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Breeding phenology in Great and Blue Tits (*Parus* spp.): are urban populations more resistant to climate change than rural ones?

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Urbanization and climate change are two environmental factors that have most prominently affected breeding phenology of birds during recent decades. We examined such relationships in rural, suburban and urban nest box populations of Great Tits *Parus major* and Blue Tits *P. caeruleus* in the capital region of Finland in the 1980s and 1990s. We expected that mild winters and high spring temperatures may advance the breeding season of tits, but less so in urban habitats, where breeding should in any case start earlier than elsewhere. On average, Blue Tits began egg laying a few days earlier in spring than Great Tits. Contrary to expectations, tits bred later in the urban parks of the city than in other habitats, whereas breeding was earliest in suburban areas. It seems that these intermediate habitats, in some way, offer the advantages of both rural and urban habitats. During the study period, the timing of breeding in tits showed advancing temporal trends in rural habitats, and in the Blue Tit also in urban habitats. The effect of increasing winter temperatures on laying dates was mainly minor, but a significant delay emerged in urban Great Tits. The main effect of increasing April temperatures on laying dates was a significant advancement. In urban habitats, however, the advancing effect was in Great Tits significantly stronger and in Blue Tits significantly weaker than in other habitats. The results suggest that breeding of tits may advance also with warming climate but some urban populations might be more resistant to climate change than rural ones.

1. Introduction

Timing of breeding in birds is primarily determined by the prevailing food and weather conditions (Perrins 1970, Drent & Daan 1980, Daan *et al.* 1989, Newton 1998, Dunn 2004). In addition to the photoperiodic cues (e.g., Rowan 1926, Chmielewski *et al.* 2013), the rise of ambient temperatures after winter to a certain level seems to be the common key factor activating reproductive behaviour (von Haartman 1963, Lofts & Murton 1968, Crick *et al.* 1997, Sokolov & Payevsky 1998, Dunn & Winkler 1999, Svensson 2004, Both *et al.* 2005). Early onset of breeding seems to be a favourable trait evolved to ensure the best feeding conditions for the forthcoming young (e.g., Lack 1968, Perrins 1970, Drent & Daan 1980, Daan *et al.* 1989). It may also allow parents to produce more clutches and young within one season (e.g., Halupka *et al*. 2008, Møller *et al.* 2010). However, sudden shifts to earlier breeding may also be disadvantageous, if the peak periods for reproduction change to less suitable ones (Visser *et al.* 1998, 2004, 2012, Sanz 2003, Both *et al.* 2005, 2009, Both & Visser 2005).

Recent long-term advancements in timing of breeding in birds seem to be largely human-induced and appear either as changing spatial gradients or temporal trends. The former changes can mainly be linked with urbanization (e.g., Marzluff *et al*. 2001, Partecke *et al*. 2004, Chamberlain *et al*. 2009), while the latter can be ascribed to changes in climate (e.g., Møller *et al*. 2004, 2010). Global climate warming has been the most commonly advocated factor behind advanced breeding in birds, including Great Tits *Parus major* and Blue Tits *P. caeruleus* (e.g., Crick & Sparks 1999, Coppack & Both 2002, Sanz 2002, 2003, Visser *et al.* 2003, Both *et al.* 2004, Crick 2004, Dunn 2004, Svensson 2004, Schaefer *et al.* 2006, Leech & Crick 2007, Halupka *et al*. 2008, Chmielewski *et al.* 2013). Understanding variation among populations in their response to climate change is crucial, if we want to understand the capacity of populations to adapt to these changes in the environment.

The Great Tit and Blue Tit are two widespread bird species in rural and urban habitats of Europe (Cramp & Perrins 1993). They commonly occupy habitats in the vicinity of human settlements and regularly use the easily available food and breeding resources provided by Man (e.g., Cowie & Hinsley 1988, Schmidt 1988, Orell 1989, Solonen 2001). Great and Blue Tits seem to move into urban areas in winter, probably largely due to improved feeding conditions, and many of them settle there to breed (van Balen 1980, Orell 1989, Hõrak 1993). The numbers of both species have considerably increased during the recent decades in Finland, apparently due to intensified winter feeding at bird tables (Hildén 1990, Väisänen & Solonen 1997, Väisänen *et al.* 1998). The breeding season of the species usually starts in late April or early May across Europe (Cramp & Perrins 1993). The onset of egg laying varies depending on habitat (e.g., Hinsley *et al*. 2008, Chamberlain *et al*. 2009).

In the present study, we examined breeding phenology of rural and urban populations of Great Tits and Blue Tits in southern Finland. Our goal was to demonstrate the potential role of weather conditions parallel to global warming in timing of breeding in tits. We expected that mild winters and high spring temperatures may advance the breeding season of tits, but less so in conditions of abundant winter food supply, such as in urban habitats, where breeding in any case should start earlier than elsewhere due to the better body condition of birds (Cresswell & McCleery 2003, Visser *et al.* 2003, Partecke *et al.* 2004, Hinsley *et al*. 2008, Chamberlain *et al*. 2009). Accordingly, our predictions were as follows:

1) The urban populations of tits breed earlier than the rural ones.
2) If there are long-term trends in the laying dates of tits, they should be parallel to long-term trends in winter and spring temperatures.
3) Independently of habitat, tits breed earlier after mild winters and in warm, favourable springs.
4) The effects of climatic factors (the severity of the preceding winter and the level of prevailing spring temperatures) on the timing of breeding in tits decrease in relation to the level of urbanization due to more benign and stable climatic conditions of urbanized areas. Thus, the advancement in the timing of breeding should be less in the urban populations than in the rural ones, suggesting that urban populations were more resistant to warming climate than rural ones.

2. Material and methods

2.1. Study areas and field work

Our rural and urban study areas were situated near the southern coast of Finland (60°N, 24–25°E), about 20–25 km apart (see Fig. 1 in Solonen 2001). The rural nest box area (2.5 km^2) was established in the 1960s in the municipality of Kirkkonummi some 25 km west of Helsinki city centre (Hildén 1981, 1990). This study area consisted mainly of mixed woodland, alternating from purely coniferous hills, to predominantly deciduous forest in lowlands and near the sea. The forest was sporadically broken up by logging and more continuously by gardens of scattered residential houses and some agricultural landscape. In all, 230–257 nest boxes were monitored throughout our study period (1981–1993) in Kirkkonummi.

The urban area in Helsinki was studied during two time periods: 1981–1983 (Hildén 1988) and 1987–1993 (Solonen 2001). For the first period, 117 nest boxes were set out in urban parks of the city (Kaivopuisto–Töölönlahti area; 0.44 km^2). This study area consisted of old managed parks with planted deciduous trees, closely surrounded by densely built-up areas and intense traffic (i.e., the city centre, with virtually no suitable habitat for tits outside the parks). For the second period, in 1987–1988, 323 new nest boxes were mounted, in part to compensate for lost or deteriorated boxes from the earlier study in the urban city parks, but also to supply for two new suburban study plots (Ruskeasuo, Maunula; in total 0.31 km^2). The plots were situated within a fairly large, less managed urban park dominated by natural deciduous and coniferous trees, especially spruce *Picea*. There were moderately densely populated urban settlements in the surroundings, and roadways were situated further away from the study plots than buildings and streets were from the parks of the city area.

To ensure breeding opportunities for both bird species studied, two kinds of (standard) nest boxes were used; in each area, 75–80% of the boxes had entrance holes measuring 32 mm in diameter and floor areas of approximately 144 cm^2, while the dimensions for the rest of the boxes were 28 mm and 100 cm^2, respectively. The larger boxes are suitable for the Great Tit, while the smaller Blue Tit can use both kinds of boxes. The nest boxes were mounted at a height of about 3–4 m above ground in the urban parks and approximately at 1.5 m above ground in the rural area, where the risk for disturbance by humans was only minor. The density of nest boxes was set to a level high enough to reveal the local population fluctuations – there were always boxes that were left unoccupied. In the rural area, the average distance between boxes was 100 m, while in the urban and suburban areas it was 50 m. These densities were determined by earlier experience from studies in rural and urban habitats, which suggested that even high densities of nest boxes could not increase the numbers of tits in rural areas, not even in the most productive habitats, to such high levels as in urban areas (Solonen 1986, 2001, Hildén 1988). All the study areas can therefore be regarded as having been saturated with nest boxes. There were only a few other nest sites suitable for tits within the study areas, except for the nest boxes. The number of nest boxes remained relatively stable throughout the study periods, due to efforts to compensate for nest box losses.

Each year, the field work included at least four inspections of the nest boxes, to determine the number of boxes occupied by each species, the onset of egg laying, clutch size, hatching success, and the number of young fledged. By the last visit, old nests were removed to keep the parasite load in the nest boxes at a minimum.

In the present study, only the first clutches laid before the end of May were considered. Laying dates of the first eggs were calculated primarily on the basis of records of incomplete clutches, assuming that the laying interval between two successive eggs laid is one day. The onset of laying could in some cases also be calculated based on information on clutch size and the hatching date or the age of nestlings recorded. For analyses, the laying dates were converted to ordinal dates, beginning the first day of April. The total data included 1265 Great Tit nests (483 rural, 418 suburban, 364 urban) and 596 Blue Tit nests (330 rural, 99 suburban, 167 urban).

2.2. Statistical methods

To test the predictions, linear mixed effects models were fitted to the data (Pinheiro & Bates 2000) using the statistical package "nlme" in R (version 3.1.1; R Development Core Team 2013, Venables *et al.* 2014). The response variable consisted of the individual ordinal laying dates. The fixed effects included categorical explanatory variables "species" (Great Tit, Blue Tit) and "habitat" (rural, suburban, urban), as well as continuous variables "year" and two temperature variables. The temperature variables included an indicator of the strength of winter – the mean temperature in January, February and March – and an indicator of the weather conditions in spring – the mean temperature in April (°C). Temperatures were measured in the urban study area in Helsinki (Kaisaniemi, Finnish Meteorological Institute). "Year" and both

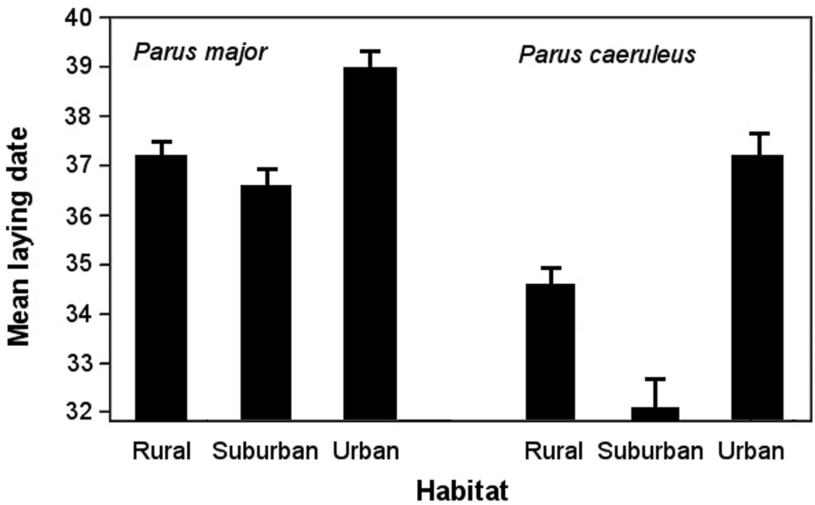

Fig. 1. Mean ordinal laying dates (beginning the first day of April) (+ SE) in the rural, suburban and urban populations of the Great Tit *Parus major* and Blue Tit *P. caeruleus* in southern Finland between 1981 and 1993. The total data included 1,265 Great Tit nests (483 rural, 418 suburban, 364 urban) and 596 Blue Tit nests (330 rural, 99 suburban, 167 urban).

temperature variables were centered to zero mean, describing average conditions. Both separate main effects and interactions between variables were considered. The territory ID, indicating impacts of the local habitat (including nest box design *etc.*) and individual birds, as well as the categorical variable "year", indicating other annually varying unknown factors, characterised random effects on the intercepts of the laying dates.

3. Results

Overall, Blue Tits began egg laying on average 2.4 days earlier than Great Tits (mean ordinal laying dates 35.3 ± 0.4 SE *vs*. 37.7 ± 0.5 SE; $t_{716} = 4.73$, $P < 0.001$). The difference was even larger in suburban parks (4.3 d), whereas in the rural area it was less (2.2 d) (Fig. 1). Blue Tits laid significantly earlier in suburban parks than in rural habitats (mean ordinal date 32.2 ± 0.7 SE *vs.* 34.6 ± 0.4 SE) and significantly later in urban parks than in rural habitats (36.7 ± 0.5 SE) (Table 1). Great Tits laid earlier in rural habitats (36.9 ± 0.4 SE) and suburban parks (36.5 ± 0.8 SE) than in the city area (39.2 ± 0.6 SE) (Table 1).

Timing of breeding in tits fluctuated considerably within and between years but significant trends emerged as well (Fig. 2, Table 1). In the Blue Tit the timing of breeding showed a signifi-

Table 1. Main effects and interaction effects (:) of species (Great Tit *Parus major* and Blue Tit *P. caeruleus*), habitat (rural, suburban, urban), and year (trend) on the laying date in tits in southern Finland between 1981 and 1993, based on a linear mixed effects model with a random intercept for territory ID (see main text for details). Random effects: SD = 0.001, residual SD = 6.659.

Fixed effects	Value	± SE	df	*t*	*P*
Blue Tit, rural (Intercept)	34.644	0.367	1368	94.512	< 0.001
Species = Great Tit	2.213	0.477	1368	4.644	< 0.001
Habitat = Suburban	–2.428	1.139	1368	–2.132	0.033
Habitat = Urban	2.013	0.659	1368	3.056	0.002
Year (Trend)	–0.439	0.089	1368	–4.928	< 0.001
Great Tit:Suburban	2.072	1.278	1368	1.622	0.105
Great Tit:Urban	0.367	0.819	1368	0.449	0.654
Great Tit:Year	–0.285	0.117	1368	–2.443	0.015
Suburban:Year	0.378	0.395	1368	0.955	0.340
Urban:Year	0.079	0.148	1368	0.536	0.592
Great Tit:Suburban:Year	0.395	0.440	1368	0.899	0.369
Great Tit:Urban:Year	0.786	0.187	1368	4.205	< 0.001

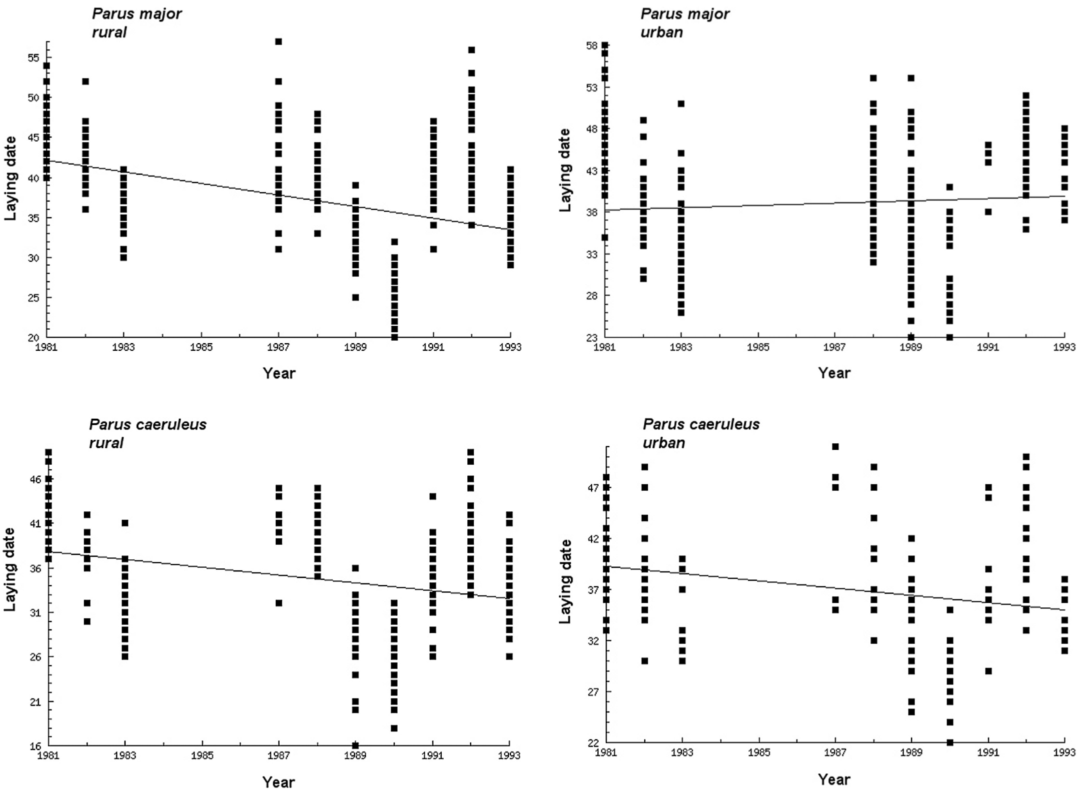

Fig. 2. Fluctuations and trends in the ordinal laying dates (beginning the first day of April) in rural and urban populations of the Great Tit *Parus major* and Blue Tit *P. caeruleus* between 1981 and 1993 in southern Finland.

cant advancing trend both in the rural ($b = -0.44 \pm 0.08$ SE, $t_{198} = -5.34$, $P < 0.001$) and urban ($b = -0.36 \pm 0.10$ SE, $t_{68} = -3.47$, $P < 0.001$) habitats but not in the suburban area ($b = -0.06 \pm 0.36$ SE, $t_{51} = -0.17$, $P = 0.865$). In the Great Tit the trend was significantly advancing in the rural habitat ($b = -0.72 \pm 0.07$ SE, $t_{310} = -9.91$, $P < 0.001$), while the relationship was not significant in the suburban ($b = 0.05 \pm 0.19$ SE, $t_{289} = 0.25$, $P = 0.800$) and urban ones ($b = 0.14 \pm 0.09$ SE, $t_{170} = 1.57$, $P = 0.119$). During the study period, there was a nearly significant increasing trend in the mean winter temperature ($t_8 = 1.75$, $P = 0.059$) but no trend in the mean temperature of April ($t_8 = 0.53$, $P = 0.305$).

The effect of increasing winter temperatures on laying dates of tits was in general minor but a significant delaying effect emerged in the Great Tit in urban habitats (Table 2). The main effect of increasing April temperatures on laying dates was a significant advancement (Table 2, Fig. 3). In urban habitats, however, the advancing effect was in the Great Tit significantly stronger and in the Blue Tit significantly weaker than in other habitats.

4. Discussion

There were significant differences in the breeding phenology of tits between species and between habitats. Blue Tits started egg laying earlier than Great Tits and in moderately urbanized habitats breeding was earlier than elsewhere. The timing of breeding fluctuated considerably but showed advancing trends both in rural and urban habitats. These trends were significant for rural and urban Blue Tits and for rural Great Tits. Similar trends, suggested to be in causal relationship to the warming of climate, have been reported from various populations of tits also elsewhere in Europe (e.g., Winkel & Hudde 1997, McCleery & Perrins 1998,

Table 2. Main effects and interaction effects (:) of species (Great Tit *Parus major* and Blue Tit *P. caeruleus*), habitat (rural, suburban, urban), and mean temperatures in winter and April (°C) on the laying date in tits in southern Finland between 1981 and 1993 based on a linear mixed effects model with a random intercept for territory ID and year (see main text for details). Random effects: SD = 1.596 and 1.812, respectively, residual SD = 4.069.

Fixed effects	Value	± SE	df	*t*	*P*
Blue Tit, rural (Intercept)	34.303	0.757	1718	45.299	< 0.001
Species = Great Tit	2.696	0.378	113	7.140	< 0.001
Habitat = Suburban	–2.101	0.648	113	–3.247	0.002
Habitat = Urban	2.628	0.554	113	4.746	< 0.001
Winter temperature	–0.415	0.280	6	–1.482	0.189
April temperature	–2.897	0.461	6	–6.286	< 0.001
Great Tit:Suburban	1.977	0.740	113	2.672	0.009
Great Tit:Urban	–0.312	0.675	113	–0.462	0.645
Great Tit:Winter temperature	–0.171	0.157	113	–1.090	0.278
Suburban:Winter temperature	0.123	0.316	113	0.388	0.699
Urban:Winter temperature	0.041	0.219	113	0.185	0.853
Great Tit:April temperature	–0.045	0.233	113	–0.195	0.846
Suburban:April temperature	–0.197	0.476	113	–0.414	0.680
Urban:April temperature	0.755	0.322	113	2.346	0.021
Winter temperature:April temperature	–0.056	0.205	6	–0.273	0.794
Great Tit:Suburban:Winter temperature	0.303	0.349	113	0.868	0.387
Great Tit:Urban:Winter temperature	1.102	0.273	113	4.038	< 0.001
Great Tit:Suburban:April temperature	–0.176	0.530	113	–0.331	0.741
Great Tit:Urban:April temperature	–0.921	0.396	113	–2.325	0.022
Great Tit:Winter temperature:April temperature	–0.114	0.104	113	–1.092	0.277
Suburban:Winter temperature:April temperature	0.430	0.256	113	1.679	0.096
Urban:Winter temperature:April temperature	–0.251	0.144	113	–1.744	0.084
Great Tit:Suburban:Winter temperature:April temperature	–0.120	0.280	113	–0.428	0.670
Great Tit:Urban:Winter temperature:April temperature	0.364	0.176	113	2.065	0.041

Sanz 2002). The short period of the present study and the large variation in laying dates and temperatures do not warrant any firm conclusions about long-term changes, but independently of habitat tits bred earlier in warm springs.

4.1. Effects of urbanization

Urbanization appears to have both advancing and delaying effects on the timing of breeding in tits. Being a widespread and still ongoing process all over the world (Marzluff *et al.* 2001, Niemelä *et al.* 2011), it drastically and continuously modifies habitats of birds in rural and wilderness areas. In spite of limiting the availability of original habitats of various species, urban habitats may provide beneficial circumstances and essential resources that are scanty elsewhere in the surroundings (e.g., Marzluff *et al.* 2001, Jones & Reynolds 2008, Solonen 2008). Therefore, urbanization may provide tempting alternative habitats for various bird species. In such conditions, birds may also be able to breed earlier than they would elsewhere (Schoech & Bowman 2001, Partecke *et al.* 2004, Chamberlain *et al*. 2009, Solonen 2014).

Contrary to our predictions, suburban populations of tits bred earliest, relative to populations in urban and rural areas. The present urban populations might, in addition to heavy urbanization, have been affected by a marine cooling effect (Solonen 2001). Excluding the extremely urban (and, in the present case, the most marine) environments, however, it can be stated that breeding early is a common phenomenon in birds breeding in moderately urban (including suburban) habitats (Cresswell & McCleery 2003, Visser *et al.* 2003, Partecke *et al.* 2004, Hinsley *et al*. 2008, Chamberlain *et al*. 2009). However, the factors that trigger early onset of breeding in urban environments are not quite clear. Possible explanations include a better general availability of food due to feeding

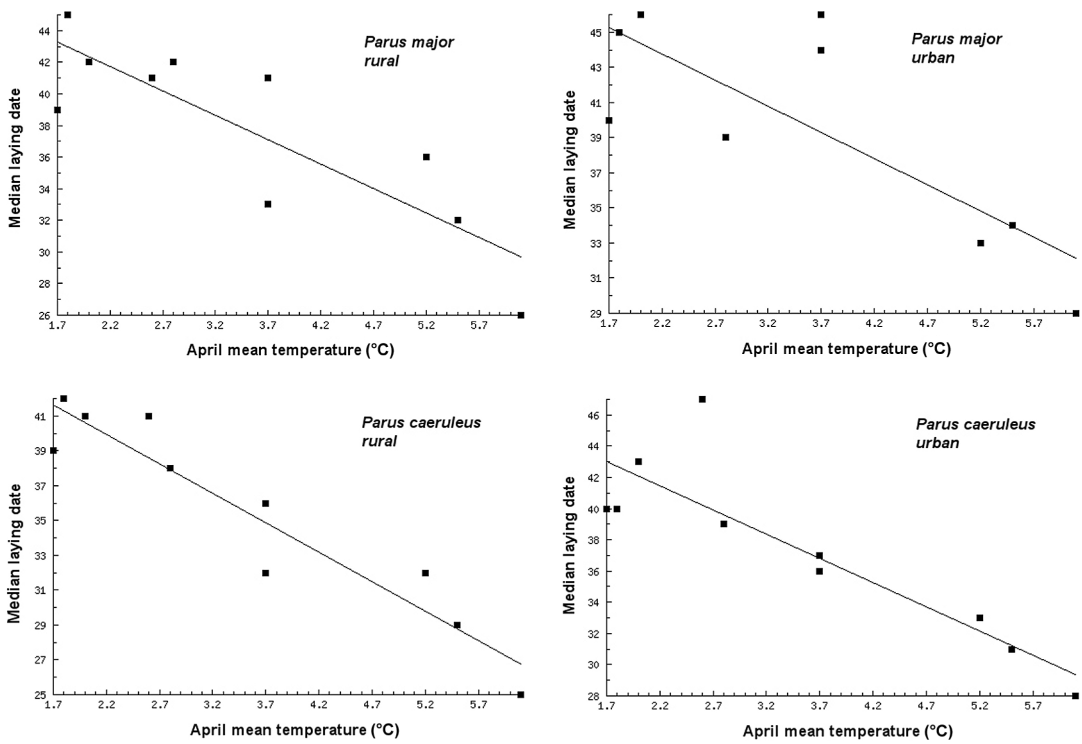

Fig. 3. Relationships between the April mean temperature (°C) and seasonal median ordinal laying dates of Great Tits *Parus major* and Blue Tits *P. caeruleus* in rural and urban habitats in southern Finland.

by humans and some other human-provided resources (e.g., van Balen 1980, Cowie & Hinsley 1988, Schmidt 1988, Orell 1989, Hõrak 1993, Solonen 2001). In addition, higher (mean) ambient temperatures (e.g., Marzluff *et al*. 2001) and anthropogenic light sources in towns and cities may physiologically activate birds earlier in spring, compared to more natural conditions (e.g., Partecke *et al*. 2004, Grandāns *et al*. 2009).

Urbanization is likely to decrease essential resources for some species and increase resources for others (e.g., Schoech & Bowman 2001). The most essential resource to birds is surely food, the availability of which may decrease or increase with urbanization. Natural foods important to birds, such as arthropods, often decline with urbanization (Blair & Launer 1997, Deny & Schmidt 1998). However, anthropogenic sources of food are often plentiful and may be readily available to birds in urban habitats (Cowie & Hinsley 1988, Schmidt 1988, Orell 1989, Chamberlain *et al*. 2005, Jones & Reynolds 2008, Robb *et al*. 2008). The increased feeding of wild birds is no doubt of profound importance in particular to urban populations of birds (Jones & Reynolds 2008). It may have for its part had an impact also on the advancement of breeding in urban tits. For many bird species, access to supplemental food often advances laying date (Boutin 1989).

Birds breeding early often enjoy a reproductive advantage, and anthropogenic foods may therefore directly benefit some species by increasing their potential fecundity (Schoech & Bowman 2001, Robb *et al*. 2008). However, the availability of anthropogenic food decreases after winter, as a result of less artificial feeding by humans in spring. Arthropod prey, essential for developing young of tits, decreases with increasing degree of urbanization (Blair & Launer 1997, Deny & Schmidt 1998). Accordingly, clutch size and fledgling production may be lower in dense populations in urban habitats than elsewhere (Perrins 1965, Berressem *et al.* 1983, Cowie & Hinsley 1987, Hõrak 1993, Solonen 2001). Thus, the final profitability of urban habitats may be questioned (e.g., Jones & Reynolds 2008, Robb *et al*. 2008, Rutz 2008, Harrison *et al*. 2010).

4.2. Effects of climatic factors

The timing of breeding in rural Great Tits and in rural and urban Blue Tits showed significantly advancing trends during the study period, but there were no clear temporal trends either in the severity of the preceding winter or in the mean temperature of April. However, the latter variable was significantly associated with the onset of laying in tits. Thus, our expectation, that mild winters and high spring temperatures might advance the breeding of tits, was partly supported by our results. Significant relationships between spring temperatures and laying dates have been demonstrated also elsewhere in various species and populations (e.g., Crick & Sparks 1999, Sanz 2002, 2003, Hussell 2003, Visser *et al.* 2003, Leech & Crick 2007, Potti 2009, Dolenec *et al.* 2011, Matthysen *et al.* 2011). These results suggest that in various cases the laying dates of birds should advance with warming climate.

There were also expected differences between habitats. Tits were less affected by climate variation in the urban area than in other habitats, suggesting that urban populations were more resistant to warming climate than rural ones. This seemed to be in accordance with recent observations of breeding having advanced according to changes in climate in many but not in all populations of a species (Visser *et al.* 2003). In England and Germany, for example, the Great Tit has shown a clear shift towards earlier breeding (Winkel & Hudde 1997, McCleery & Perrins 1998), while in the Netherlands, the same species has not altered its laying date (Visser *et al.* 1998).

4.3. Conclusions

The present study suggests, in particular, that suburban habitats profit from characteristics of both rural and urban environments, and that urbanized habitats may have some buffering influences over climatic effects. It provides some insights into how populations may vary in their responses to climate change at a relatively local scale. However, it suffers from potentially confounding effects of habitat and other gradients such as distance to the sea. Thus, there is still a need for more information on the effects of urbanization on birds, particularly into how urban versus rural birds respond to climate change at various spatial and temporal scales.

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Talitiaisen ja sinitiaisen pesinnän ajoittuminen: ovatko tiaiset kaupunkiympäristössä vähemmän alttiita ilmaston muutoksen vaikutuksille kuin maaseudulla?

Viime vuosikymmeninä lintujen pesinnän ajoittumiseen ovat vaikuttaneet voimakkaimmin kaupungistuminen ja ilmaston lämpeneminen. Tutkimme kaupungistumisen ja ilmaston lämpenemisen vaikutusten suhteita tali- ja sinitiaispopulaatioissa Helsingissä ja Kirkkonummella 1980- ja 1990-luvuilla. Odotimme, että tiaiset pesisivät leutojen talvien jälkeen ja lämpiminä keväinä aikaisemmin kuin viileämmissä olosuhteissa, ja että aikaistuminen olisi maaseudulla voimakkaampaa kuin kaupunkiympäristöissä, missä pesintä olisi (aiempiin tutkimuksiin ja havaintoihin perustuen) joka tapauksessa aikaisempaa kuin muualla.

Sinitiaiset aloittivat pesinnän keskimäärin talitiaisia aikaisemmin ja niiden pesintä aikaistui merkitsevästi tutkimusjakson (1981–1993) aikana sekä maaseudulla että kaupungissa. Talitiaisen pesintä aikaistui vain maaseudulla. Hieman odotusten vastaisesti tiaiset pesivät Helsingin ydinkeskustan puistoissa myöhemmin kuin muissa ympäristöissä. Toisaalta esikaupunkialueen puistometsissä tiaisten pesintä oli kaikkein aikaisinta. Näyttääkin siltä, että tällaiset ympäristöt voivat tarjota linnuille sekä maaseudun että kaupunkiympäristön parhaat puolet. Talven lämpötila vaikutti yleensä vain vähän tiaisten pesintäaikaan, mutta se näytti jotenkin liittyvän talitiaisen pesinnän myöhentymiseen kaupunkiympäristössä. Tiaisten muninnan aloitus myötäili merkitsevästi huhtikuun keskilämpötiloja. Kaupunkiympäristössä lämpötilan munintaa aikaistava vaikutus oli talitiaisella merkitsevästi suurempi, mutta sinitiaisella merkitsevästi pienempi kuin muissa ympäristöissä. Tulokset viittaavat siihen, että tiaisten pesintä voi aikaistua myös ilmaston lämmetessä, mutta kaupungeissa pesivät tiaiset voivat olla vähemmän alttiita ilmaston lämpenemisen vaikutuksille kuin maaseudulla pesivät lajitoverinsa.

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