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Article

Urbanisation lowers great tit *Parus major* breeding success at multiple spatial scales

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While numerous studies have reported negative effects of urbanisation on birds, few have examined the role of urban scale in influencing breeding success. Furthermore, many studies have relied on qualitative rather than quantitative assessments of urbanisation. This study sought to address these issues by testing the effects of urbanisation, measured at two spatial scales, on the breeding success of great tits *Parus major*. A nested study design, incorporating over 400 nestboxes, was used in study sites across northern Belgium with a priori quantified degrees of urbanisation at both local and regional scales. All measured breeding parameters were found to vary at one or both spatial scales of urbanisation; in more urbanised areas great tits displayed advanced laying dates but lower breeding success compared to rural areas, with smaller clutch sizes, lower nestling masses and fewer fledglings per egg. Importantly, urbanisation effects were not limited to big cities as birds breeding in gardens or parks in small towns also had comparatively low success. We found that both regional- and local-scale urbanisation had consistent significant effects on laying date, clutch size and nestling mass, while the number of fledglings per egg was negatively influenced by local-scale urbanisation only. Results of this study therefore highlight the importance of utilising multiple spatial scales in analysing urbanisation effects, as well as the potential negative impact of local urbanisation on breeding success. This calls for further investigation into mechanisms driving urbanisation effects and how these may vary at different scales.

Keywords: avian, bird, city, fledgling, phenology, urban gradient

Introduction

The urbanisation of natural landscapes is accelerating worldwide, changing the physical structure, local climates and ecological processes of once natural habitats and irreversibly altering patterns of biodiversity (Marzluff 2001, McKinney 2002, Seto et al. 2011). Urban impacts on wildlife are wide-ranging; increasing household density is strongly correlated with negative effects on wildlife (Peterson et al. 2007), while urban-driven shifts in land use result in the decline and local extinction of numerous



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taxonomic groups (Ree and McCarthy 2005, Hahs et al. 2009) and drive biotic homogenisation (McKinney 2006, Aronson et al. 2014, Ibáñez-Álamo et al. 2017). The negative effects of urbanisation on birds have been well studied (Chace and Walsh 2006, Chamberlain et al. 2009, Gil and Brumm 2013) and numerous studies have reported poor breeding success in urban birds compared with their rural counterparts (Horak 1993, Mennechez and Clergeau 2006, Chamberlain et al. 2009, Seress et al. 2012, Wawrzyniak et al. 2015, Bailly et al. 2016).

While urban landscapes are markedly different from their natural surroundings (Marzluff 2001) they still encompass substantially variable habitats (Chamberlain et al. 2009). Urban environments represent a continuum 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 (Clergeau et al. 2006). A combination of urban spread and the colonisation of these new urban environments has given rise to 'urban-positive' species (Stracey 2011) – the phenomenon whereby a species occurs in higher densities in urban areas compared with their natural habitats. This phenomenon has been observed for a variety of taxa (Francis and Chadwick 2011) and is particularly well documented for several bird species (Johnston 2001, Stracey 2011, Hedblom and Söderström 2012, Stracey and Robinson 2012). In contrast, 'urban-negative' or 'absent' species occur in lower densities or are absent from urban areas (Stracey 2011) due to, for example, the removal of native vegetation (and a resulting scarcity of food sources or nesting sites) or high disturbance (McKinney 2006, Bonier et al. 2007, Croci et al. 2008).

Cities represent potentially attractive areas to urban-positive birds, offering several positive cues for habitat selection: they comprise concentrated sources of food such as bird 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 and convenient nesting sites in the form of nestboxes or crevices in houses (Reynolds et al. 2019). However, despite these positive cues, urban areas can act as 'ecological traps' (Dwernychuk and Boag 1972, Gates and Gysel 1978). This phenomenon can occur when an environmental change (e.g. urbanisation) acts to uncouple the cues that individuals use to assess the environment from its true quality; thus individuals mistakenly prefer habitats where their fitness is lower than in other available habitats (Gates and Gysel 1978, Robertson and Hutto 2006, Hale and Swearer 2016). For birds in an urban context, this can occur when individuals settle in built-up areas (rather than more natural areas) despite artificially high levels of disturbance, insufficient resources and/or novel sources of mortality (Stracey 2011, Stracey and Robinson 2012). If ecological traps are also sink habitat – areas with negative net population growth reliant on immigration from surrounding source populations to sustain their existence (Pulliam 1988) – then such traps can drive regional

populations to extinction (Kristan 2003, Robinson and Hoover 2011, Stracey and Robinson 2012).

Observations of poor breeding success of many bird species in urban areas have stimulated a growing interest in urban bird ecology (Chace and Walsh 2006, Chamberlain et al. 2009, Rodewald et al. 2011). Several studies have highlighted smaller clutch sizes (Perrins 1965, Solonen 2001, Chamberlain et al. 2009, Gładalski et al. 2015, Wawrzyniak et al. 2015) and poorer nestling condition in cities (Cowie and Hinsley 1988, Mennechez and Clergeau 2006, Chamberlain et al. 2009, Hedblom and Söderström 2012). Additionally, urbanisation effects have been found to influence avian phenology (Deviche and Davies 2014) with multiple studies having reported earlier breeding attempts in urban birds compared with rural conspecifics (Dhondt et al. 1984, Cowie and Hinsley 1987, Antonov and Atanasova 2003, Liker et al. 2008, Hedblom and Söderström 2012, Solonen and Hilden 2014, Møller et al. 2015, Wawrzyniak et al. 2015). A set of strongly contrasting environmental pressures in cities and birds' native habitats may underlie the observed differences in breeding success and phenology (McKinney 2002, Bailly et al. 2016, Marzluff et al. 2016). Widely discussed in urban ornithological literature are the respective roles of food (quality and quantity), environmental cues (such as light and temperature), predation and habitat structure (Chamberlain et al. 2009). Urban-induced changes in these factors, such as higher temperatures, greater food abundance or a reduction in native vegetation, can influence the breeding success and phenology of city birds (Table 1).

While numerous studies have sought to observe and explain urbanisation effects on birds by contrasting strongly urbanized areas with much less disturbed peripheral urban or even rural areas, few studies have examined the role of urban spatial scale. The various effects of urbanisation (e.g. changes in temperature, pollution, insect abundance, and/or nest sites) can operate at a variety of scales, each driven by unique processes (Clergeau et al. 2006, Merckx et al. 2018) and therefore may influence birds in a scale-dependent manner. The role of urban-induced temperature change illustrates this point: urban heat island effects significantly increase temperatures in urban areas over several kilometres (Deviche and Davies 2014, McDonnell and Hahs 2015) and therefore may compound local-scale temperature effects. As an example of the latter, fragmented tree cover in urban parks may allow for increased direct sunlight on nestboxes (Banbura and Banbura 2012) and thus raise nest temperatures in already warm urban micro-climates. Such scale effects become particularly interesting when examining birds breeding in highly contrasting environments; for example semi-natural forest remnants nested in the heart of highly urbanised areas, versus gardens in small built-up areas surrounded by a rural landscape. As such, to account for potential scale dependencies, urban research should attempt to include multiple spatial scales when analysing urbanisation effects (Hostetler 2001, Goddard et al. 2010).

Table 1. Changes in key factors in urban environments (relative to more rural environments), the potential underlying reasons for these changes, and the potential effects of the changes on the breeding success and phenology of great tits *Parus major* in urban areas. Arrow symbols: ↑ = increased; ↓ = decreased; → = no apparent change.

Factor	Urban habitat change	Potential reason	Potential effect
Food quantity ¹	↑ food abundance ↑ food types	Anthropogenic food sources e.g. bird feeders, refuse and exotic fruiting plants	Advanced laying dates; increased attraction to urban habitat
Food quality ²	↓ food quality ↓ caterpillar abundance	Anthropogenic food sources often energy rich but protein poor. Caterpillars limited by lack of (native) trees and vegetation	Poorer laying capacity and egg quality; poorer nestling condition and survival
Environmental cues ³	↑ temperature ↑ light	Urban 'heat island' effect maintains higher urban temperatures relative to rural surroundings. City lights artificially lengthen daily photoperiod	Advanced laying dates
Predation ⁴	↑ predator abundance → predation rate	Greater urban food availability and presence of domestic predators (e.g. cats), but supplementary food sources (e.g. refuse or deliberately provided food) may decouple predator abundance and predation rates	Increase in whole nest failures (but pattern of predation rates unclear in urban areas)
Habitat structure ⁵	↑ built habitat ↑ fragmentation ↓ (native) vegetation	Increased human population density, road density and impervious sealed surface (pavement, asphalt and buildings), increases in urban gardens and parks with managed, exotic, ornamental vegetation	Habitat loss, increase in deleterious effects of fragmentation (e.g. edge effects), poorer natural prey availability (e.g. Winter Moth <i>Operophtera brumata</i>)

¹References: Lack 1954, Perrins 1965, Cowie and Hinsley 1988, Chace and Walsh 2006, Leston and Rodewald 2006, Isaksson and Andersson 2007, Marciniak and Nadolski 2007, Robb et al. 2008a,b, Chamberlain et al. 2009, Harrison et al. 2010, Amrhein 2014, Deviche and Davies 2014, Mackenzie et al. 2014, Gładalski et al. 2015, Wawrzyniak et al. 2015.

²References: Perrins 1991, Williams 1996, Solonen 2001, Isaksson and Andersson 2007, Peach et al. 2008, Chamberlain et al. 2009, Harrison et al. 2010, Hedblom and Söderström 2012, Bailly et al. 2016, Narango et al. 2018.

³References: McKinney 2002, Partecke et al. 2004, Schochat et al. 2006, Kempnaers et al. 2010, Seto et al. 2011, Deviche and Davies 2014, Solonen and Hilden 2014.

⁴References: Gering and Blair 1999, Jokimäki and Huhta 2000, Haskell et al. 2001, Marzluff 2001, Solonen 2001, Thorington and Bowman 2003, Baker et al. 2008, Chamberlain et al. 2009, Stracey 2011.

⁵References: Friesen et al. 1995, McIntyre 2000, Naef-Daenzer et al. 2000, Fernández-Juricic and Jokimäki 2001, Mörtberg 2001, McKinney 2002, Chace and Walsh 2006, Wilkin et al. 2007, Chamberlain et al. 2009, Evans et al. 2009, Banbura and Banbura 2012, Helden et al. 2012.

In addition to the previous, many urban bird studies lack a quantitative characterisation of degree of urbanisation (Chamberlain et al. 2009), instead deriving conclusions from qualitative urban–rural contrasts, typically by comparing urban parks to forests (Isaksson and Andersson 2007, Björklund et al. 2010, Gładalski et al. 2015, Wawrzyniak et al. 2015, Bailly et al. 2016, Biard et al. 2017, Salmón et al. 2017). To address these issues, in this study we utilised a nested sampling design involving study sites with a priori quantified degrees of urbanisation at two different scales (Merckx et al. 2018). Moreover, instead of focusing on a single large city, we collected data from a large urbanised region in northern Belgium containing several large urban centres but also smaller towns and traditional rural areas. This design was used to test urbanisation effects on breeding success of great tits *Parus major* at two distinct spatial scales. Based on previous studies, we hypothesised that great tits would lay earlier, but also show poorer breeding success in all measured breeding parameters (clutch size, nestling mass and fledglings per egg and per nest) with increasing urbanisation at one or both measured spatial scales. We did not make predictions of scale-specific effects on breeding success, given a lack of information on underlying drivers at different scales (e.g. food availability).

Material and methods

Study design and data collection

Data were collected from 27 plots (each 3 × 3 km) scattered in northern Belgium, encompassing the major urban areas of Antwerp, Ghent and Brussels over two years (2014 and 2015) (Fig. 1). Plots were chosen as part of a multi-taxon research project (Brans et al. 2017, Piano et al. 2017, Merckx et al. 2018). In this design, nine plots were chosen in each of three urbanisation categories according to percentage built-up area. The choice to use built-up area as the sole criterion was driven by the need to use a general characterisation of the urban gradient that would be useful for widely different organisms and at multiple spatial scales (see below). Information on % built-up area was derived from an object-oriented reference map with precise contours of all buildings, excluding roads and parking infrastructures as a vector layer (GRB, <www.agiv.be/international/en/products/grb-en>). The cut-off points were arbitrarily defined as 0–3% built-up area for 'low' urbanisation, 5–10% for 'moderate' urbanisation and > 15% for 'high' urbanisation. Given that only buildings are considered for the calculation of percentage built-up area, values of 15% can be considered highly

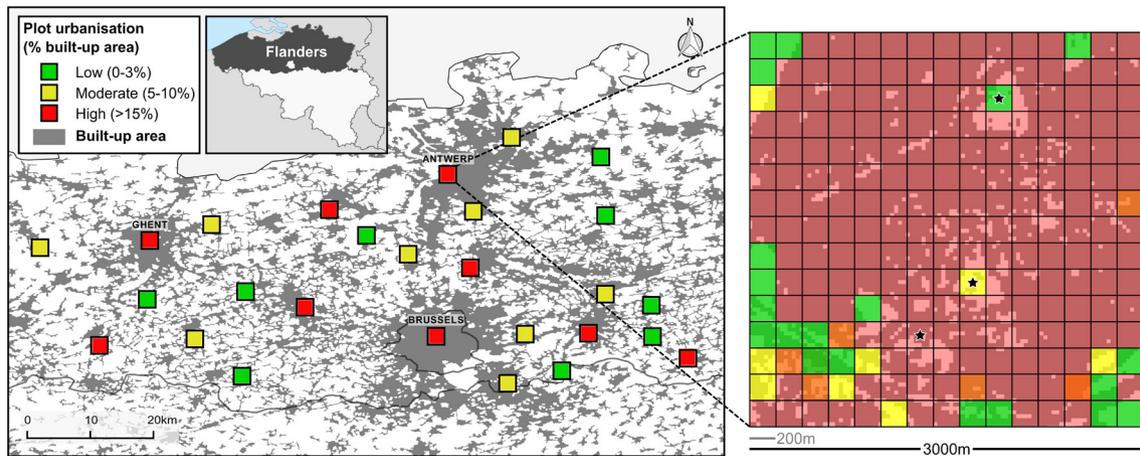


Figure 1. Left: Map of northern Belgium showing the 27 study plots (3×3 km – boxes not to scale) with degree of urbanisation in colour (based on % built up area – Agency for Geographical Information Flanders 2016). Right: enlargement of the Antwerp plot (3×3 km) with subplots (200×200 m) colour-coded in the same way as the plots (green, yellow, and red; orange subplots were intermediate [10–15% built-up area] and not used in the study) similarly overlaid on coarse-scale urban build up. Star symbols indicate subplots containing nestboxes used in this study.

urbanised. To ensure that ‘low’ urbanisation areas had high natural value and were likely to harbour local populations of multiple taxa of interest, these plots comprised > 20% ‘ecologically valuable areas’ (Vriens et al. 2011). For simplicity, the three degrees of urbanisation (low, moderate, high) are henceforth referred to as colours: low = green; moderate = yellow; and high = red. ‘Red’ plots were characteristically embedded in large to medium-sized cities or towns, ‘yellow’ plots were typically a mixture of farmland or wooded areas and small villages or residential areas, while ‘green’ plots were dominated by larger wooded areas and/or farmland. Each of the 27 plots was further divided into 200 m by 200 m subplots which were again classified into the three degrees of urbanisation (green, yellow, red) as defined above. Within each plot, nestboxes were installed (or in some cases, existing boxes were used) in at least one subplot of each urbanisation level, resulting in a total of 81 locations (3 subplots in each of the 27 plots). Thus, all locations were characterized by two hierarchical levels of urbanization (e.g. nestboxes in a small town would be in a ‘red’ 200×200 m subplot within a ‘green’ 3×3 km plot). An illustration of the land-cover in plots and subplots characterised as urban, suburban and rural can be found in Supplementary material Appendix 1.

The number of nestboxes varied among locations. For reasons of logistical feasibility and statistical power, 20 of these locations were chosen to hold a larger number of nestboxes (typically 15–20 boxes in one or possibly two adjacent subplots of the same urbanisation level). These 20 locations 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’). Due to the heterogeneous nature of the various locations in terms of size, shape and habitat (e.g. city parks or large gardens with scattered trees or large open spaces) no attempt was made to standardize nestbox densities, but

nearby boxes were typically at least 20–30 m apart regardless of urbanization level. In two cities (Ghent and Sint-Niklaas), boxes were not concentrated in a small area, but scattered in gardens and small greenspaces across the city; here, all boxes with the same urbanisation level were considered as belonging to a single location. Since we did not investigate any effects of habitat patch sizes or local population characteristics per se, nor investigated interactions between neighbouring nests, this alternative design is unlikely to have affected our results. Supplementary material Appendix 1 Table A1 gives a brief characterization of the habitat and surrounding landscape for each of these 20 locations, which accounted for 281 of all analysed nests. In each of the remaining 61 subplots three or four nestboxes were installed with the main purpose of sampling nest parasites (not a part of this study). Data on breeding success of these nests were also incorporated in the present study, adding 150 nests to the dataset. The final data set thus comprised 430 nests: 104 in green plots (according to subplot ‘colour’: 46 green, 29 yellow and 29 red), 191 in yellow plots (88 green, 71 yellow and 32 red) and 135 in red plots (30 green, 30 yellow and 75 red).

Breeding data were collected over two consecutive breeding seasons (2014 and 2015). Nestboxes were visited approximately weekly before egg laying. 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). Nestlings were ringed and weighed to the nearest 0.1 g on day 14 (or as close to day 14 as logistics allowed), the number of nestlings (alive and dead) recorded, and any unhatched eggs were noted.

Statistical analyses

Since individual parents were not ringed and pairs often re-nest in a different nestbox, we were unable to link potential second or replacement broods with a previous nesting

attempt. Conversely, we could not identify whether early failed nests were potentially compensated by replacement nests. We therefore decided to focus only on the success of first broods where at least one young hatched. First clutches were defined as all clutches laid within six weeks of the first clutch of the season (2014: day 72–114, 2015: day 78–120; $n=430$). 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 the large range of first clutch dates among plots of differing urbanisation degree. Laying dates were converted to ordinal dates (Julian day = days elapsed since 1st January).

Five response variables – laying date (LD), clutch size (CS), mean nestling mass (MNM), fledglings per egg (FPE) and fledglings per nest (FPN) – were analysed using generalised linear mixed-effects models (GLMMs) in R ver. 3.3.3 (R Core Team), using the lme4 package (ver. 1.1-12). GLMMs were fitted by restricted maximum likelihood estimation; LD, CS, MNM and FPN models were specified with normal distributions (clutch size [CS] and fledglings per nest [FPN], despite being count data, reflected a normal distribution), while the FPE model was specified with a binomial distribution. Prior to model selection, normality of model residuals was validated using quantile–quantile plots and histograms (Zuur et al. 2009). Model selection was undertaken in R using the dredge function ('MuMIn' package – Bartoń 2016) to identify the most parsimonious (henceforth 'best-fit') model (Katzenberger et al. 2015, Oleksy et al. 2019), whereby all possible combinations of variables within the full model were ranked using the second order Akaike information criterion (AICc) (Burnham and Anderson 2002). Results are reported from best-fit models, i.e. models with the lowest AICc values. Where best-fit models did not outrank competing models by $\Delta\text{AICc} > 2$, the average parameter estimates of the 'equivalent' top-ranked models (i.e. $\Delta\text{AICc} < 2$) were calculated for comparison (Symonds and Moussalli 2011, Bartoń 2016).

Full models were fitted for each response variable and were built by regressing a response variable (e.g. clutch size) against urban factor variables 'plot' (urbanisation level at a 3×3 km scale with three levels: green, yellow, red) and 'subplot' (urbanisation at a 200 m by 200 m scale with three levels: green, yellow, red), an interaction term of the two urban scales, 'year' (accounting for inter-annual variation between field seasons), a random effect 'location' (the identity of the 3×3 km plot in which nestboxes were located) and appropriate covariates (e.g. brood size) deemed important in explaining variation in the relevant response variable. Additionally, we tested full models without covariates – 'no-covariate models' – to determine whether urbanisation effects might be masked by effects on other traits (e.g. laying date or brood size).

The full LD model did not include additional individual-level covariates. The full CS model included 'laying date' (Julian day) given its potential importance in explaining variation in clutch sizes (Boyce and Perrins 1987, Kempenaers et al. 2010). MNM and FPE full models were

fitted with several additional explanatory variables; 'laying date' and 'laying date squared' (a second order polynomial term) were included as breeding success has been 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). However, the 'laying date squared' term was dropped from the binomial FPE full model to aid model convergence. 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 (mean \pm SD: 14.90 ± 0.78 , range: 9–18) and 'brood size' (number of nestlings in the nest at the time of weighing) to incorporate effects of within-nest competition between nestlings for food. The FPN model did not include any individual-level covariates, as we used this to assess overall productivity per nest.

Results

Breeding analyses were based on a data set of 430 first-clutch nests with at least one young hatched: 181 nests in 2014 and 249 nests in 2015. Laying was considerably earlier in 2014 than 2015 (average first egg laid on 3 April 2014 and 14 April 2015). The laying date model of best fit ($df=12$, $\Delta\text{AICc}=13.0$, $R^2=0.63$) showed a significant interaction term between the two urban scales, with an additional year effect (Table 2). Laying dates were observed to be earlier with increasing urbanisation at plot level, with a less clear effect of subplot level; average model-predicted laying dates within plots were 7 April in red plots, 9 April in yellow plots and 11 April in green plots. Model estimates predicted the earliest laying dates in 'yellow in red' areas and the latest laying dates in 'green in green' areas, almost six days later on average (Fig. 2).

The average clutch size (CS) across the two years was 8.5 ± 1.8 eggs (range: 4–14). The CS model of best fit ($df=8$, $\Delta\text{AICc}=3.1$, $R^2=0.31$) retained plot, subplot (no interaction) and laying date (Table 2). CS model estimates suggested progressively smaller clutches along the urban gradient at both urban scales (Fig. 3). When comparing extremes, the additive effects of both scales amounted to a difference of 1.65 eggs between green-in-green and red-in-red clutches. Additionally, clutch sizes decreased with later laying dates (Table 2). The CS model without laying date showed a significant plot effect (no subplot effects or interaction) and a significant year term (Supplementary material Appendix 1 Table A2).

The mean nestling mass (MNM) was 16.2 ± 1.8 g. The MNM model of best fit ($df=14$, $\Delta\text{AICc}=0.6$, $R^2=0.30$) retained all explanatory variables including the plot–subplot interaction, with the exception of year and laying date squared, and all variables were significant (Table 2). Model selection indicated three alternate candidate models deemed equivalent ($\Delta\text{AICc} < 2$) to the MNM best-fit model (Supplementary material Appendix 1 Table A3). Differences between candidate models were minimal; all four top-ranked models retained the same urban explanatory

Table 2. Model summaries for 'best-fit' generalised linear mixed-effects models regarding the significance of urbanisation (at plot and subplot scale) and other relevant covariates for great tit laying dates, clutch sizes, mean nestling mass and fledglings per egg.

Explanatory variables	Response variables (n)											
	Laying date (430)		Clutch size (395)		Mean nestling mass (340)		Fledglings per egg (395)					
	df, den-df	F-value	p	df, den-df	F-value	p	df, den-df	F-value	p	χ^2	p	
Subplot	2, 407	2.10	0.124	2, 252	9.25	< 0.001	2, 235	11.85	< 0.001	2	87.45	< 0.001
Plot	2, 22	4.40	0.025	2, 19	9.86	0.001	2, 22	7.00	0.004	-	-	-
Plot x Subplot	4, 405	2.53	0.040	-	-	-	4, 216	3.22	0.014	-	-	-
Year	1, 414	507.03 (12.16 ± 0.54)	< 0.001	-	-	-	-	-	-	1	46.30 (-0.63 ± 0.09)	< 0.001
Laying date	n/a	n/a	n/a	1, 389	85.06 (-0.72 ± 0.08)	< 0.001	1, 324	10.42 (-0.53 ± 0.10)	0.001	-	-	-
Laying date ²	n/a	n/a	n/a	n/a	n/a	n/a	-	-	-	n/a	n/a	n/a
Brood size	n/a	n/a	n/a	n/a	n/a	n/a	1, 328	15.65 (-0.39 ± 0.10)	< 0.001	n/a	n/a	n/a
Weighting age	n/a	n/a	n/a	n/a	n/a	n/a	1, 323	5.94 (0.20 ± 0.08)	0.015	n/a	n/a	n/a
Clutch size	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Parameter estimates and their standard errors indicated in parentheses, parameter estimates not shown for non-significant and urban scale terms (for model estimates of urbanisation effects see Fig. 3–6). Significant values ($p < 0.05$) shown in bold. 'n/a' values indicate explanatory variables not included in full/no covariate models, while '-' indicates variables not supported by best-fit models. Degrees of freedom (df) and denominator degrees of freedom (den-df) reported (Pinheiro and Bates 2006).

variables (Supplementary material Appendix 1 Table A3), and averaged parameter estimates (Table 3) showed similar trends to those of the best fit model (Table 2). Nestling mass was generally low in red plots for any level of subplot urbanization; while green subplots nested within green and yellow plots contained the highest nestling masses (Fig. 4). As expected, MNM models estimated that mean nestling masses were likely to increase in smaller broods and with increasing weighing age, and decrease with later laying dates (Table 3). As for all top-ranked MNM models, the MNM no-covariate model found the plot-subplot interaction term to explain significant variation in nestling mass (Supplementary material Appendix 1 Table A2) and estimated an analogous relationship between urbanisation and nestling mass.

Nests over the two seasons produced an average of 6.3 ± 3.0 fledglings, corresponding on average to 0.73 ± 0.31 fledglings per egg. The FPE model of best fit ($df=5$, $\Delta AIC_C=0.3$, $R^2=0.21$) retained covariates subplot (no interaction) and year with both found to be significant (Table 2). Model estimates predicted an average of 0.84 fledglings per egg in green subplots compared with 0.62 in red subplots (Fig. 5). Model selection indicated an additional candidate model to the FPE best-fit model ($\Delta AIC_C=0.3$). This second-ranked FPE model retained the same urban covariates as the best-fit FPE model, but included the laying date covariate (Supplementary material Appendix 1 Table A3). Irrespective of this addition, models were highly similar in their estimation of subplot-scale urban effects and the averaged parameter estimates maintained that the number of fledglings per egg decreased with increasing urbanisation (Table 3). The FPE model without individual-level covariates confirmed the subplot-level urbanisation effect combined with a significant year effect (Supplementary material Appendix 1 Table A2). Similarly, the FPN no-covariate model (Supplementary material Appendix 1 Table A2) found subplot-level urbanisation to explain significant variation in the number of fledglings per nest, and predicted 7.2 fledglings per nest in green subplots, 5.9 fledglings in yellow subplots and 5.0 fledglings in red subplots.

Discussion

This study provides novel insight into how great tit breeding success varies with urbanisation at two spatial scales. Results across measured breeding parameters suggest a clear negative relationship between breeding success and urbanisation at one or both measured spatial scales – with negative effects notable even at relatively low levels of urbanisation. All measured breeding parameters were significantly correlated with local (subplot) and/or regional (plot) scale urbanisation. As hypothesised, laying dates (LD) were found to be more advanced in more urbanised areas than in rural ones, a well-studied phenomenon with important repercussions (Deviche and Davies 2014). As further hypothesised, breeding success was found to be consistently lower with increasing

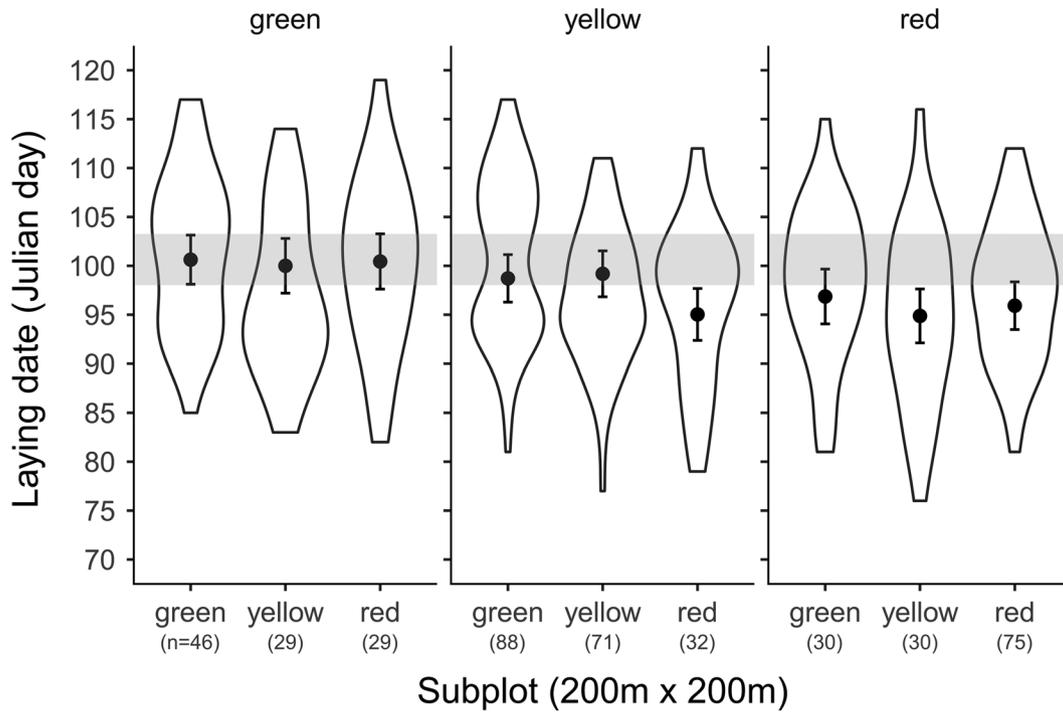


Figure 2. Model-fitted estimates (points with bars indicating 95% confidence intervals) and violin plots of great tit laying date in relation to urbanisation degree (green, yellow, red) at subplot scale, grouped by plot scale. Violin plots depict the data's distribution (kernel probability density), i.e. the width of the shape represents the proportion of the data located there. For reference, the grey-shaded area indicates the model-predicted 95% confidence interval for laying dates in 'green in green' areas. Sample size (n) indicated in brackets along the x axis. For reference, day 70 = 11th March.

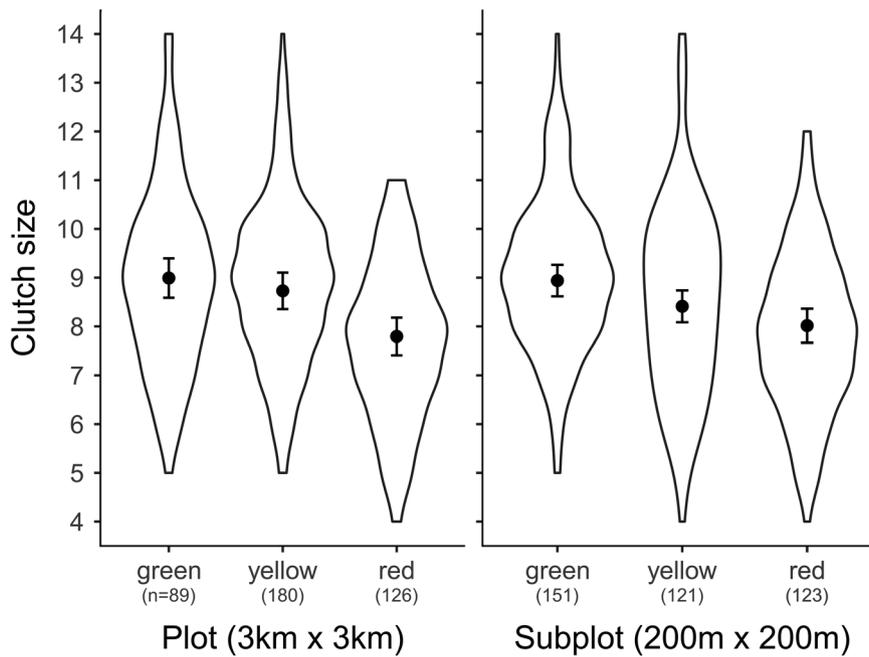


Figure 3. Model-fitted estimates (points with bars indicating 95% confidence intervals) and violin plots of great tit clutch sizes in relation to urbanisation degree (green, yellow, red) at both plot and subplot scales.

Table 3. Average parameter estimates of top-ranking equivalent models (Supplementary material Appendix 1 Table A3) for great tit mean nestling mass (MNM) and fledglings per egg (FPE).

Model	Fixed effect	Estimate	SE	z value	p
MNM	Intercept	17.334	0.336	51.40	< 0.001
	Brood size	-0.388	0.098	3.96	< 0.001
	Laying date	-0.401	0.145	2.75	0.006
	Plot				
	Yellow	-0.329	0.428	0.77	0.444
	Red	-2.133	0.497	4.28	< 0.001
	Subplot				
	Yellow	-1.945	0.447	4.34	< 0.001
	Red	-1.344	0.474	2.83	0.005
	Weighing age	0.109	0.117	0.93	0.352
	Year	0.198	0.281	0.70	0.482
	Plot × subplot				
	Yellow × yellow	1.103	0.540	2.04	0.042
	Red × yellow	2.317	0.662	3.49	< 0.001
Yellow × red	-0.323	0.622	0.52	0.605	
Red × red	0.758	0.639	1.18	0.238	
FPE	Intercept	1.987	0.185	10.69	< 0.001
	Laying date	-0.042	0.065	0.65	0.52
	Subplot				
	Yellow	-0.838	0.125	6.70	< 0.001
	Red	-1.187	0.132	8.94	< 0.001
	Year	-0.574	0.131	4.39	< 0.001

Low-level urbanisation (i.e. Green) set as the reference category. Significant values ($p < 0.05$) shown in bold. SE standard error.

urbanisation, as reflected by smaller urban clutch sizes (CS), lower mean nestling masses (MNM), and fewer fledglings per egg (FPE) when compared with more rural areas along the urbanisation gradient. Mean nestling mass, an important predictor of fledging success (Tinbergen and Boerlijst 1990), decreased with urbanization at both scales, highlighting that negative urbanisation effects on breeding success are not limited to large cities but also extend to localised areas of urban build-up such as suburban settlements or even small residential areas outside major cities.

The finding that urbanisation lowers the breeding success in great tits – a potential model study species for many urban passerines – is an anticipated phenomenon which aligns with previous studies (Chamberlain et al. 2009). Importantly, this study confirmed that urbanisation effects persisted throughout the breeding season; models without individual-level covariates confirmed that the ‘gross’ effects of urbanisation were evident at subsequent stages of the breeding cycle. This rules out the possibility that effects early in the breeding season, on laying date or clutch size for example, are compensated for at a later stage in the breeding season at least regarding first clutches. While urban scale interactions were present (for LD and MNM), their effects were relatively

subtle and did not markedly change the overall influence of additive urban scale effects.

Our study highlights that urbanisation effects are not confined to major cities, but that birds breeding in small residential areas are also negatively affected by localised urbanisation, and often equally as severely as birds in broad-scale urbanised environments. For example, low nestling masses in sites with localised urban build-up in a broader rural context (‘red’ subplots in a ‘green’ plot) were comparable with highly urbanised sites such as city parks (‘red’ plots) (Fig. 4). In addition, localised urbanisation was correlated with the number of fledglings, with a relatively low average number of fledglings per egg in more urbanised settings at a local scale (Fig. 5). Importantly, several of these findings indicate how urbanisation effects can negatively influence breeding success at low levels of urbanisation (Peach et al. 2008, Seress et al. 2012), an insight often overlooked by previous urban ecology research on birds which has largely focused on dichotomous comparisons of highly urbanised areas with (semi-)natural environments outside or at the periphery of major cities (Chamberlain et al. 2009, Sprau et al. 2017). Results regarding birds breeding in major cities also reveal important patterns, particularly with regards to the role of small forested areas or city parks nested in the heart of highly urbanised areas. Laying dates within highly urbanized regions were largely similar regardless of the urbanisation degree at local (subplot) level (Fig. 2), as were mean nestling masses (Fig. 4). This suggests that despite comprising > 20% ‘ecologically valuable areas’ (Vriens et al. 2011), local-scale green areas in cities are low-quality habitats – containing non-native plant species and less preferred dietary items of lower nutritional value (de Satgé unpubl., Narango et al. 2018) – and are subject to the effects of regional-scale urbanisation (Strohbach et al. 2013).

Advanced laying dates in urbanised areas, as observed in this study, are hypothesised to be caused by various factors such as increases in light, temperature and food in urban areas (Deviche and Davies 2014, Sprau et al. 2017). These factors all illustrate spatial variance in urban environments: higher urban temperatures are driven by the large-scale urban heat-island effect (McDonnell and Hahs 2015) which may compound the effects of warm urban microclimates (Banbura and Banbura 2012); increases in urban light result from regional artificial light emission or ‘sky-glow’ effects (Longcore and Rich 2004) which likely compound the effects of localised light sources such as street lamps (Kempnaers et al. 2010); and increases in urban food sources (e.g. refuse and bird feeders) are exploited by adult great tits at both regional scales (during winter and pre-laying periods) and local scales (during the breeding season) (Gosler 1993, Wilkin et al. 2009a). Our data show that advancement in laying date is largely linked with urbanization at the plot level, suggesting that factors affecting laying date operate mostly at the larger scale. However, within the intermediate category of urbanization, the most urban subplots are as early as the heavily urbanized plots, while the least urban subplots are similar to the rural plots (Fig. 2). Thus, there is still evidence for a

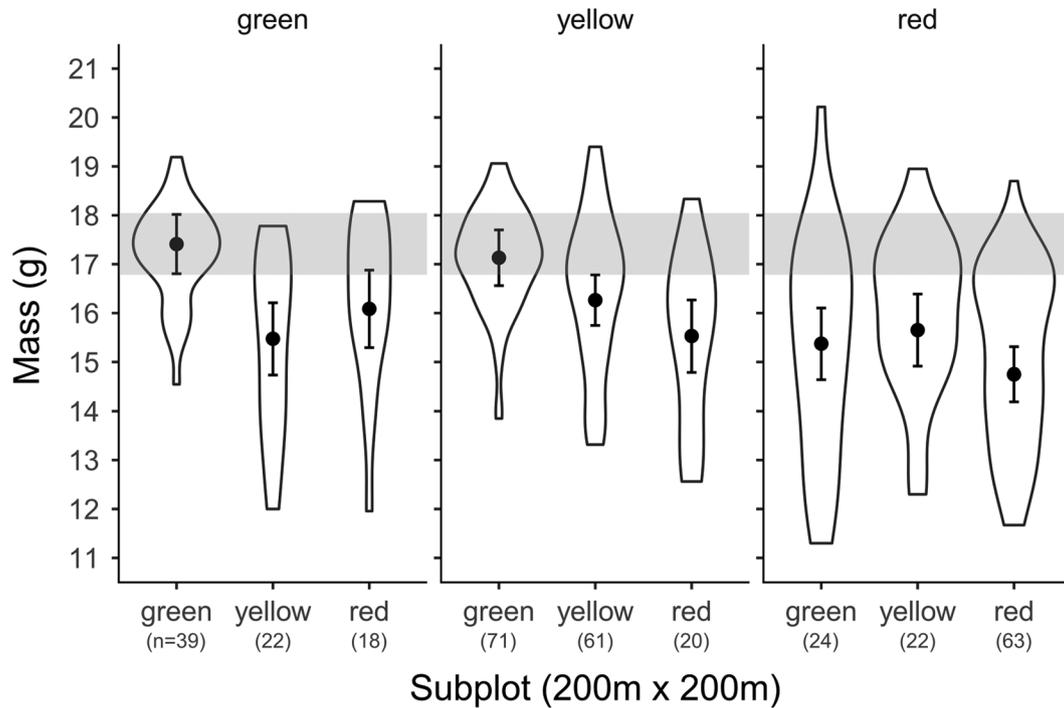


Figure 4. Model-fitted estimates (points with bars indicating 95% confidence intervals) and violin plots of great tit nestling mass in relation to urbanisation degree (green, yellow, red) at subplot scale, grouped by plot scale. For reference, the grey-shaded area indicates the model-predicted 95% confidence interval for laying dates in 'green in green' areas.

possible additive effect of low-scale urbanisation. Recently, Sprau et al. (2017) showed that differences among great tits breeding in urban and forest areas persisted after controlling for temperature, humidity, light and noise. This suggests that food abundance may be the most important driver of laying-date differences at both spatial scales. This is indirectly supported by our results on nestling condition and clutch size.

Our results found smaller clutch sizes with increasing levels of urbanisation, with clearly additive effects at regional

and local scale, but only in the model controlling for laying date (Fig. 3). The model without laying date shows that overall clutches decreased with regional, but not local urbanization. The phenomenon of small urban clutches has been hypothesised to be food related: despite the potential availability of supplementary food in urban environments, the poor quality of urban-sourced foods may result in a lack of key nutrients required for egg formation (Williams 1996, Bailly et al. 2016) thereby limiting clutch sizes and reducing egg quality (Isaksson et al. 2008, Banbura et al. 2010, Harrison et al. 2010). Our findings thus suggest that this effect operates mostly at a larger scale. This might be either because food availability is affected by urbanization at relatively large scale, and/or that female birds forage over relatively wide areas while building up reserves for egg laying. In winter great tits are not bound to breeding territories and may travel over 500m from roost sites to visit garden feeders in a peri-urban landscape (Matthysen unpubl.). Cox et al. (2016) showed that movements among feeders are highly influenced by features such as vegetation cover and roads. An alternative explanation which we could not test in this study, might be that birds strategically produce smaller clutches in response to lower food availability for rearing young (without success, given lower nestling mass in urban areas) and/or higher survival prospects for themselves (Sepp et al. 2018). Yet another alternative, which may also apply to other breeding success measures, is that urban areas are settled by birds of lower or different phenotypic quality (Rodhouse et al. 1997, Chamberlain et al. 2009).

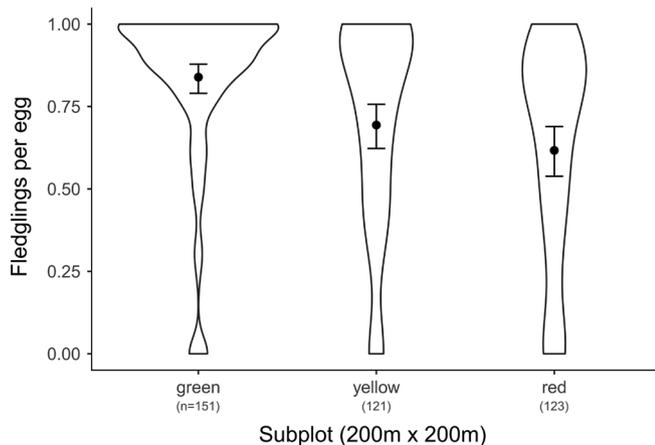


Figure 5. Model-fitted estimates (points with bars indicating 95% confidence intervals) and violin plots of great tit fledglings per egg in relation to urbanisation degree (green, yellow, red) at subplot scale.

In addition to smaller clutch sizes, we observed that nestling mass decreased with increasing urbanisation at both spatial scales (Fig. 4), a finding hypothesised to be linked with urban-driven changes in food availability. Foods obtained from anthropogenic sources like refuse or bird feeders are relatively rare in nestling diets (O’Leary and Jones 2006, Chamberlain et al. 2009) and are thus unlikely to compensate for a potential lack of natural foods – such as high-quality prey items like caterpillars – in urban areas (Marciniak and Nadolski 2007, Kaliński et al. 2009, Wawrzyniak et al. 2015, Seress et al. 2018). Indeed, analyses of 51 two to three hour video-recordings made in 2015 and 2016 on a subset of nests showed a strong reduction in proportion of caterpillars in the provisioned food in yellow (67%) and red (68%) compared to green (90%) subplots, though prey sizes did not differ significantly (de Satgé unpubl.). Urban declines in natural food sources are thought to be linked to urbanisation effects at multiple scales; localised absences of native vegetation in cities and gardens can substantially lower the presence of important arthropod species (Wilkin et al. 2009b, Helden et al. 2012, Mackenzie et al. 2014), while increases in regional levels of pollution can both change arthropod community composition (Eeva et al. 2005) and potentially result in prey items of lower nutritional value (Isaksson and Andersson 2007). A recent study using the same spatial sampling design – though not the actual locations – showed that arthropod abundance and diversity generally decreased with urbanisation but that different groups were affected by different scales (Merckx et al 2018). These authors found that macro-moths – a main source of food for great tit nestlings in natural areas (Table 1) – were comparatively strongly affected relative to other groups such as spiders or beetles, and were most sensitive to urbanisation at rather broad (3 km) scales.

While multi-scale urbanisation effects were found to influence great tit laying date, clutch size and nestling mass, nest productivity (fledglings per egg and nest) was only significantly related to localised urbanisation. However, the effect of this reduced reproductive output on fitness may be compounded by urbanisation at regional scales given that lower nestling mass is deemed to be an important factor after fledging in terms of future survival until the first breeding season (Tinbergen and Boerlijst 1990, Naef-Daenzer and Keller 1999, Bouwhuis et al. 2015). For example, long-term data on recruitment from one of our study areas in a moderately urbanized landscape (Matthysen 2002) show that a reduction in fledging mass of 2 g – equal to the difference between most and least urbanized sites – would correspond with a reduction of more than 65% in recruitment (unpubl.). In conclusion, our study suggests that urbanisation effects at different scales likely work in tandem to additively reduce breeding success of great tits at successive stages of the breeding season.

An important restriction of our study is that we did not measure productivity per season, but only for first broods that succeeded at least to the stage of hatching. Thus, we cannot fully exclude the possibility that urban birds may compensate for poor initial breeding success by successfully re-nesting later

in the breeding season. However, other studies have similarly shown poorer success in great tit second broods in urban compared to rural areas (Bailly et al. 2016, Seress et al. 2018). Furthermore, productivity of second broods – and recruitment to the next year – is typically much lower in second than first broods (Verboven and Visser 1998, Matthysen et al 2011). Conversely, we did not include data on early failed nests since we have no information which of these pairs re-nested. However, inspection of the data shows that these early failures were relatively uncommon (less than 10%) and occurred in almost all (16 out of 20) of the main study locations, so it is very unlikely that their inclusion would have changed the outcomes. Other factors than re-nesting might also potentially compensate for lower productivity, such as reduced competition among first-year birds (Reed et al. 2013). Given that we have no information on actual population densities in urban areas, especially in relation to the available resources, we cannot speculate on the role of density-dependence. We do want to point out, however, that given the strong gradients in breeding success and offspring quality over relatively short distances (i.e. urbanisation effects operating at the subplot scale) it is well possible that young birds fledging in urban conditions and in poor condition, will already compete with dispersers from more productive areas early in life, thus reducing any beneficial effects of relaxed competition.

As poor urban breeding success is unlikely to be compensated for by higher post-fledging survival or re-nesting, urban areas may be sinks reliant on immigration from surrounding source habitats (i.e. forests) to maintain their existence (Pulliam 1988, Bailly et al. 2016, Seress et al. 2018). Furthermore, if individuals show consistent preference towards sink habitats, these habitats may become ecological traps – poor quality habitats that nonetheless attract individuals despite reduced fitness relative to alternate habitats (Schlaepfer et al. 2002, Kristan 2003, Hale and Swearer 2016). For both sinks and ecological traps we expect poorer breeding success relative to alternate (source) habitats, hence our findings of reduced breeding success in urban environments relative to rural ones are compatible with both source–sink and ecological trap hypotheses. However our findings do not explicitly support these theories, since establishing whether cities are sinks requires habitat-specific information on survival and recruitment of great tits (Horak and Lebreton 1998, Seress et al. 2018), while ecological trap theory stipulates the measurement of habitat preference (Robertson and Hutto 2006).

Our findings have important implications for urban research and management. Firstly, this study makes a strong case for re-evaluating the relationship between urbanisation and breeding success by including multiple spatial scales. While several studies have compared avian breeding success between rural and urban areas (Solonen 2001, Isaksson and Andersson 2007, Björklund et al. 2010, Gładalski et al. 2015, Wawrzyniak et al. 2015, Bailly et al. 2016) and some along urbanisation gradients (Peach et al. 2008, Brahmia et al. 2013), the majority lack information regarding spatial scale, thereby excluding the potential for additive urban effects or

local–regional urbanisation interactions. Secondly, this study highlights the importance of a quantitative definition for urbanisation (Marzluff 2001, Chamberlain et al. 2009); the fluid use of the term ‘urban’ among various studies incorporates a variety of inconsistent classifications across studies, making cross-study comparisons challenging (Moll et al. 2019). To improve the development of urban ecological theory and enable comparison among studies, Moll et al. (2019) propose that urban ecological studies follow conceptual frameworks which identify: (a) the urban component measured (this study: built structures), (b) the method of measurement (this study: a singular measurement – the proportion of built-up area), (c) the metric’s spatial scale (this study: two explicitly defined scales) and (d) the metric’s temporal nature (this study: a static snapshot of urban build-up). In this study, we chose a single structural component (buildings) rather than multiple (green, grey, blue) components as advocated by Moll et al. (2019), driven by the need for a simple metric that could be easily quantified at multiple spatial scales. Similar built-structure urban classifications have been used in many other studies (Coelho et al. 2012, Hager et al. 2012, Calegaro-Marques and Amato 2014, Vaugoyeau et al. 2016); and built-up area correlates strongly with other land-cover types across our study plots (Supplementary material Appendix 1). We nevertheless agree with Moll et al. (2019) that there is a need to evaluate multiple metrics at multiple scales, but this was not feasible within our study. Thirdly, our study makes apparent that spatial variation of key urban factors such as light, temperature and food is likely highly relevant to understanding poor avian breeding success in cities and requires further investigation. Finally, given that our findings indicate that urbanisation, even at low levels, has negative effects on breeding performance of great tits, there are important implications for urban management. For example, the public should be aware that the placement of nest boxes in (sub-) urban environments does not guarantee the support of urban bird populations, given the negative consequences on fledging success and the potential for increased nestling starvation. Moreover, campaigns which advocate the distribution of urban nestboxes should simultaneously promote the planting of native trees or other measures of enhancing insect populations (Seress et al. 2018). Our results also show that remnant patches of forest in highly urbanised areas are unlikely to buffer the effects of surrounding urbanisation, giving weight to the argument that large-scale native forest patches should be protected.

Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.xgxd254bw>> (de Satgé et al. 2019).

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Conflict of interest – The authors declare that they have no conflict of interest.

Author contributions – The research idea was conceptualised by EM. The sampling design was developed and coordinated by DS and FA with input from EM, JE and JDL. JE, FA and JDL contributed to data collection in the field. FA was responsible for environmental variables and quality control of the final dataset. JDS performed statistical analyses and wrote the majority of the manuscript, with input and editorial guidance from EM. All authors provided input to draft versions of the manuscript.

Permits – All applicable institutional and/or national guidelines for the care and use of animals were followed. The ANB (Agentschap Natuur & Bos) permit number for research was ANB/BL/FF-V13-00194.

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Supplementary material (available online as Appendix jav-02108 at <www.avianbiology.org/appendix/jav-02108>). Appendix 1.