuk and Boag 1972; Gates and Gysel 1978; Robertson and Hutto 2006). Literature suggests that cities comprise a number of elements which may bait individuals into settling, including supplementary food, an increase in available nesting and shelter sites, and accessible water (Isaksson and Andersson 2007; Robb et al. 2008b; Stracey and Robinson 2012). However, these positive cues are not representative of future conditions. This study has underlined the relative negative fitness consequences of breeding in urban areas: great tit breeding success was found to be consistently lower in urban areas as measured by a series of breeding parameters (clutch size, nestling mass and fledgling per egg). Earlier laying dates were also observed in cities. While this phenomenon is usually regarded as advantageous in the wild (Robb et al. 2008a), in urban birds it can represent a maladaptation leading to a mismatch between breeding timing and prey abundance (Lambrechts et al. 1997). Furthermore, the role of food was explored and shown to play a potentially strong role in determining the conditions which 'bait' and 'trap' birds in urban areas. Food, while likely more abundant in urban areas ('baiting') has been shown by this study to be of poorer quality and not necessarily more abundant during the breeding season. This finding is also reflected in literature (e.g. Isaksson and Andersson 2007; Wawrzyniak et al. 2015).

In short, it is likely that positive urban food and environmental cues are misrepresentative, and the reality for great tits breeding in cities is that these environments are poorer than rural counterparts with significant negative consequences on breeding success.

Acknowledgements

Several people have helped make this thesis a reality, and I would like to extend my thanks to them all:

I am grateful to my supervisor Professor Erik Matthysen for giving me the opportunity to work with the UA EvoEco research group, for helping me to establish the foundations of this Master's project, and for providing detailed, insightful and meaningful feedback on thesis drafts. I would like to extend thanks to Frank Adriaensen for his tireless help at multiple stages of this thesis, and particularly for his work in establishing fieldwork protocol, organising and collecting data, and the many hours he spent gathering, building and fine-tuning the equipment for the technical aspects of this thesis.

Several people from or associated with the University of Antwerp (and the EvoEco research group) have made valuable contributions to this project in one form or another. I would like to thank Joris Elst, Lisa Baardsen, Sofie Philtjens, Aimeric Teyssier and Milena Trosch for their assistance with field work, as well as additional advice and know-how which made the thesis process smoother. In addition, thank you to Diederik Strubbe for his GIS work, to Jonas Reijniers whose work with Matlab to edit videos undoubtedly saved me hours of additional work, and to Stefan Van Dongen for helping me overcome a stats-related hurdle. Thanks also go to the two assessors of this thesis, Professor Ivan Nijs and Professor Patrick Meire, whose feedback during the mid-project assessment was highly useful.

A big thank you to my scholarship provider Erasmus Mundus EUROSA, and the associated staff at the international office, for making my Masters in Belgium possible in the first place.

Finally, I want to thank my friends and family for their support, as their cumulative contributions and kindness have helped me immeasurably during this process. Particularly, Lisa Bloss for her never-ending supply of motivation, thoughtfulness and readiness to help. Many thanks to Jakob Katzenberger as well, whose statistical advice was as welcome as his friendship support. And last but not least, a heartfelt thank you to Laura, Rick and Francis for supporting me throughout this Master's degree.

References

Agency for Geographical Information Flanders (2016) GRBgis dataset. https://www.agiv.be/catalogus/datasetfolder/7c823055-7bbf-4d62-b55e-f85c30d53162. Accessed 25 May 2016

Ahola MP, Laaksonen T, Eeva T, Lehikoinen E (2009) Great tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. J Anim Ecol 78:1298–1306. doi: 10.1111/j.1365-2656.2009.01596.x

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

Bailly J, Scheifler R, Berthe S, et al (2016) From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. J Ornithol 157:377–392. doi: 10.1007/s10336-015-1293-3

Baker PJ, Molony SE, Stone E, et al (2008) Cats about town: is predation by free-ranging pet cats Felis catus likely to affect urban bird populations? Ibis (Lond 1859) 150:86–99. doi: 10.1111/j.1474-919X.2008.00836.x

Banbura J, Banbura M (2012) Blue tits Cyanistes caeruleus and great tits Parus major as urban habitat breeders. Int Stud Sparrows 36:66–72. doi: 10.1515/isspar-2015-0014

Bańbura M, Sulikowska-Drozd A, Kaliński A, et al (2010) Egg size variation in blue tits Cyanistes caeruleus and great tits Parus major in relation to habitat differences in snail abundance. Acta Ornithol 45:121–129. doi: 10.3161/000164510X551264

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. doi: 10.18637/jss.v067.i01

Björklund M, Ruiz I, Senar JC (2010) Genetic differentiation in the urban habitat: the great tits (Parus major) of the parks of Barcelona city. Biol J Linn Soc 99:9–19. doi: 10.1111/j.1095-8312.2009.01335.x

Both C, Visser ME, Verboven N (1999) Density-dependent recruitment rates in great tits: the importance of being heavier. Proc R Soc Lond B 266:465–469. doi: 10.1098/rspb.1999.0660

Boyce MS, Perrins CM (1987) Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142–153.

Breininger DR (1999) Florida Scrub-Jay demography and dispersal in a fragmented landscape. Auk 116:520–527. doi: 10.2307/4089384

Carpintero S, Reyes-López J (2014) Effect of park age, size, shape and isolation on ant assemblages in two cities of Southern Spain. Entomol Sci 17:41–51. doi: 10.1111/ens.12027

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69. doi: 10.1016/j.landurbplan.2004.08.007

Chamberlain DE, Cannon a. R, Toms MP, et al (2009) Avian productivity in urban landscapes: a review and meta-analysis. Ibis (Lond 1859) 151:1–18. doi: 10.1111/j.1474-919X.2008.00899.x

Clergeau P, Croci S, Jokimäki J, et al (2006a) Avifauna homogenisation by urbanisation: analysis at different European latitudes. Biol Conserv 127:336–344. doi: 10.1016/j.biocon.2005.06.035

Clergeau P, Jokima J, Snep R (2006b) Using hierarchical levels for urban ecology. Trends Ecol Evol 21:660–661. doi: 10.1016/j.tree.2006.09.001

Collins JP, Kinzig A, Grimm NB, et al (2000) A new urban ecology. Am Sci 88:416–425. doi: 10.1511/2000.5.416

Cowie R, Hinsley S (1988) Feeding ecology of great tits (Parus major) and blue tits (Parus caeruleus), breeding in suburban gardens. J Anim Ecol 57:611–626.

Cowie RJ, Hinsley SA (1987) Breeding success of blue tit and great tit in suburban gardens. Ardea1 75:81–90.

Crooks KR, Suarez A V., Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biol Conserv 115:451–462. doi: 10.1016/S0006-3207(03)00162-9

Deng WH, Gao W (2005) Edge effects on nesting success of cavity-nesting birds in fragmented forests. Biol Conserv 126:363–370. doi: 10.1016/j.biocon.2005.06.013

Deviche P, Davies S (2014) Reproductive phenology of urban birds: environmental cues and mechanisms. In: Gil D, Brumm H (eds) Avian Urban Ecology, First. Ox, Oxford, pp 98–115

Dhondt AA, Adriaensen F, Matthysen E, Kempenaers B (1990) Nonadaptive clutch sizes in tits. Nature 348:723–725.

Dhondt AA, Eyckerman R (1979) Temperature and date of laying by tits Parus spp. Ibis (Lond 1859) 121:329–331.

Dhondt AA, Kempenaers B, Adriaensen F (1992) Density dependent clutch size caused by habitat heterogeneity. J Anim Ecol 61:643–648.

Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. Trends Ecol Evol 11:255–260. doi: 10.1016/0169-5347(96)20047-3

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Dwernychuk LW, Boag DA (1972) Ducks nesting in association with gulls - an ecological trap? Can J Zool 50:559–563.

Eeva T, Ryömä M, 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 JP, et al (2008) Environmental pollution affects the plumage color of great tit nestlings through Carotenoid Availability. Ecohealth 5:328–337. doi: 10.1007/s10393-008-0184-y

Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. Ibis (Lond 1859) 151:19–39. doi: 10.1111/j.1474-919X.2008.00898.x

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Environ Syst 34:487–515. doi: 10.1146/132419

Fernández-Juricic E, Jokimäki J (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodivers Conserv 10:2023–2043.

Fox J (2003) Effect displays in R for generalised linear models. J Stat Softw 8:1–27. doi: 10.2307/271037

Friesen LE, Eagles PFJ, Mackay RJ (1995) Effects of residential development on forest-dwelling neotropical migrant songbirds. Conserv Biol 9:1408–1414.

Garnett MC (1981) Body size, its heritability and influence on juvenile survival among great tits, Parus major. Ibis (Lond 1859) 123:31–41.

Gates JE, Gysel LW (1978) Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv 106:91–100. doi: 10.1016/S0006-3207(01)00232-4

Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol Evol 25:90–98. doi: 10.1016/j.tree.2009.07.016

Goodenough AE, Elliot SL, Maitland DP, Hart AG (2009) Variation in the relationship between lay date and clutch size in three cavity-nesting woodland passerines. Acta Ornithol 44:27–36. doi: 10.3161/000164509X464858

Gosler A (1993) The Great Tit. Reed International Books Limited, London

Gosler A (1987) Some aspects of bill morphology in relation to ecology in the great tit Parus major. University of Oxford

Gosler A, Clement P, Christie DA (2013) Great Tit (Parus major). In: del Hoyo J, Elliott A, Sargatal J, et al. (eds) Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona,

Haggard WH (1990) Urban weather. Int J Environ Stud 36:73–82.

Hamer AJ, McDonnell MJ (2008) Amphibian ecology and conservation in the urbanising world: a review. Biol Conserv 141:2432–2449. doi: 10.1016/j.biocon.2008.07.020

Hargitai R, Nagy G, Nyiri Z, et al (2016) Effects of breeding habitat (woodland versus urban) and metal pollution on the egg characteristics of great tits (Parus major). Sci Total Environ 544:31–38. doi: 10.1016/j.scitotenv.2015.11.116

Harrison TJE, Smith J a., Martin GR, et al (2010) Does food supplementation really enhance productivity of breeding birds? Oecologia 164:311–320. doi: 10.1007/s00442-010-1645-x

Hedblom M, Söderström B (2012) Effects of urban matrix on reproductive performance of Great Tit (Parus major) in urban woodlands. Urban Ecosyst 15:167–180. doi: 10.1007/s11252-011-0204-5

Helden AJ, Stamp GC, Leather SR (2012) Urban biodiversity: comparison of insect assemblages on native and non-native trees. Urban Ecosyst 15:611–624. doi: 10.1007/s11252-012-0231-x

Horak P, Lebreton J-D (1998) Survival of adult Great Tits Parus major in relation to sex and habitat: a comparison of urban and rural populations. Ibis (Lond 1859) 140:205–209. doi: 10.1111/j.1474-919X.1998.tb04380.x

Hostetler M (2001) The importance of multi-scale analyses in avian habitat selection studies in urban environments. In: Marzluff JM, Bowman R, Donelly R (eds) Avian ecology and conservation in an urbanising world2. Kluwer Academic, New York, pp 139–154

Husby A, Nussey DH, Visser ME, et al (2010) Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (Parus major) populations. Evolution (N Y) 64:2221–2237. doi: 10.1111/j.1558-5646.2010.00991.x

Isaksson C, Andersson S (2007) Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. J Avian Biol 38:564–572. doi: 10.1111/j.2007.0908-8857.04030.x

Isaksson C, Johansson A, Andersson S (2008) Egg yolk carotenoids in relation to habitat and reproductive investment in the great tit Parus major. Physiol Biochem Zool 81:112–118.

Kempenaers B, Borgstrom P, Loes P, et al (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. Curr Biol 20:1735–1739. doi: 10.1016/j.cub.2010.08.028

Krist M (2011) Egg size and offspring quality: a meta-analysis in birds. Biol Rev Cambridge Philos Soc 86:692–716. doi: 10.1111/j.1469-185X.2010.00166.x

Kutschbach-Brohl L, Washburn BE, Bernhardt GE, et al (2010) Arthropods of a semi-natural grassland in an urban environment: the John F. Kennedy International Airport, New York. J Insect Conserv 14:347–358. doi: 10.1007/s10841-010-9264-8

Lack D (1954) The natural regulation of animal numbers. Oxford University Press, Oxford

Lambrechts MM, Blondel J, Maistre M, Perret P (1997) A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. Proc Natl Acad Sci U S A 94:5153–5155. doi: 10.1073/pnas.94.10.5153

Leston LF V, Rodewald AD (2006) Are urban forests ecological traps for understory birds? An examination using Northern cardinals. Biol Conserv 131:566–574. doi: 10.1016/j.biocon.2006.03.003

Liker A, Papp Z, Bókony V, Lendvai ÁZ (2008) Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. J Anim Ecol 77:789–795. doi: 10.1111/j.1365-2656.2008.01402.x

Mackenzie J a., Hinsley S a., Harrison NM (2014) Parid foraging choices in urban habitat and their consequences for fitness. Ibis (Lond 1859) 156:591–605. doi: 10.1111/ibi.12166

Mägi M, Mänd R, Tamm H, et al (2009) Low reproductive success of great tits in the preferred habitat: a role of food availability. Ecoscience 16:145–157. doi: 10.2980/16-2-3215

Marri V, Richner H (2014) Yolk carotenoids increase fledging success in great tit nestlings. Oecologia 176:371–377. doi: 10.1007/s00442-014-3051-2

Marzluff JM (2001) Worldwide urbanisation and its effects on birds. In: Marzluff JM, Bowman R, Donelly R (eds) Avian ecology and conservation in an urbanising world. Kluwer Academic, New York, pp 19–48

Matthysen E, Adriaensen F, Dhondt A a. (2011) Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (Cyanistes caeruleus, Parus major). Glob Chang Biol 17:1–16. doi: 10.1111/j.1365-2486.2010.02213.x

McDonnell MJ, Hahs AK (2015) Adaptation and adaptedness of organisms to urban environments. Annu Rev Ecol Evol Syst 46:261–280. doi: 10.1146/annurev-ecolsys-112414-054258

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Ann Entomol Soc Am 93:825–835. doi: 10.1603/0013-8746(2000)093[0825:EOUAAR]2.0.CO;2

McKinney ML (2002) Urbanisation, biodiveristy and conservation.

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. doi: 10.1016/j.biocon.2005.09.005

Mennechez G, Clergeau P (2001) Settlement of breeding European Starlings in urban areas: importance of lawns vs anthropogenic wastes. In: Marzluff JM, Bowman R, Donelly R (eds) Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, New York, pp 275–287

Miller JR, Hobbs RJ (2002) Conservation where people live and work. Conserv Biol 16:330–337. doi:

10.1046/j.1523-1739.2002.00420.x

Misenhelter MD, Rotenberry JT (2000) Choices and consequences of habitat occupancy and nest site selection in sage sparrows. Ecology 81:2892–2901.

Møller AP, Erritzøe J, Karadas F (2010) Levels of antioxidants in rural and urban birds and their consequences. Oecologia 163:35–45. doi: 10.1007/s00442-009-1525-4

Mörtberg UM (2001) Resident bird species in urban forest remnants: landscape and habitat perspectives. Landsc Ecol 16:193–203. doi: 10.1023/A:1011190902041

Naef-Daenzer B, Keller LF (1999) The foraging performance of Great and Blue Tits (Parus in relation major and P . caeruleus) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim Ecol 68:708–718.

Naef-Daenzer L, Naef-Daenzer B, Nager RG (2000) Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. J Avian Biol 31:206–214. doi: 10.1034/j.1600-048X.2000.310212.x

Nager RG, Ruegger C, Noordwijk AJ Van (1997) Nutrient or energy limitation on egg formation: a feeding experiment in great tits. J Anim Ecol 66:495–507. doi: 10.2307/5944

Nour N, Currie D, Matthysen E, et al (1998) Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit). Oecologia 114:522–530. doi: 10.1007/s004420050476

Oberg M, Arlt D, Part T, et al (2014) Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. Ecol Evol 5:345–356. doi: 10.1002/ece3.1345

Pagani-Núñez E, Senar JC (2013) One hour of sampling is enough: great tit Parus major parents feed their nestlings consistently across time. Acta Ornithol 48:194–200. doi: 10.3161/000164513X678847

Partecke J, Van't Hof T, Gwinner E (2004) Differences in the timing of reproduction between urban and forest European blackbirds (Turdus merula): result of phenotypic flexibility or genetic differences? Proc R Soc London B 271:1995–2001. doi: 10.1098/rspb.2004.2821

Paton PWC (1994) The effect of edge on avian nest success: how strong is the evidence? Conserv Biol 8:17–26. doi: 10.1046/j.1523-1739.1994.08010017.x

Perrins CM (1965) Population fluctuations and clutch-size in the Great Tit, Parus major L. J Anim Ecol 34:601–647.

Perrins CM (1970) The timing of birds' breeding seasons. Ibis (Lond 1859) 112:242–255.

Perrins CM (1991) Tits and their caterpillar food supply. Ibis (Lond 1859) 133:49–54. doi: 10.1111/j.1474-919X.1991.tb07668.x

Peterson MN, Peterson MJ, Peterson TR, Liu J (2007) A household perspective for biodiversity conservation. J Wildl Manage 71:1243–1248. doi: 10.2193/2006-207

Postma E, van Noordwijk AJ (2005) Gene flow maintains a large genetic difference in clutch size at a small spatial scale. Nature 433:65–68. doi: 10.1038/nature03083

R Core Team (2015) R: A language and environment for statistical computing. http://www.r-project.org/.

Radford AN, Mccleery RH, Woodburn RJW, Morecroft MD (2001) Activity patterns of parent Great Tits Parus major feeding their young during rainfall. Bird Study 3657:214–220. doi:

10.1080/00063650109461220

Ree R, McCarthy M a. (2005) Inferring persistence of indigenous mammals in response to urbanisation. Anim Conserv 8:309–319. doi: 10.1017/S1367943005002258

Riddington R, Gosler A (1995) Differences in reproductive success and parental qualities between habitats in the Great Tit Parus major. Ibis (Lond 1859) 137:371–378. doi: 10.1111/j.1474-919X.1995.tb08035.x

Robb GN, McDonald R a, Chamberlain DE, et al (2008a) Winter feeding of birds increases productivity in the subsequent breeding season. Biol Lett 4:220–223. doi: 10.1098/rsbl.2007.0622

Robb GN, McDonald R a., Chamberlain DE, Bearhop S (2008b) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front Ecol Environ 6:476–484. doi: 10.1890/060152

Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085. doi: 10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Rytkönen S, Krams I (2003) Does foraging behaviour explain the poor breeding success of Great Tits Parus major in northern Europe? J Avian Biol 34:288–297. doi: 10.1034/j.1600-048X.2003.03041.x

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480. doi: 10.1016/S0169-5347(02)02580-6

Schoech SJ, Bridge ES, Boughton RK, et al (2008) Food suplpementation: a tool to increase reproductive output? A case study in the threatened Florida scrub-jay. Biol Conserv 141:162–173.

Seto KC, Fragkias M, Guneralp B, Reilly MK (2011) A meta-analysis of global urban land expansion. PLoS One 6:1435–1439. doi: 10.1371/Citation

Shochat E, Warren PS, Faeth SH, et al (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191. doi: 10.1016/j.tree.2005.11.019

Solonen T (2001) Breeding of the Great Tit and Blue Tit in urban and rural habitats in southern Finland. Ornis Fenn 78:49–60.

Solonen T, Hilden M (2014) Breeding phenology in Great and Blue Tits (Parus spp.): Are urban populations more resistant to climate change than rural ones? Ornis Fenn 91:209–219.

Stracey CM (2011) Resolving the urban nest predator paradox: The role of alternative foods for nest predators. Biol Conserv 144:1545–1552. doi: 10.1016/j.biocon.2011.01.022

Stracey CM, Robinson SK (2012) Are urban habitats ecological traps for a native songbird? Season-long productivity, apparent survival, and site fidelity in urban and rural habitats. J Avian Biol 43:50–60. doi: 10.1111/j.1600-048X.2011.05520.x

Stuber EF, Grobis MM, Abbey-Lee R, et al (2014) Perceived predation risk affects sleep behaviour in free-living great tits, Parus major. Anim Behav 98:157–165. doi: 10.1016/j.anbehav.2014.10.010

Swinnen KRR, Reijniers J, Breno M, Leirs H (2014) A novel method to reduce time investment when processing videos from camera trap studies. PLoS One. doi: 10.1371/journal.pone.0098881

Tinbergen JM, Boerlijst MC (1990) Nestling weight and survival in individual great tits (Parus major). J Anim Ecol 59:1113–1127.

United Nations (2014) World Urbanization Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352). New York

Van Balen JH (1973) A comparative study of the breeding ecology of the great tit Parus major in different habitats. Ardea 61:1–93.

Van Dongen S, Backeljau S, Matthysen E, Dhondt AA (1994) Effects of habitat fragmentation on the population structure of the winter moth Operophetera brumata L. (Lepidoptera, Geometridae). Acta Oecologica 15:193–206.

Van Noordwijk AJ, McCleery RH, Perrins CM (1995) Selection for the timing of Great Tit breeding in relation to caterpillar growth and temperature. J Anim Ecol 64:451–458. doi: 10.2307/5648

Verboven N, Tinbergen JM, Verhulst SI (2001) Food, reproductive success and multiple breeding in the Great Tit Parus major. Ardea 89:387–406.

Visser ME, Adriaensen F, Van Balen JH, et al (2003) Variable responses to large-scale climate change in European Parus populations. Proc R Soc B Biol Sci 270:367–372. doi: 10.1098/rspb.2002.2244

Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172.

Vriens L, Bosch H, De Knijf G, et al (2011) De Biologische Waarderingskaart. Biotopen en hun verspreiding in Vlaanderen en het Brussels Hoofdstedelijk Gewest. Het Instituut voor Natuur- en Bosonderzoek (INBO), Brussels

Wawrzyniak J, Kaliński A, Glądalski M, et al (2015) Long-Term variation in laying date and clutch size of the great tit Parus major in central Poland: A a comparisonfbetween urban parkland and deciduous forest. Ardeola 62:311–322. doi: 10.13157/arla.62.2.2015.311

Wilkin T a., King LE, Sheldon BC (2009a) Habitat quality, nestling diet, and provisioning behaviour in great tits Parus major. J Avian Biol 40:135–145. doi: 10.1111/j.1600-048X.2009.04362.x

Wilkin TA, Garant D, Gosler AG, Sheldon BC (2006) Density effects on life-history traits in a wild population of the Great Tit Parus major: analysis of long-term data with GIS techniques. J Anim Ecol 75:604–615.

Wilkin TA, Garant D, Gosler AG, Sheldon BC (2007a) Edge effects in the great tit: analyses of long-term data with GIS techniques. Conserv Biol 21:1207–1217. doi: 10.1111/j.1523-1739.2007.00767.x

Wilkin TA, Gosler AG, Garant D, et al (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 159:463–472. doi: 10.1007/s00442-008-1222-8

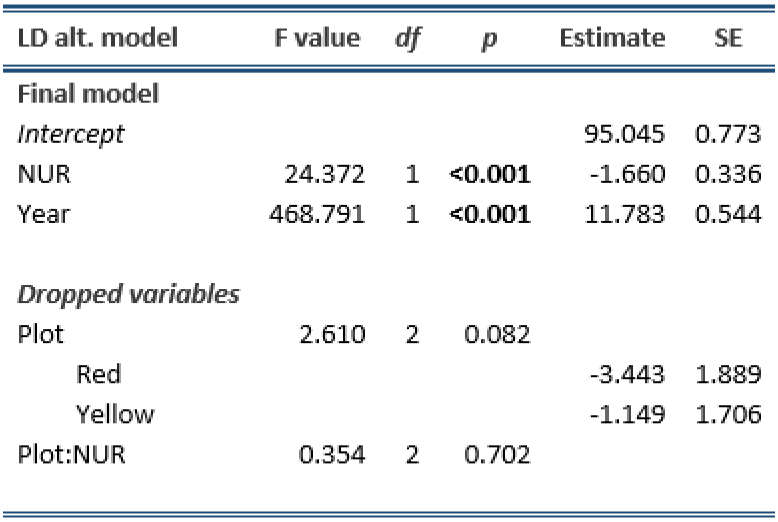
Wilkin TA, Perrins CM, Sheldon BC (2007b) The use of GIS in estimating spatial variation in habitat quality: a case study of lay-date in the Great Tit Parus major. Ibis (Lond 1859) 149:110–118. doi: 10.1111/j.1474-919X.2007.00757.x

Williams T (1996) Variation in reproductive effort of female zebra finches in relation to nutrient-specific dietary supplements during egg laying. Physiol Zool 69:1255–1275.

Zuur AF, Ieno EN, Walker NJ, et al (2009) Mixed effects models and extensions in ecology with R. Springer, New York

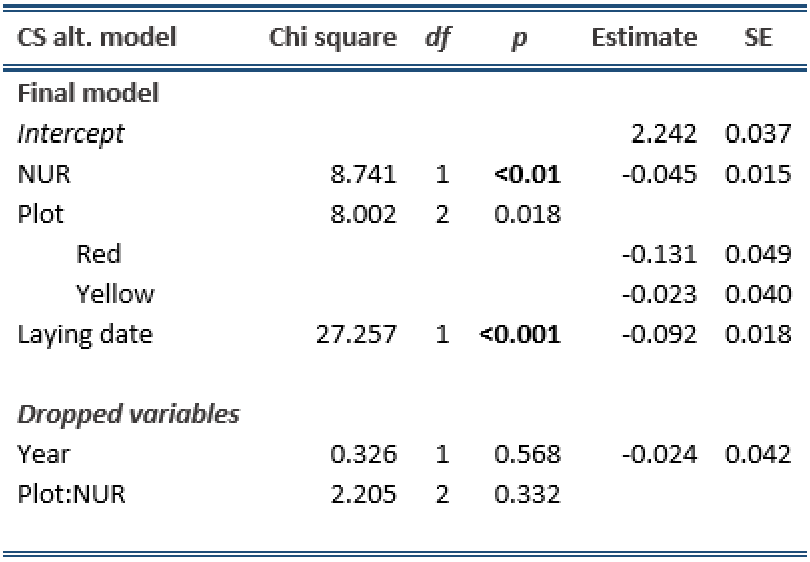
Appendix I

Table 13: GLMM summaries and analyses of variation for the effects of urbanisation and relevant breeding and measurement parameters on great tit laying dates (LD; n=421) recorded during the 2014 and 2015 breeding seasons. Dropped variables indicate terms removed in reducing full models to final models, as determined by step-wise ANOVA testing. Bold values indicate statistically significant terms (*p* < 0.05). Presented model represents 'alternate' LD model, incorporating covariate 'NUR' in place of 'subplot'



LD alt. model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				95.045	0.773
NUR	24.372	1	**<0.001**	-1.660	0.336
Year	468.791	1	**<0.001**	11.783	0.544
Dropped variables					
Plot	2.610	2	0.082		
Red				-3.443	1.889
Yellow				-1.149	1.706
Plot:NUR	0.354	2	0.702		

Table 14: GLMM summaries and analyses of variation for the effects of urbanisation and relevant breeding and measurement parameters on great tit clutch sizes (CS; n=434) recorded during the 2014 and 2015 breeding seasons. Presented model represents 'alternate' CS model, incorporating covariate 'NUR' in place of 'subplot'



CS alt. model	Chi square	*df*	*p*	Estimate	SE
Final model					
Intercept				2.242	0.037
NUR	8.741	1	**<0.01**	-0.045	0.015
Plot	8.002	2	0.018		
Red				-0.131	0.049
Yellow				-0.023	0.040
Laying date	27.257	1	**<0.001**	-0.092	0.018
Dropped variables					
Year	0.326	1	0.568	-0.024	0.042
Plot:NUR	2.205	2	0.332		

Table 15: GLMM summaries and analyses of variation for the effects of urbanisation and relevant breeding and measurement parameters on great tit mean nestling mass (MNM; n=369) recorded during the 2014 and 2015 breeding seasons. Presented model represents 'alternate' MNM model, incorporating covariate 'NUR' in place of 'subplot'

MNM alt. model	F value	*df*	*p*	Estimate	SE
Final model					
Intercept				19.289	0.540
NUR	26.319	1	**<0.001**	-0.876	0.202
Plot	4.299	2	**0.019**		
Red				-1.592	0.543
Yellow				-0.560	0.477
Brood size	19.493	1	**<0.001**	-0.207	0.047
Laying date	13.632	1	**<0.001**	-0.332	0.090
Weighing age	5.287	1	**0.022**	0.180	0.078
Dropped variables					
Laying date^2	1.162	1	0.282	0.102	0.094
Year	1.636	1	0.202	0.284	0.222
Plot:NUR	3.003	2	0.056		
Green				-0.876	0.202
Red				-0.249	0.157
Yellow				-0.493	0.181

Table 16: GLM summaries and analyses of variation for the effects of urbanisation and relevant breeding and measurement parameters on great tit nest productivity, as measured by fledglings per egg (FPE; n=403), in the 2014 and 2015 breeding seasons. Presented model represents 'alternate' FPE model, incorporating covariate 'NUR' in place of 'subplot'

FPE alt. model	Chisq	*df*	*p*	Estimate	SE
Final model					
Intercept				1.872	0.145
NUR	139.213	1	**<0.001**	-0.556	0.087
Plot	8.157	2	**0.017**		
Red				-0.388	0.239
Yellow				-0.064	0.172
Laying date	33.551	1	**<0.001**	-0.237	0.041
Plot:NUR	11.148	2	**<0.01**		
Green				-0.556	0.087
Red				-0.248	0.067
Yellow				-0.511	0.054
Dropped variables					
Laying date^2	0.914	1	0.339	0.046	0.048
Year	0.183	1	0.669	-0.045	0.106

Table 17: Degree of variance explained by random effect 'area' for full alternate breeding models. Marginal (fixed effects) and conditional (fixed and random effects) coefficients of determination (R^2) for breeding models reported

Alt. Model	Random effect variance (±SD)	Marginal R^2	Conditional R^2
LD	6.959 ± 2.638	0.53	0.63
CS	$1.292e^{-18} \pm 1.137e^{-09}$	0.12	0.12
MNM	0.399 ± 0.632	0.19	0.32
FPE	NA	0.12	NA