GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Loss of migration and urbanization in birds: a case study of the blackbird (*Turdus merula*)

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Abstract Many organisms have invaded urban habitats, although the underlying factors initially promoting urbanization remain poorly understood. Partial migration may facilitate urbanization because such populations benefit from surplus food in urban environments during winter, and hence enjoy reduced fitness costs of migratory deaths. We tested this hypothesis in the European blackbird *Turdus merula*, which has been urbanized since the 19th century, by compiling information on timing of urbanization, migratory status, and population density for 99 cities across the continent. Timing of urbanization was spatially auto-correlated at scales up to 600 km. Analyses of timing of urbanization revealed that urbanization occurred earlier in partially migratory and resident populations than in migratory populations of blackbirds. Independently, this effect was most pronounced in the range of the distribution that currently has the highest population density, suggesting that urbanization facilitated population growth. These findings are consistent with the hypothesis that timing of urbanization is facilitated by partial migration, resulting in subsequent residency and population growth.

Keywords European blackbird · Migration · Residency · Spatial autocorrelation · Urbanization

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Introduction

Urban areas have existed for 10,000 years, but most have developed during the last 1,000 years (Francis and Chadwick 2013). Now conversion of rural habitats into urban areas happens at an unprecedented rate, with countries such as the Netherlands having more than 15 % of the surface covered by urban habitats (European Commission 2006; United Nations 2007; Schneider et al. 2009). More than half of all humans were living in urban areas in 2008 (Handwerk 2008), and this trend is predicted to increase in the near future. The current world population of close to 7 billion is projected to reach 10.1 billion in the next 90 years, reaching 9.3 billion by the middle of this century (United Nations 2011). By 2030, global urban land cover will increase to between 430,000 and 12,568,000 km^2, with an estimate of 1,527,000 km^2 most likely (Seto et al. 2011). Biological urbanization is the process by which rural species invade, become established and expand their populations in urban areas, and as such, urbanization is similar to other biological invasion processes (Croci et al. 2007; Davis 2009; Evans et al. 2010b; Møller 2013).

Many factors have been implicated in the process of urbanization (Klausnitzer 1989; Møller 2009, 2010; Evans et al. 2010a). These range from habitat choice, generalism, dispersal and lack of fear responses to human proximity, to innovation and cognitive ability. Some of these

predictions have been evaluated in comparative studies that take similarity due to common phylogenetic descent into account (Møller 2009), or by comparison of characteristics of ancestral rural and derived urban populations. Tomialojc (1976), Jerzak (2001) and Evans et al. (2010b) made pioneering collections of information on year of urbanization of wood pigeon *Columba palumbus*, magpie *Pica pica* and blackbird *Turdus merula*, showing that urbanization varied with latitude and longitude, although the nature of such latitude and longitude effects remained obscure. However, estimates from individual towns and cities are only statistically independent observations if there is no spatial auto-correlation in the data, an analysis that has so far not been considered in the study of urbanization and only rarely in the temporal analysis of biological invasions in general.

Distribution range and its correlates may predict spontaneous invasion of urban areas (Croci et al. 2007; Møller 2009, 2013). The urban heat island effect and anthropogenic feeding of birds might enable some species to expand their natural range limits. Migration may play a role in urbanization, because urbanization implies that some individuals move to new urban areas (Croci et al. 2007), and because the extent of dispersal increases with migration distance (Paradis et al. 1998; Belliure et al. 2000), even within species (Balbontín et al. 2009). Migration has a quantitative genetic basis (Berthold 2001), and populations can readily change from partially migratory (some individuals being resident and others migratory) to resident in a few generations, as shown by selection experiments (Pulido et al. 1996). Establishment of urban populations during winter could select for residency, if such urban wintering individuals enjoyed increased survival due to availability of food during winter (von Haartman 1968), milder micro-climate, and reduced mortality of resident birds compared to migratory conspecifics. Migration entails significant mortality costs (Newton 2008), and the frequency of residents and migrants can be viewed as the equilibrium reflecting the relative costs of residency and migration, respectively. Thus, we propose that an initially migratory winter population eventually becomes resident breeders, with food availability during winter causing an increase in survival prospects and hence population size. Several observations of the chain of events from partial migration to residency of urban birds are consistent with such a scenario. Högberg (1863) wrote that European blackbirds started to spend the winter in Örebro, Sweden in the 1860s, continuing until the 1950s as reported by a number of naturalists. Then some wintering birds remained until spring and started to breed, followed by the establishment of an increasing winter population (R. Gyllin pers. comm.). Likewise, in Rovaniemi, Finland, the blue tit *Parus caeruleus* started to over-winter in 1954–1955, with the first birds remaining in summer and starting to breed in 1981 (J.

Jokimäki pers. obs.). The greenfinch *Carduelis chloris* was very rare in Rovaniemi until the winter 1976–1977. After that winter, the number of wintering greenfinches increased rapidly, and in spring 1980, the species was already a common breeder (J. Jokimäki pers. obs.). Indeed, the distribution range of blue tit and greenfinch has expanded northwards because of the intensified winter feeding in Finland (Väisänen 2003; Valkama et al. 2011). Likewise, Pulliainen (1963) described how mallards *Anas platyrhynchos* started to over-winter in urban areas, followed by many of these subsequently remaining in spring and eventually starting to breed. These observations on four different species suggest that migratory birds first start to over-winter while exploiting food provided by or derived from human habitation. Subsequently, following periods of up to 90 years, as in the case of blackbirds from Sweden, some of these over-wintering individuals remain during spring and summer and reproduce in the urban environment. Initial establishment of urban populations was followed by dramatic population increases in all cases (Pulliainen 1963; von Haartman 1968; R. Gyllin pers. comm.; J. Jokimäki pers. obs.). These observations are unique because they show a sequence of events that allow inference about causation that has so far eluded studies of urbanization. Pulido (2012) and Chapman et al. (2011) showed that large amounts of genetic variation can be maintained in partially migratory populations, and the threshold of migration may be modified by environmental factors, such as availability of food, as we have suggested here. If an increase in the abundance of food allows establishment of wintering populations, this will eliminate the fitness costs of migration, further increasing population size. Indeed, because urban birds generally have much higher population densities than rural populations of the same species (Møller et al. 2012), overall population size should increase as a consequence of urbanization.

The objective of this study was to test whether migratory status predicted timing of urbanization, using the European blackbird as a model system. There is a long history of the study of urbanization of the European blackbird dating back to the 1960s (Dyrcz 1963; Gliwicz et al. 1994; Graczyk 1974; Luniak et al. 1990; Stephan 1985), with more recent contributions by Partecke et al. (2004), Partecke and Gwinner (2007) and Evans et al. (2009, 2010a, b). We used extensive information on the approximate year of urbanization of the European blackbird (from Evans et al. 2010b and our own data) to test to what extent migratory status, population density, latitude and longitude were correlated with timing of urbanization. We predicted that the transition from migration to partial migration and residency would facilitate urbanization. In addition, we predicted that such urbanization would result in an overall increase in population density. We made these tests in explicit spatial analyses that took spatial auto-correlation in response and

predictor variables into account (Legendre 1993; Lichtstein et al. 2002; Dorman et al. 2007; Diniz-Filho et al. 2008). Importantly, spatially auto-correlated data are not statistically independent, and are treated as independent constitutes pseudo-replication (Hurlbert 1984). Spatial (and temporal) autocorrelation analysis can resolve problems of statistical dependence of data (Dorman et al. 2007; Diniz-Filho et al. 2008). Here, we analyze spatial patterns of year of urbanization and population density using spatial autocorrelation analysis. First, we quantify the degree of spatial autocorrelation and the scale of such autocorrelation. Second, having found evidence of spatial autocorrelation for year of urbanization and population density, we proceed by resolving this problem by inclusion of auto-regressive terms in the analyses (Dorman et al. 2007; Diniz-Filho et al. 2008).

Materials and methods

Data

We used approximate year of urbanization of European blackbirds in different towns and cities defined as the year when blackbirds were first recorded breeding in urban areas by relying on information provided by Evans et al. (2010b) combined with our own data. In order to obtain additional data, we contacted numerous ornithologists in Portugal, Spain, Italy, France, Denmark, Norway, Sweden and Finland in order to expand this information during the period 2010–2013, and among the 52 requests sent by email, a total of 42 responded by stating that they had no data, or by providing additional data. For each location, we extracted latitude and longitude from Google. Estimated year of urbanization across a large number of different bird species based on requests to amateur ornithologists is highly repeatable among observers (Møller 2008; Møller et al. 2012), but also between observers and older published data (Møller 2008), suggesting that such information is reliable.

We classified blackbird populations with respect to migration in countries with information on timing of urbanization using a three point scale from (1) resident, when all individuals remain in the same area during breeding and winter (an example is Spain); (2) partially migratory, when a significant fraction of individuals migrates (typically 10–90 %) while the remainder stays (an example is Denmark); and (3) migratory, when all individuals migrate away from the breeding sites (an example is Finland). We used Cramp (1988) and Glutz von Blotzheim and Bauer (1988) as sources for this information, and if there was information dating back to the beginning of the nineteenth century, we used that information, because that is the period during

which urbanization mainly took place. Because blackbirds are common breeding birds throughout Europe, there is extensive information on the migratory status of different countries (review in Stephan 1985). Although there may be some arbitrariness in this classification, we relied on published and unpublished sources to obtain this information (as reported in Electronic Supplementary Material [ESM] Table S1). We see no reason why there should be any consistent bias in our classification using these predefined criteria.

We recorded current minimum and maximum breeding population sizes for all countries in Europe using Burfield and van Bommel (2004) as a source. They report the minimum and the maximum breeding population sizes for all countries, and we subsequently calculated the mean of these two estimates for the analyses presented here. Such national estimates of breeding population sizes have been used in a large number of studies, and they form the basis of national and continental conservation policy. Population density was simply the mean size of the national breeding population divided by the area of the country as reported by the CIA World Fact Book (https://www.cia.gov/library/publications/the-world-factbook/geos/html). The entire data set is reported in ESM Table S1.

Statistical analyses

We analyzed the data at the level of cities because we had estimates of year of urbanization for cities. We note that Evans et al. (2009) reported and analyzed independent events of urbanization of different cities, but did not consider spatial autocorrelation. Here, we adopted spatial autoregressive terms in our analyses to address problems of dependence due to spatial auto-correlation.

The variables were not strongly collinear, with the strongest correlation between variables only being $r = -0.49$ (year of urbanization and $\log_{10}$-transformed population density). Variance inflation factors were all below ten. The first analytical goal was to describe the spatial aggregation for the variables using Moran's I correlograms (Legendre 1993). The spatial autocorrelation value at a given distance class indicates how predictable (positively or negatively) the value of a given variable is at a given point of the sampling framework. Autocorrelation using Moran's I varies between -1 and 1, with non-significant values being close to zero. To test the significance of the autocorrelation, we estimated P values based on 500 Monte Carlo simulations.

We used general linear models and mixed models (SAS 2012) to identify factors predicting year of urbanization. The response variable was year when a town or city started to have a permanent breeding population of blackbirds, while predictor variables were migration status, population

Fig. 1 Timing of urbanization of the European blackbirds in the Western Palearctic region based on the data reported in Electronic Supplementary Material Table S1. The map shows smoothed values using the inverse distance weighting procedure (Bailey and Gatrell 1995)

1820 - 1845
1846 - 1870
1871 - 1895
1896 - 1920
1921 - 1945
1946 - 1970
1971 - 1995
1996 - 2010
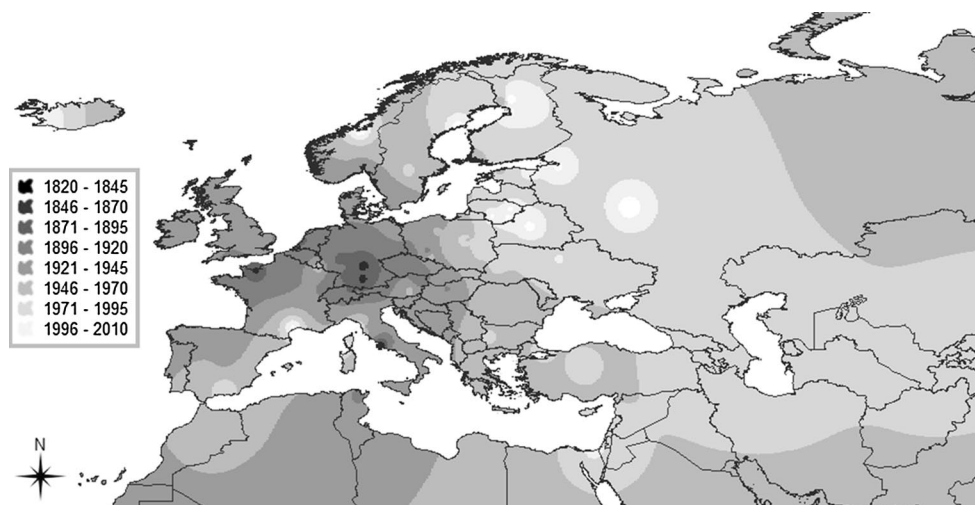
density and geographical latitude and longitude. We also included the interaction between latitude and longitude, because there is a trend in climate and hence in conditions for staying during winter from SW to NE. Population density was included to account for density-dependent effects. Latitude and longitude were included to account for other linear and quadratic spatial effects than those included in year of urbanization and population density. To take spatial autocorrelation into account, we included a spatial term that was added to the models (Dorman et al. 2007; Diniz-Filho et al. 2008). The spatial variable was defined as an autoregressive term given by ρWY, where W is the connectivity matrix, Y the response variable, and ρ the autoregressive coefficient. A spatial term was also calculated for independent variables, when necessary, and was defined as $WX\tau$, where W is the connectivity matrix, X the explanatory variable, and τ the autoregressive coefficient. Thus, our spatial model was similar to the lagged-predictor regression model (Dorman et al. 2007): $Y = \rho WY + \beta X + WX\tau + e$, where β is the estimated ordinary least square function slope and e an error term. When necessary, we used square-root or natural log-transformation to reduce the effects of outlier observations (Quinn and Keough 2002).

Spatial autocorrelograms and spatial terms were obtained in SAM 4.0 statistical software (Rangel et al. 2010). Spatial interpolation of year of urbanization was performed by the inverse distance weighting method in Quantum GIS software to illustrate the spatial pattern of urbanization (Quantum GIS Development Team 2012).

We determined final reduced models by relying on model selection based on Akaike's Information Criterion, excluding variables if they increased AICc values >2 (Burnham and Anderson 2002). All estimates of statistical parameters (means, betas) are quoted with standard errors (SE) and 95 % confidence intervals (CI).

Results

The first observation of urbanized breeding European blackbirds dates from the 1820s, when Bonaparte (1828) observed the species as breeding commonly in Rome. Early and apparently independent cases of urbanization occurred in different parts of Central Europe, as judged by areas between such early epicenters only being urbanized much later (Fig. 1). There was significant spatial auto-correlation in timing of urbanization, with year of urbanization being spatially correlated according to Moran's I at distances of up to 600 km (Fig. 2a). Migration status showed spatial auto-correlation with significant positive values up to a distance of 1,200 km (Fig. 2b). Finally, population density of blackbirds was also spatially auto-correlated with Moran's I being significant up to a distance of 1,200 km (Fig. 2c). These findings imply that neighboring populations were similar with respect to year of urbanization, migration status and population density, and that this similarity extended twice as far for migration status and population density compared to year of urbanization. In other words, urbanization took place more locally than change in migration status or population density.

The minimal model of timing of urbanization explained 62 % of the variance and included three predictors (Table 1). Partial migration was associated with earlier urbanization, residency with intermediate urbanization and migration with the latest urbanization (Fig. 3). The categories of residents and partial migrants differed significantly ($P < 0.05$) from migrants using Tukey HSD differences. In addition, urbanization occurred earlier in more dense populations, and this effect remained after inclusion of the autoregressive term. There was a strong effect of auto-regressive term of year of urbanization (Table 1), implying that year of urbanization showed evidence of spatial auto-correlation. There were no significant linear or quadratic effects
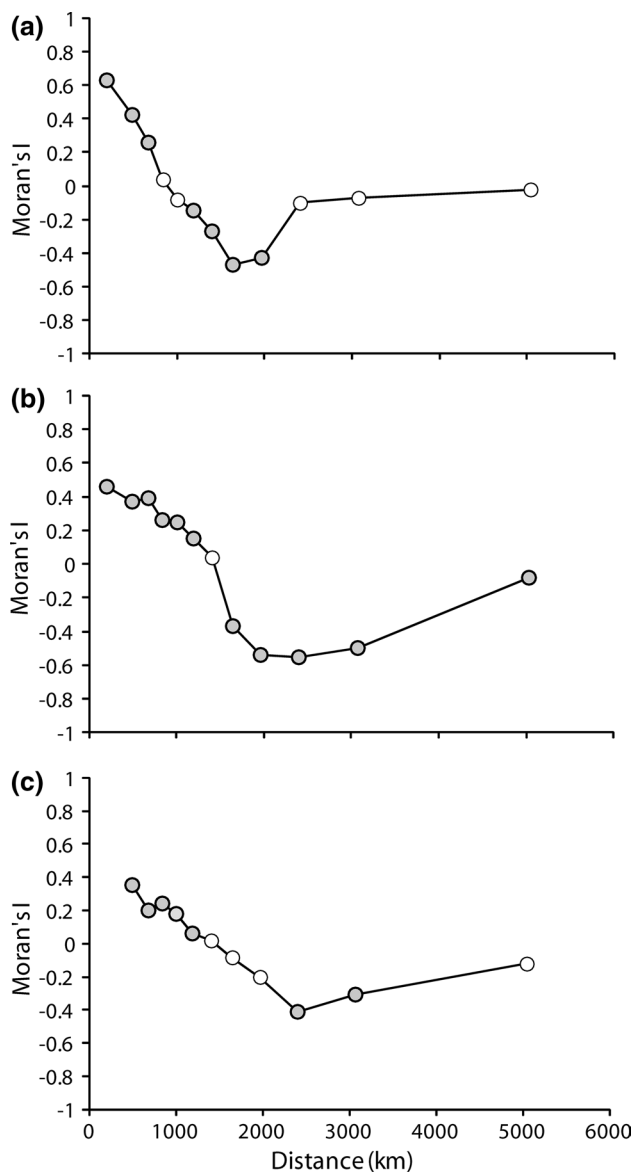
Fig. 2 Correlograms of spatial auto-correlation for **a** year of urbanization, **b** migration status and **c** population density of the European blackbird. Estimates shown in *dark color* differ significantly from zero. Values are Moran's I for different classes of distances

of latitude or longitude, or their interaction, and these variables were therefore not included in the final model (their partial effects are reported in Table 1). The extreme value for Reykjavik, Iceland was not a statistical outlier (Cook's $D = 0.02$), and exclusion of this observation did not affect the conclusions (results not shown).

Population density in different countries was explained by two factors accounting for 61 % of the variance (Table 2). Population density increased sevenfold across the range of years of urbanization, implying that population density increased with time since urbanization. In addition, there was an effect of latitude (higher density at lower latitudes), a linear, but non-significant effect of longitude (higher density at more easterly longitudes) and a quadratic effect of longitude (peak density at 18°E) (Table 2). There were no significant auto-regressive terms (Table 2). Non-significant effects are reported in Table 2.

Discussion

The main findings of this study of the spatial patterns of urbanization of the European blackbird were that year of urbanization showed significant spatial auto-correlation at a scale of 600 km and migration status and population density at a scale of 1,200 km. We included these patterns of spatial auto-correlation in analyses of the timing of urbanization, showing that migration pattern and population density explained significant variation in when different populations became urbanized. Change from migration to partial migration and residency was consistently associated with year of urbanization. The auto-regressive term for year urbanized was an important predictor of year of urbanization, showing that a spatially explicit model provides better and more detailed information than a model without this spatial effect.

The analyses of timing of urbanization that we conducted do not rely on the assumption that migration status in the past is similar to the current situation. We explicitly assigned migration status to different countries by using historical information (ESM Table S1). As concerns population density, we have shown that density increased linearly with time since initial urbanization. Indeed, year of urbanization is correlated with difference in breeding population density between neighboring urban and rural habitats of different species of birds, including the European blackbird (Møller et al. 2012). The year of urbanization of blackbirds was strongly spatially auto-correlated, as shown by a significant positive Moran's I at distances up to 600 km. This finding implies that timing of urbanization shows spatial similarity across considerable distances, and that individual records of timing of urbanization for individual cities cannot be considered statistically independent observations, as shown by our analyses of the auto-regressive term of year of urbanization. This scale of spatial auto-correlation is almost three orders of magnitude longer than the geometric mean natal dispersal distance of 0.8 km (Paradis et al. 1998). Therefore, spatial auto-correlation of that scale must reflect phenomena other than dispersal, such as the scale of climatic conditions allowing survival during winter and therefore the spatial scale at which residency is favored over migration. Interestingly, we also found spatial auto-correlation in migration status and population density, but at much longer distances of 1,200 km, implying that similarity in timing of urbanization occurred at a spatial scale

Table 1 Minimal model of year of urbanization of the European blackbird as predicted by migration status and population density ($F = 36.76$, $df = 4, 83$, $r^2 = 0.62$, $P < 0.0001$)

Variable	Sum of squares	df	F	P	Estimate (SE)
Intercept		1		<0.0001	1,943.12 (5.53)
Migration status	10,606.85	2	5.55	0.0055	
Migration status [0]		1	0.01	0.93	0.52 (5.97)
Migration status [1]		1	9.73	0.0025	−15.76 (5.06)
Density	7,528.97	1	7.87	0.0063	−16.06 (5.72)
Spatial auto-regressive year of urbanization	25,329.15	1	26.47	<0.0001	24.83 (4.83)
Error	220,103.09	83			

The spatial auto-regressive term represents the spatial auto-correlation

The effect of migration was still significant ($F = 5.75$, $df = 1, 76$, $P = 0.0047$) when latitude ($F = 0.13$, $df = 1, 76$, $P = 0.72$), latitude squared ($F = 0.20$, $df = 1, 76$, $P = 0.65$), longitude ($F = 0.38$, $df = 1, 76$, $P = 0.54$), longitude squared ($F = 0.20$, $df = 1, 76$, $P = 0.54$), latitude by longitude interaction ($F = 0.69$, $df = 1, 76$, $P = 0.41$), density ($F = 4.47$, $df = 1, 76$, $P = 0.04$), spatial auto-regressive term of migration ($F = 1.94$, $df = 1, 76$, $P = 0.17$) and spatial auto-regressive term of density ($F = 1.23$, $df = 1, 76$, $P = 0.27$) were included in the model
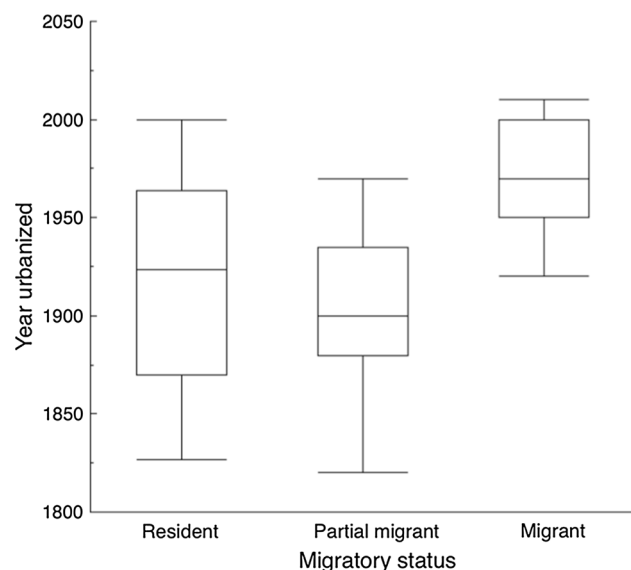
Fig. 3 *Box-plot* of year of urbanization for the three categories of migration status of the European blackbird, showing medians, quartiles and 5-percentiles and 95-percentiles

Table 2 Minimal model of population density of the European blackbird as predicted by year of urbanization, spatial auto-regressive year of urbanization, spatial auto-regressive density, latitude, latitude squared, longitude, longitude squared, and latitude by longitude interaction ($F = 34.97$, $df = 4, 83$, $r^2 = 0.61$, $P < 0.0001$)

Variable	Sum of squares	df	F	P	Estimate (SE)
Intercept		1		<0.0001	11.63 (1.98)
Year of urbanization	3.03	1	16.61	0.0001	−0.004 (0.001)
Latitude	6.53	1	35.71	<0.0001	−0.04 (0.007)
Longitude	0.28	1	1.52	0.22	0.01 (0.005)
Longitude × longitude	10.44	1	57.15	<0.0001	−0.002 (0.0002)
Error	15.17	83			

The effect of year of urbanization was still significant ($F = 6.07$, $df = 1, 79$, $P = 0.016$) when latitude ($F = 12.06$, $df = 1, 79$, $P = 0.0008$), latitude squared ($F = 0.003$, $df = 1, 79$, $P = 0.90$), longitude ($F = 5.53$, $df = 1, 79$, $P = 0.021$), longitude squared ($F = 12.56$, $df = 1, 79$, $P = 0.0007$), latitude by longitude interaction ($F = 3.56$, $df = 1, 79$, $P = 0.06$), spatial auto-regressive term of year urbanized ($F = 0.61$, $df = 1, 79$, $P = 0.44$) and spatial auto-regressive term of density ($F = 0.56$, $df = 1, 79$, $P = 0.46$) were included in the model

that was much finer than the scale at which migration status and population density varied. These observations are consistent with the hypothesis that timing of urbanization is not constrained by migration status and population density.

Year of urbanization showed a clear spatial pattern with different foci in Central and Southern Europe (Fig. 1). This finding is consistent with molecular analyses showing evidence of independent evolution of urbanization in different parts of Europe (Partecke et al. 2004; Evans et al. 2009). Migration has been suggested to play a role in urbanization of birds (Dyrcz 1963; Pulliainen 1963; Tomialojc 1976), because initial establishment of wintering populations may arise from reduced fitness loss caused by migration (Newton 2008). For example, migration has been shown

to prevent establishment of introduced species on oceanic islands (Veltman et al. 1996).

Partially migratory populations of the blackbird started to winter in urban habitats following decades of some of these wintering individuals staying to reproduce during summer. In several cases, wintering blackbirds in specific sites became residents in exactly the same sites (see "Introduction"). Such a transition was associated with exploitation of food found near human habitation or provided by humans (Dyrcz 1963; Pulliainen 1963) and reduced fear responses (Møller 2010; Díaz et al. 2013). Similar patterns were observed for mallard, greenfinch and blue tit (see "Introduction").

Many urban bird species use anthropogenic food that may help establish winter populations, as described here, and subsequently establish breeding populations (Jokimäki and Kaisanlahti-Jokimäki 2012). In the blackbird, we found significantly earlier urbanization in resident and partially migratory populations. It is likely that urbanization has been favored by loss of migration rather than long-distance migration having a negative effect on urbanization, as shown by studies of blackbirds and other species showing that urbanization facilitates residency (Berthold 2001; Partecke and Gwinner 2007; see also three examples in the "Introduction"). Blackbirds are known since long to be residents or partial migrants in urban areas and partial migrants or migrants in nearby rural areas (Stephan 1985). This raises questions about causality and whether urbanization facilitates residency or the reverse. Given our explicit review of the literature from Scandinavia in the "Introduction," we can conclude that urban breeding populations became established when wintering birds from other populations (presumably further north, where the birds are migrants) not only stayed during winter, as facilitated by availability of food provided by humans, but remained during spring and summer to reproduce. The underlying mechanism resulting in initial population growth is the elimination of mortality caused by migration (Newton 2008). Indeed, the fitness benefits of residency or partial migration can be illustrated by the exponential increase in the abundance of winter blackbirds in Finland since 1956–1957, followed by a significantly slower increase in size of the breeding population (Väisänen 2003; Valkama et al. 2011). These effects are independent of latitude and longitude as measures of spatial variation in other factors that might explain variation in timing of urbanization, because linear and quadratic effects of latitude and longitude do not enter any of the statistical models as significant predictors.

Higher population density was associated with earlier timing of urbanization independent of the effects of latitude and longitude. We found evidence of spatial auto-correlation for population density up to distances of 1,200 km. Population density predicted year of urbanization, with higher density being associated with earlier urbanization. There are two interpretations of this effect of population density at large spatial scales. First, density-dependent processes such as intraspecific competition, dispersal or parasitism may have selected for early colonization of urban areas. Second, population density may have increased as a consequence of urbanization because population densities of blackbirds in urban habitats may reach levels that exceed densities in rural habitats by more than two orders of magnitude (Dyrcz 1963; Stephan 1985; Møller et al. 2012). Our data do not allow discrimination between these two possibilities, although future analyses of spatial patterns of urbanization for other species may help resolve this question.

Urbanization had implications for population growth and hence overall population size of blackbirds in different European countries. Population density increased by 30 % across the range of years of urbanization reported here, as in urban bird populations in general (Stephan 1985; Evans et al. 2010a; Møller et al. 2012). Interestingly, there were additional effects of latitude and longitude with southern and Central European population densities being larger than northern and eastern densities. These findings are consistent with mortality costs of migration and/or mortality costs of residency in more cold climates, prevailing for instance in Northern and Eastern Europe.

There are alternative explanations for the spatial and temporal patterns of urbanization reported here. First, climate change may facilitate a change from migration to residency, because warmer winters allow residents to survive even during the part of the year when food is least abundant. Because climate is strongly related to latitude and longitude, inclusion of linear and quadratic terms of latitude and longitude should account for such effects. None of these linear or quadratic terms were retained as significant predictors of timing of urbanization in the statistical models (Møller et al. 2010). Second, urbanization may have facilitated a transition from migration to residency, reversing the causality (Berthold 2001; Partecke and Gwinner 2007). We consider this alternative explanation to be unlikely given the observations of the sequence of events reported in the "Introduction".

In conclusion, we have shown strong patterns of spatial auto-correlation of timing of urbanization by the European blackbird, migration status and population density have contributed to patterns of urbanization across the Western Palearctic, and population size has increased as a consequence of adaptation to urban environments. These patterns deserve further study in other urbanized species.

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