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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

High urban population density of birds reflects their timing of urbanization

**Anders Pape Møller · Mario Diaz · Einar Flensted-Jensen ·
Tomas Grim · Juan Diego Ibáñez-Álamo · Jukka Jokimäki ·
Raivo Mänd · Gábor Markó · Piotr Tryjanowski**

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Abstract Living organisms generally occur at the highest population density in the most suitable habitat. Therefore, invasion of and adaptation to novel habitats imply a gradual increase in population density, from that at or below what was found in the ancestral habitat to a density that may reach higher levels in the novel habitat following adaptation to that habitat. We tested this prediction of invasion biology by analyzing data on population density of breeding birds in their ancestral rural habitats and in matched nearby urban habitats that have been colonized recently across a continental latitudinal gradient. We estimated population density in the two types of habitats using extensive point census bird counts, and we obtained information on the year of urbanization when population density in urban habitats reached levels higher than that of the ancestral rural habitat from published records and estimates by experienced ornithologists. Both the difference in population density between urban and rural habitats and the year of urbanization were significantly repeatable when analyzing multiple populations of the same species across Europe. Population density was on average 30 % higher in urban than in rural habitats, although density reached as much as 100-fold higher in urban habitats in some species. Invasive urban bird species that colonized urban environments over a long period achieved the largest increases in population density compared to their ancestral rural habitats. This was independent of whether species were anciently or recently urbanized, providing a unique cross-validation of timing of urban invasions. These results

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A. P. Møller (✉)
Laboratoire d'Ecologie, Systématique et Evolution,
CNRS UMR 8079, Université Paris-Sud,
Bâtiment 362, 91405 Orsay Cedex, France
e-mail: anders.moller@u-psud.fr

M. Diaz
Museo Nacional de Ciencias Naturales (MNCN-CSIC),
28006 Madrid, Spain

E. Flensted-Jensen
Cypresvej 1, 9700 Brønderslev, Denmark

T. Grim
Department of Zoology and Laboratory of Ornithology,
Palacky University, 77146 Olomouc, Czech Republic

J. D. Ibáñez-Álamo
Departamento de Zoología, Facultad de Ciencias,
Universidad de Granada, Campus Universitario de Fuentenueva
s/n, 18071 Granada, Spain

J. Jokimäki
Arctic Centre, University of Lapland,
FI-96101 Rovaniemi, Finland

R. Mänd
Department of Zoology, Institute of Ecology and Earth Sciences,
University of Tartu, 51014 Tartu, Estonia

G. Markó
Behavioral Ecology Group, Department of Systematics, Zoology
and Ecology, Eötvös Loránd University, 1/C Pázmány Péter
sétány, Budapest 1117, Hungary

G. Markó
Department of Plant Pathology, Corvinus University
of Budapest, Ménesi út 44, Budapest 1118, Hungary

P. Tryjanowski
Institute of Zoology, Poznań University of Life Sciences,
Wojska Polskiego 71C, 60-625 Poznan, Poland

suggest that successful invasion of urban habitats was associated with gradual adaptation to these habitats as shown by a significant increase in population density in urban habitats over time.

Keywords Adaptation · Birds · Cross-validation · Invasion · Population density

Introduction

Urban habitats cover increasingly large fractions of land, especially in Europe and North America (European Commission 2006; Schneider et al. 2009), with a further increase predicted (United Nations 2007). Conversion of natural habitats into areas partly covered by buildings, heavily fragmented and with a high level of edges, has increased dramatically and hence exposed many animals to human proximity worldwide. Many ecological consequences of habitat conversion to urban areas have long been recognized, such as altered disturbance regimes, light conditions, habitat distributions, and species composition (Rebele 1994; Turner et al. 2004; Alberti 2005; Miller 2005). In addition, urban environments have more anthropogenic food resources, and the climate of urban areas differs from that in nearby rural environments (Gilbert 1989; Rebele 1994) due to the so-called urban heat island phenomenon (Gilbert 1989). Therefore, urban areas have longer growing seasons than nearby rural habitats. Such changes in urban habitats have forced animals and plants to either adapt or disappear (Coppedge et al. 2001).

Conversion to urban habitats favors the occurrence of very abundant animal species including birds (Bezzel 1985; Marzluff et al. 2001; Chace and Walsh 2006; Møller 2009). In general, habitat conversion has a negative effect on rare and specialist species, while it favors generalists and behaviorally flexible species (Møller 2009). These changes in abundance and association with humans are often accompanied by changes in behavior, physiology, and life history (Dyrcz 1963; Klausnitzer 1989; Møller 2008b, 2009; Møller et al. 2009; Zhang et al. 2011). This phenomenon of organismal changes we term the biological process of urbanization. Urban birds may be better adapted to urban environments than rural conspecifics, even when these urban birds are introduced to a novel area, as was the case when blackbirds *Turdus merula* were introduced to a city that previously did not have this species breeding (Graczyk 1974).

Some species are better able to live in and colonize urban habitats than others (Klausnitzer 1989; Stephan 1999; Gliwicz et al. 1994; Anderies et al. 2007; Møller 2009, 2010a; Carrete and Tella 2011). Because environmental conditions have changed due to habitat conversion, species that have lived for a long time in urban environments such as feral pigeons *Columba livia domestica*, house sparrows *Passer domesticus*, and blackbirds have become adapted to urban environments, causing such urban populations to reach higher population densities than populations in nearby rural habitats. For example, blackbirds now reach densities that are more than two orders of magnitude higher in urban habitats compared to the ancestral forested rural habitats, where this species exclusively bred until 180 years ago (Dyrcz 1963; Klausnitzer 1989; Luniak et al. 1990; Stephan 1999; Gliwicz et al. 1994).

Species of birds that currently live in cities can be categorized as anciently associated with humans for thousands of years, such as feral pigeons and house sparrows, because they are pre-adapted to urban habitats with many and large buildings (e.g., Parmelee 1959 on the birds of the bible; Gesner 1669 on birds in general; Møller 1992 on pre-fossil finds of barn swallows *Hirundo rustica* from a Danish flint mine), or they have more recently become established in cities from rural open parkland habitats. Thus urbanization of birds may either constitute a gradual process that have been going on for a different period of time for different species, or it may differ qualitatively between species that have lived for millennia in urban environments.

Different criteria have been used for successful invasion of urban environments. Møller (2009) used the criterion for urbanization of breeding birds that at least one urban population has higher population density than nearby rural populations. Croci et al. (2008) defined urbanized species of those that were able to breed in city centers. Finally, Evans et al. (2010) analyzed British census data and used the population density in urban habitats and the difference in density between all urban and all rural habitats to investigate determinants of degree of urbanization. Here, we extend this approach by comparing nearby urban and rural habitats in a paired design that controls statistically for the fact that urban and rural habitats may differ in many other respects than urbanization. Indeed, the approach that we adopt here relies on the fact that nearby areas differing in whether they are urban or rural will be similar in other respects such as habitat, geology, weather, and history of human exploitation including pollution. However, it remains to be tested whether adaptation to the invaded novel habitat as reflected by population density generally increases over time, although such a test would provide much needed cross-validation of a central assumption in invasion biology (e.g., Davis 2009; Lockwood et al. 2006). Such an increase may not necessarily be linear, but rather be gradual followed by a rapid increase (e.g., Stephan 1999; Vuorisalo et al. 2003).

The objectives of this study were to test for gradual adaptation to novel habitats in invasive species by analyzing extensive data on breeding birds occupying urban environments. To this end, we first provide two independent estimates of the degree of urbanization of different species: the difference in population density between urban and nearby rural habitats, and the estimated year of urbanization. The difference in population density between urban and nearby rural habitats provides an estimate of the extent to which a species has adapted to the urban environment, with a value of zero indicating no difference, a positive value an increase in density in urban habitats, and a negative value that the species has not become adapted to urban habitats. Second, we assess to which extent these measures of degree of urbanization are repeatable among cities, thereby testing if one estimate from a comparison between an urban and a nearby rural area has any predictive power for estimating the degree of urbanization by the same species in other cities elsewhere in Europe. Third, we test if urban species of birds can be considered to consist of two different categories of species that have either been urbanized for millennia or only more recently. Finally, we assess whether there is gradual adjustment to urban environments by testing if the difference in population density between urban and rural habitats increases with the time since known time of initial urbanization (based on literature information and data collected by local ornithologists). Here, we assess these predictions, using birds in nine pairs of European cities and nearby rural habitats as a model system for invasion biology. While urban ecosystems may differ from other ecosystems by their high and unpredictable disturbance regimes, they are not so different from high and unpredictable disturbance in agricultural, forest, or lagoon ecosystems exploited by humans.

Materials and methods

Study areas

We recorded population density of breeding birds in nine cities (each paired with a nearby rural area) across Europe by using consistent methods across all spatial replicates (Fig. 1). The distance between urban and rural study sites was 1–20 km, which can be considered small, given the flying ability of birds. The benefits of this matched design is that neighboring rural and urban study sites will share most characteristics including weather, altitude, soil, and many others.

All urban study sites included areas with multi-storey buildings, single-family houses, roads, and parks, while nearby rural areas had open farmland and woodland and did not contain continuous urban elements like multi-storey buildings, single-family houses, roads, and parks. This simple operational definition was also adopted in other studies (e.g., Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999), and our definitions of urban (percent of built-up area >50, building density >10/ha, and residential human density >10/ha) and rural habitats (percent of built-up area 5–20, building density >2.5/ha, and residential human density 1–10/ha) follow the suggestion made by Marzluff et al. (2001). A list of cities, coordinates, and their human population sizes is provided in electronic appendix Table 1.

Fig. 1 Location of the nine paired localities with urban and rural study sites for urbanization of birds

Ancient or recently urbanized species

We classified all species as being ancient urban species if they are known to have inhabited urban settlements since ancient times in the Mediterranean basin and the Middle East. The species belonging to this category were rock dove, jackdaw *Corvus monedula*, barn swallow, house martin *Delichon urbicum*, house sparrow, spotless starling *Sturnus unicolor*, and starling *S. vulgaris*. All other species were classified as recently urbanized.

Estimating urbanization level of species I: timing of urbanization

Bird species that have been urbanized for a long period will have spent more generations in urban areas, and hence will have had a longer time to adapt to this environment.

We estimated the approximate year of urbanization in the different cities, as described in detail by Møller (2008a, 2009, 2010a). Timing of urbanization will result from colonization followed by establishment or extinction and re-colonization. Obviously, information is rarely available for such processes, and empirical information on development of urban population sizes is also scarce (but see Stephan 1999; Vuorisalo et al. 2003). In the following, we assume that colonization of urban environments can be approximated from observations by keen ornithologists that habitually closely follow changes in composition and distribution of birds. Any heterogeneity in colonization processes or increase in population size will cause noise in the data, and ultimately make it more difficult to discern any patterns. We estimated the year when different species became urbanized using two different approaches. First, we asked keen amateur ornithologists living in our study areas to state which year different species of birds were first recorded breeding in urban areas. This estimate was used as an approximate year of urbanization, with a conservative value of 1950 assigned to species that were known to breed in urban habitats before the observers started watching birds. Previously, Møller (2008a) asked two keen Danish amateur ornithologists (William C. Årestrup and E. Flensted-Jensen) living in a study area in Denmark to state when different species of birds were first recorded breeding in urban areas. An approximate year of urbanization was recorded, with a value of 1950 assigned to species that were known to breed in urban habitats before the two observers started watching birds. Independently, Møller also recorded these years for all species before asking for estimates from the two independent observers. These three datasets were highly consistent in assignment of year (all three Pearson $r > 0.96$, $n = 44$ species). Second, we recorded timing of invasion of urban environments from old published records. Although urbanization is likely to have occurred much earlier for many species such as house sparrow and rock pigeon, these estimates are conservative. Previouslyn Møller (2008a) recorded the timing of invasion of urban environments in Copenhagen, Denmark, and Paris, France, from old published records (Gram 1908; Fløystrup 1920, 1925 for Copenhagen, and an extensive literature survey of ornithological journals and handbooks such as Cramp and Perrins 1977–1994 and Glutz and Bauer 1985–1997). If the year of urbanization was before records reported in these sources, Møller assigned 1850 as the year of urbanization (because Gram's observations date back to 1850, and many species were urbanized before the start of his study). Although urbanization is likely to have occurred much earlier for many species such as house sparrow and rock pigeon, these estimates are conservative. This dataset provided independent estimates of the time of urbanization, but these were still strongly positively correlated with Møller's own estimates from Northern Jutland (Pearson $r = 0.72$, $n = 41$ species). For all populations with urbanized populations, we used an estimate of 2010 as the year of urbanization for populations that were not yet urbanized. We included in the analyses all populations for which we could obtain information on year of urbanization.

Estimating urbanization level of species II: density in urban and rural areas

Bird species that have higher densities in urban versus rural areas could be considered to have adapted successfully because a hallmark of adaptation to local conditions is high local and global population densities (Brown 1995; Brown and Lomolino 1998). We performed standard point count censuses of breeding birds with unlimited recording distance (e.g. Voříšek et al. 2010), twice with an interval of 3–4 weeks, during spring 2010 in both urban and rural habitats in all study locations. Point counts provide highly reliable estimates of relative population density that is comparable among habitats (Voříšek et al. 2010). First, we placed 25–50 points (depending on the size of the particular urban area because some smaller urban areas did not allow allocation of 50 points) in each urban and rural study plot at a distance of 100 m between consecutive points, using a stratified random sampling design to ensure that all locally available habitats were included. The exact location of each point was determined with a GPS, allowing us to make the second census in exactly the same sites as the first census. Second, we made a first census in early spring starting early April in southern Spain, delaying the census at higher latitudes so it was completed in northern Finland in late May. The census started at local sunrise, while remaining 5 min at each point recording all birds seen or heard. Censuses were finished before 1000 hours (Voříšek et al. 2010). Censuses started on alternate days in urban and rural study plots ensuring that there was no difference in timing of censuses between habitats.

Vegetation cover (trees, shrubs, herbs, and grass) and cover with buildings and other man-made structures were quantified to the nearest 10 % in the field within 50 m of each survey point. In estimates of population density, we obtained quantitatively similar results when controlling or not controlling for differences in coverage for the three vegetation layers (results not shown).

As an estimate of relative population density in urban compared to rural habitats, we used $\log_{10}$-transformed population density in urban areas minus $\log_{10}$-transformed population density in rural areas, adding a constant of 0.01 to avoid problems with a few estimates of zero. The density for each of the two habitats was the mean number of individuals recorded per census point during the two point count censuses made in 2010. The data are provided in electronic appendix Table 2.

Statistical analyses

All analyses were made with JMP (SAS Institute 2000). We $\log_{10}$-transformed population densities from point counts, adding a constant of 0.01 in order to be able to include population densities of zero to achieve distributions that did not differ from normality. The variable classifying species as anciently or recently urbanized was treated as a dichotomous dummy variable with levels of 0 (recent) or 1 (ancient).

We tested for repeatability of difference in population density and year of urbanization using species as a predictor for those species that had at least two pairs of urban and rural populations, using statistics in Falconer and Mackay (1996).

We tested if the difference in population density between urban and nearby rural habitats could be predicted from the year of urbanization, using a GLM with difference in density as the response variable and year of urbanization and species as a random effect to avoid problems of non-independence of different cases of urbanization by the same species. This might not constitute a serious problem because Evans et al. (2009) have shown for the blackbird that different urban populations have become established independently rather than through migration from a single urban source population to other urban areas, and several studies have shown that even neighboring populations of urban birds are genetically differentiated (Baratti et al. 2009; Björklund et al. 2010; Fulgione et al. 2000; Rutkowski et al. 2005), suggesting recent divergence even within urban areas. Finally, we included the dichotomous dummy variable reflecting ancient or recent urbanization in these models. We entered the interaction between this dummy variable and year of urbanization, but also constructed a model that excluded anciently urbanized species to test for a qualitative difference between anciently and recently urbanized species.

Values reported are means (SE).

Results

Estimates of degree and timing of urbanization

The mean difference in density between urban and rural habitats on a log-scale was 0.112 (SE = 0.039, range −1.656 to +2.021, $n = 250$ populations, differing significantly from zero (one-sample *t* test, $t = 2.90$, $df = 249$, $P = 0.004$). This implies that population density in urban areas varied from 2.2 % of the density of the same species in rural habitats to 105 times the density in rural habitats. The mean of 0.112 implies that density in urban habitats was 1.29 times the density in rural habitats. The five species with the relatively largest density in urban habitats were tree sparrow *Passer montanus* in Denmark (105 times density in rural habitat), house sparrow in Norway (83 times), jackdaw *Corvus monedula* in Poland (77 times), rock dove in Finland (63 times) and black-headed gull *Larus ridibundus* in Finland (36 times). The frequency distribution of differences in population density only deviated marginally from a normal distribution (Shapiro–Wilk test, $W = 0.971$, $P = 0.012$). Breeding population density in urban habitats was positively correlated with density in nearby rural habitats [$F = 115.71$, $df = 1, 248$, $r^2 = 0.32$, $P < 0.0001$, slope (SE) = 0.766 (0.071)]. This implies that urban species already had high population densities in their ancestral rural habitats, under the assumption that current density in rural habitats also reflects past density in these habitats. Difference in density was not significantly related to latitude in a model that also included species (partial effect of latitude: $F = 0.14$, $df = 1, 189$, $P = 0.70$).

The first year of urbanization ranged from 1850 to 2010, mean (SE) = 1966 (4 years), $n = 174$. If we excluded all values from 2010 (implying that the species had not yet become urbanized), the mean year was 1938 (4 years), range 1850 to 2005. There was a weak negative relationship between year of urbanization and latitude in a model that also included species [partial effect of latitude: $F = 4.77$, $df = 1, 122$, $r^2 = 0.03$, $P < 0.0001$, slope (SE) = −0.960 (0.439)].

Repeatability of degree and timing of urbanization

The difference in density was significantly repeatable among populations for the species with at least 2 estimates ($F = 2.44$, $df = 59, 190$, $r^2 = 0.43$, $P < 0.0001$) with a repeatability of 0.26 (SE = 0.05). The estimates of repeatability were not significantly different for anciently and recently urbanized species [ancient: $F = 2.02$, $df = 7, 32$, $r^2 = 0.31$, $P = 0.08$, $R = 0.17$ (SE = 0.10); recent: $F = 2.47$, $df = 51, 158$, $r^2 = 0.44$, $P < 0.0001$, $R = 0.27$ (SE = 0.05)].

Year of urbanization was significantly repeatable among populations for the species with at least two estimates ($F = 3.66$, $df = 50, 123$, $r^2 = 0.60$, $P < 0.0001$) with a repeatability estimate of 0.44 (SE = 0.06). The estimates of repeatability were not significantly different for anciently and recently urbanized species [ancient: $F = 3.80$, $df = 7, 20$, $r^2 = 0.57$, $P = 0.009$, $R = 0.44$ (SE = 0.15); recent: $F = 1.82$, $df = 51, 102$, $r^2 = 0.47$, $P = 0.005$, $R = 0.21$ (SE = 0.07)].

Relationship between the difference in density and year of urbanization

The difference in population density between urban and rural habitats was significantly negatively related to year of urbanization [Fig. 2; $F = 52.09$, $df = 1{,}181$, $r^2 = 0.22$, $P < 0.0001$, slope (SE) $= -0.0056$ (0.0008)]. This result implies that a 100-year difference in timing of urbanization was associated with a factor 3.64 difference in population density between urban and rural habitats (SE = 1.20). There was no significant additional partial effect of latitude ($F = 0.58$, $df = 1{,}180$, $P = 0.45$). If we excluded all populations with an estimated year of urbanization of 2010, there was still a highly significant effect of year of urbanization [$F = 18.83$, $df = 42{,}63$, $r^2 = 0.23$, $P < 0.0001$, slope (SE) $= -0.0055$ (0.0013)].

If we entered species as a random effect in this model, to account for the possible non-independence of multiple populations of the same species, the model explained 36 % of the variance ($F = 1.69$, $df = 60$, 122, $r^2 = 0.36$, $P = 0.0073$). The partial effect of year of urbanization was highly significant [$F = 39.74$, $df = 1$, 122, $r^2 = 0.25$, $P < 0.0001$, slope (SE) $= -0.0052$ (0.0008)]. The slope of -0.0052 implies that a 100-year difference in timing of urbanization was associated with a difference in density by a factor 3.31 (SE = 1.20). There was no significant additional partial effect of latitude ($F = 0.14$, $df = 1{,}189$, $P = 0.70$).

If we related difference in density to year urbanized, population and the variable reflecting ancient or recent urbanization, we find a model that explains 29 % of the variance ($F = 7.17$, $df = 10{,}172$, $r^2 = 0.29$, $P < 0.0001$). The largest effect was for year urbanized [$F = 33.97$, $df = 1{,}172$, $P < 0.0001$, slope (SE) $= -0.0055$ (0.0009)], followed by a marginal effect of population ($F = 1.93$, $df = 8{,}172$, $P = 0.06$) and a small, non-significant effect of ancient or recent urbanization ($F = 1.12$, $df = 1{,}172$, $P = 0.29$). Likewise, the interaction between year of urbanization and ancient or recent urbanization was small and non-significant ($F = 1.15$, $df = 1{,}171$, $P = 0.28$). Finally, a model that excluded all anciently urbanized species explained 54 % of the variance ($F = 2.33$, $df = 52{,}102$, $r^2 = 0.54$, $P < 0.0001$), with significant effects of year urbanized [$F = 10.09$, $df = 1{,}102$, $P = 0.002$, slope (SE) $= -0.0038$ (0.0012)] and species ($F = 1.85$, $df = 1{,}102$, $P = 0.005$). These analyses suggest that anciently urbanized species do not differ qualitatively from recently urbanized species, and that overall species that have been urbanized over a long period have a greater difference in population density between urban and rural habitats.

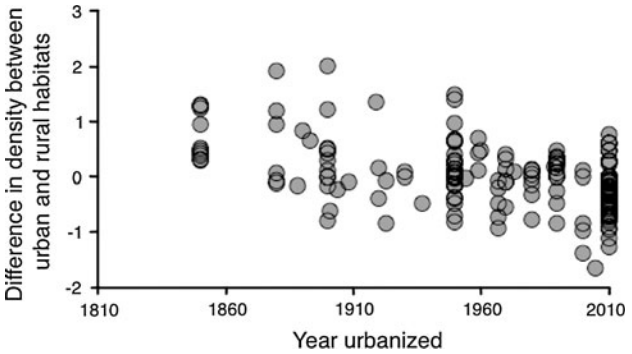

Fig. 2 Difference in breeding population density between urban and rural habitats in relation to estimated year of urbanization in different populations of species of birds. The difference in density is $\log_{10}$(population density in urban habitats) − $\log_{10}$(population density in rural habitats)

Discussion

We tested the assumptions of invasion biology that species that had invaded a novel environment had achieved higher population density in the invaded environment, and that the increase in density reflected time since invasion of the novel habitat. We did so by analyzing extensive data on density and timing of invasion of urban habitats by birds. The mean difference in population density of the same species between urban and nearby rural habitats was positive, implying that most species had higher densities in urban habitats. The difference was significantly repeatable, albeit with a small repeatability, suggesting that, when population density differed between urban and rural habitats to a certain degree in one city in Europe, this difference tended to be of similar magnitude in other cities. Likewise, the estimated year of urbanization was significantly repeatable among populations, implying that, when a species became urbanized in one city in a given year, other cities tended to become urbanized at a similar time elsewhere in Europe. Finally, we showed that the difference in population density between urban and nearby rural habitat was significantly negatively related to the estimated year of urbanization, suggesting that adaptation to urban environments results in a gradual increase in population density in the invaded environment over time, and that the difference in density is a reasonably good proxy for time of urbanization. Importantly, this relationship between difference in population density and year of urbanization was qualitatively similar in anciently and recently urbanized species, suggesting that anciently urbanized species that have been associated with humans for millennia show qualitatively similar patterns of urbanization as recently urbanized species. This provides empirical tests of critical assumptions of invasion biology, but also of repeatability of invasiveness across large geographical scales, something that has rarely if ever been tested (e.g., Davis 2009; Lockwood et al. 2006).

Urban birds have large population densities relative to the density of the same species in nearby rural habitats (e.g., Dyrcz 1963; Klausnitzer 1989; Luniak et al. 1990;

Stephan 1999; Gliwicz et al. 1994; Evans et al. 2010). On average, across the species and populations sampled here, we found an increase in population density in urban habitats by almost 30 % compared to nearby rural habitats. In addition, population density in novel urban habitats was significantly positively correlated with density in ancestral rural habitats. This effect implies that bird species that have successfully invaded urban habitats already had high population densities in their ancestral rural habitats. Indeed, a pairwise comparative analysis of phylogenetically independent cases of urbanization by birds in the Western Palearctic showed that range size, population size and population density were consistently higher in the species that became urbanized compared to a non-urbanized closely related species (Møller 2009). The difference in population density between urban and rural habitats reached more than two orders of magnitude, and similarly large differences have been reported elsewhere (Dyrcz 1963; Klausnitzer 1989; Luniak et al. 1990; Stephan 1999; Gliwicz et al. 1994; Evans et al. 2010). These differences in population density could also be generalized across populations of the same species, as shown by a statistically significant repeatability. Repeatability estimates in genetics are use to set an upper limit to the heritability (Falconer and Mackay 1996). However, repeatabilities can also be estimated in other contexts such as ecological studies. With values ranging from 0 to 1, a value of 0.26 is modest, although ecological studies consistently have small to intermediate effect sizes hence implying low repeatabilities (Møller and Jennions 2002). These findings also relate to theoretical models of population density in urban environments with low predation pressure and more predictable and abundant food resources (Sochat 2004; Anderies et al. 2007). In competition models with two phenotypes that differ in foraging ability, short periods between pulses of resources and low predation rates result in weaker competitors, while longer periods and high predation rates favor stronger competitors (Sochat 2004; Anderies et al. 2007). Indeed, species differing in susceptibility to predation are differentially successful in urbanization (Møller 2009), and urban birds with higher population densities than rural populations of the same species differ in terms of song post position, the fraction of nests found indoors inside buildings, and escape behavior by birds captured by humans (Møller 2008a, 2010a, b, 2011; Møller and Ibáñez-Álamo 2012). Interestingly, these differences in antipredator behavior are strongly correlated with time since urbanization. The findings that we report here suggest that time since urbanization may be an additional factor to consider in such models. Point counts provide reliable information about relative density, especially when comparing populations of the same species in different habitats (Voříšek et al. 2010). However, the precision of population densities based on 25–50 census points is limited, suggesting that the repeatability of difference in population density constitutes a conservative estimate. The fact that population density in urban habitats could be predicted by population density in rural habitats in a model that explained 32 % of the variance implies that the two indices of urbanization (urban density and difference in density between urban and rural habitats) provide qualitatively similar information.

Urbanization has been ongoing for a long time. For example, many species of insects, birds, and mammals have co-habited with humans for millennia (Klausnitzer 1989). Anciently urbanized birds such as rock doves, barn swallows, house martins, house sparrows, and jackdaws are known to have been associated with human settlements in the Middle East for more than 5,000 years (e.g., Parmelee 1959; Summers-Smith 1963). It is known that blackbirds were already very common in the city of Rome in the 1820s (Bonaparte 1828). Likewise, many birds have bred indoors inside human habitation for millennia, and species that are adapted to human proximity are also those that have been urbanized for a long time (Møller 2010b). Here, we analyzed the year of urbanization as estimated by amateur ornithologists and published reports in the ornithological literature. We found significant repeatability in year of urbanization among populations, with an estimate of 0.44. This implies that more than 40 % of the variance in year of urbanization is accounted for by species. Thus, the same species tended to become urbanized at the same time in different parts of Europe. Importantly, we found no significant difference between anciently and recently urbanized species, suggesting that these two categories of species behaved qualitatively similar to urbanization. This is an important finding suggesting that the process of association between birds and humans is a continuous process dating back thousands of years.

There is a currently increasing interest in the study of biological aspects of urbanization (e.g., Grimm et al. 2008), but also of invasion biology (e.g., Davis 2009; Lockwood et al. 2006). Here, we have provided significant evidence for adaptation to novel environments by invasive urban bird species, because species that invaded urban environments a long time ago are also the species that have achieved the largest increases in population density compared to their ancestral rural habitats. This finding is ecologically important because species with high local population densities tend to have high global population sizes (Brown 1995; Brown and Lomolino 1998). There have been few attempts to explicitly test to which extent different metrics of urbanization provide similar information. Møller (2008a, 2010a) has shown that the estimated year of urbanization of different species of birds is highly consistent when using observations by different observers, and also when comparing observations and published records of date of urbanization. Here, we have taken this cross-validation approach one step further by relating the difference in population density among all populations to the year of urbanization, after controlling for the fact that different populations of the same species may not constitute statistically independent observations unless urbanization has occurred independently in different cities (Evans et al. 2009). The correlation between the two metrics of urbanization of bird populations accounted for 22–25% of the variance in the data. This provides evidence for consistency in different estimates of urbanization. Clearly 22–25 % of the variance is not a large amount, although again this should be viewed in the light of the inherent uncertainty of the two estimates. We can judge the relative magnitude of these effects by comparing the estimates with the amount of variance explained by all meta-analyses in the biological sciences that was in the order of 5–10 % of the variance (Møller and Jennions 2002).

The implications of this study are that urbanized birds have shown gradual adjustment to urban environments, as shown by relative larger population densities in urban habitats in species that have been urbanized for a long time. In addition, we can predict a small, but significant, amount of variance in difference in population density and year of urbanization from just a single estimate according to the estimates of repeatability. Obviously, the precision of such estimates will improve with the number of populations used. The findings also imply that we can use differences in population density and year of urbanization for further studies, knowing that these estimates provide reliable information on two aspects of urbanization. Finally, several studies have shown significant genetic differentiation between populations in rural and urban habitats or among populations inhabiting different urban areas (e.g., Baratti et al. 2009; Björklund et al. 2010; Evans et al. 2009; Fulgione et al. 2000; Rutkowski et al. 2005). Because Crispo and Hendry (2005) have shown that isolation by distance increases with time since colonization, we make the additional prediction that the degree of such differentiation will be greater in species that show large differences in population density between urban and rural habitats and for populations that have been urbanized for a long time. However, anciently and recently urbanized species should only differ in degree rather than kind, as shown by the lack of effect of ancient or recent urbanization on the relationship between year of urbanization and difference in density between urban and nearby rural habitats in the present work.

In conclusion, urban birds provide an ideal model system for the study of invasion of novel environments, showing consistency in timing of invasion and extent of adaptation to these novel environments. In addition, we have shown that both the difference in population density between urban and rural habitats and the estimated year of urbanization are repeatable among cities in Europe, and that different species on average have almost 30 % higher population density in urban habitats. Furthermore, the difference in population density between urban and rural habitats is negatively correlated with the estimated year of urbanization, independent of whether species are anciently or recently urbanized. This result provides cross-validation of the assumption that different measures of the degree of urbanization provide similar and reliable information. These findings have implications for future studies of urbanization, and for invasion biology in general, because the high and unpredictable level of disturbance in urban ecosystems makes urban ecosystems similar to other ecosystems exploited by humans such as farmland, forests, and lagoons.

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Electronic appendix Table 1 Location of the eight cites and their current human population size extracted from www.wikipedia.org

City	Latitude	Longitude	Human population size
Rovaniemi	66° 27’ N	25° 37’ E	59,000
Oslo	59° 57’ N	10° 45’ E	1,422,000
Brønderslev	57° 12’ N	10° 00’ E	12,000
Poznan	52° 25’ N	16° 55’ E	856,000
Olomouc	49° 34’ N	17° 15’ E	110,000
Paris	48° 04’ N	2° 11’ E	11,769,000
Budapest	47° 28’ N	19° 02’ E	2,503,000
Toledo	39° 51’ N	4° 01’ W	298,000
Granada	37° 15’ N	3° 40’ W	238,000

Electronic appendix Table 2. Difference in population density between urban and rural habitats, year of urbanization, population and sample size for rural and urban habitats.

Species	Difference in density	Year urbanized	Population	Sample size rural habitat	Sample size urban habitat
Aegithalos caudatus	0.9031	.	Budapest	2	0
Aegithalos caudatus	0.1249	2000	Paris	5	3
Anas platyrhynchos	0.3424	1990	Brønderslev	4	5
Anas platyrhynchos	0.3424	1990	Budapest	0	2
Anas platyrhynchos	0.6021	.	Granada	0	20
Anas platyrhynchos	1.1761	.	Olomouc	4	37
Anas platyrhynchos	0	1900	Oslo	5	5
Anas platyrhynchos	0.5195	1900	Paris	21	50
Anas platyrhynchos	0.1761	.	Poznan	7	8
Anas platyrhynchos	0.4771	2010	Toledo	0	12
Carduelis	0	2000	Brønderslev	0	0

carduelis					
Carduelis carduelis	-0.1498	1888	Budapest	32	27
Carduelis carduelis	0.2109	.	Granada	91	210
Carduelis carduelis	-0.1597	2010	Olomouc	9	16
Carduelis carduelis	-0.9777	2000	Oslo	18	1
Carduelis carduelis	-0.4771	2010	Paris	3	2
Carduelis carduelis	0.1493	.	Toledo	82	104
Carduelis chloris	0.3245	1970	Brønderslev	30	58
Carduelis chloris	-0.0669	1923	Budapest	11	37
Carduelis chloris	0.4428	1959	Granada	58	199
Carduelis chloris	0.0241	.	Olomouc	17	31
Carduelis chloris	-0.0833	1970	Oslo	62	51
Carduelis chloris	0.6872	1950	Paris	21	102
Carduelis chloris	-0.01	1954	Rovaniemi	26	25
Carduelis	0.4629	.	Toledo	32	76

chloris					
Certhia brachydactyla	-0.8129	1950	Paris	48	4
Certhia brachydactyla	0.7782	.	Toledo	0	0
Coccothraustes coccothraustes	-0.0669	2010	Olomouc	16	7
Coccothraustes coccothraustes	0	2010	Paris	0	0
Coccothraustes coccothraustes	-0.8451	.	Poznan	8	1
Coccothraustes coccothraustes	0.4771	2010	Toledo	0	4
Columba livia	0.417	1950	Budapest	14	225
Columba livia	0.4429	1850	Granada	347	680
Columba livia	0.8129	.	Oslo	1	12
Columba livia	1.29	1850	Paris	4	48
Columba livia	1.7993	.	Rovaniemi	0	37
Columba livia	1.4624	.	Toledo	0	164
Columba oenas	-1.3802	2000	Oslo	23	0
Columba oenas	-0.699	1950	Paris	8	1
Columba palumbus	0.2666	1950	Brønderslev	135	240
Columba palumbus	-0.5119	2010	Budapest	12	16
Columba palumbus	-1.6564	2005	Granada	180	2
Columba	0.1542	.	Olomouc	19	142

palumbus					
Columba palumbus	-0.0139	1950	Oslo	94	91
Columba palumbus	-0.0711	1880	Paris	229	172
Columba palumbus	-0.0872	1908	Poznan	21	33
Columba palumbus	-0.5119	.	Toledo	252	50
Corvus cornix	-0.5482	1970	Brønderslev	64	14
Corvus cornix	0.5477	.	Budapest	9	66
Corvus cornix	0.1317	1970	Oslo	47	64
Corvus cornix	0.9294	.	Poznan	1	19
Corvus cornix	0.2414	.	Rovaniemi	23	40
Corvus corone	0.0341	1950	Paris	75	73
Corvus corone	0.9294	.	Poznan	0	0
Corvus frugilegus	0.0631	1950	Brønderslev	262	358
Corvus frugilegus	0.699	.	Poznan	0	15
Corvus monedula	1.1934	1880	Brønderslev	10	230
Corvus monedula	1.2041	.	Olomouc	4	20
Corvus monedula	-0.1047	1880	Oslo	13	1
Corvus monedula	1.8865	.	Poznan	0	99

Corvus monedula	0.2609	.	Toledo	26	16
Delichon urbica	0.9606	1850	Granada	113	83
Delichon urbica	0.4771	1850	Paris	0	2
Delichon urbica	-1.4698	.	Toledo	0	0
Dendrocopos major	-0.1761	2010	Budapest	0	1
Dendrocopos major	-0.2583	2010	Olomouc	27	15
Dendrocopos major	-0.8451	1990	Paris	16	1
Dendrocopos major	0	2010	Rovaniemi	1	1
Dendrocopos major	0.301	2010	Toledo	0	2
Emberiza citrinella	-1.2553	2010	Olomouc	33	0
Emberiza citrinella	-0.7782	2010	Oslo	5	0
Emberiza citrinella	-0.9358	1967	Rovaniemi	41	4
Emberiza schoeniclus	-0.4771	2010	Brønderslev	1	0
Emberiza schoeniclus	-1.1139	2010	Rovaniemi	7	0

Eritahcus rubecula	-0.1445	1980	Oslo	52	37
Erithacus rubecula	-0.2808	2010	Brønderslev	16	6
Erithacus rubecula	0	.	Budapest	0	1
Erithacus rubecula	0	.	Granada	0	4
Erithacus rubecula	-0.4472	2010	Olomouc	11	2
Erithacus rubecula	-0.1614	1900	Paris	142	76
Erithacus rubecula	0.4771	1990	Poznan	1	0
Ficedula hypoleuca	0	2010	Paris	0	0
Ficedula hypoleuca	-0.0678	1967	Rovaniemi	49	42
Fringilla coelebs	-0.1316	1950	Brønderslev	79	75
Fringilla coelebs	0.8451	1890	Budapest	0	16
Fringilla coelebs	-0.1687	2010	Olomouc	49	50
Fringilla coelebs	-0.3896	1950	Oslo	102	41
Fringilla coelebs	0.301	1900	Paris	59	118

Fringilla coelebs	0.0792	1990	Poznan	17	16
Fringilla coelebs	-0.1996	1967	Rovaniemi	45	28
Galerida cristata	0	.	Poznan	0	0
Galerida cristata	-0.3153	2010	Toledo	30	20
Gallinula chloropus	-0.4771	2010	Brønderslev	0	0
Gallinula chloropus	0	.	Oslo	1	0
Gallinula chloropus	0.2341	1950	Paris	11	18
Garrulus glandarius	0.301	2010	Budapest	4	1
Garrulus glandarius	0	2010	Olomouc	13	8
Garrulus glandarius	-0.243	2010	Paris	18	5
Garrulus glandarius	-0.426	2010	Poznan	6	0
Hirundo rustica	0	1950	Brønderslev	0	1
Hirundo rustica	-0.5229	2010	Budapest	2	2
Hirundo rustica	-0.6446	2010	Granada	59	13

Hirundo rustica	0.2791	2010	Toledo	60	174
Larus argentatus	0	2010	Brønderslev	0	0
Larus argentatus	0.6021	2010	Oslo	0	3
Larus marinus	0	2010	Brønderslev	0	0
Larus marinus	0	2010	Oslo	0	16
Larus ridibundus	0.9379	.	Olomouc	1	14
Larus ridibundus	0.0994	1950	Oslo	43	34
Larus ridibundus	1.5563	.	Rovaniemi	0	21
Motacilla alba	0	1950	Brønderslev	2	0
Motacilla alba	-0.0792	2010	Granada	6	4
Motacilla alba	-0.699	2010	Olomouc	8	0
Motacilla alba	0.3979	1970	Oslo	7	19
Motacilla alba	0	2010	Paris	0	0
Motacilla alba	-0.1761	2010	Poznan	2	0
Motacilla alba	0.5149	1850	Rovaniemi	6	21
Motacilla cinerea	0	2010	Olomouc	4	0
Motacilla cinerea	0.368	1990	Paris	2	6
Muscicapa striata	0	1950	Brønderslev	0	0
Muscicapa	0.301	.	Granada	4	4

striata					
Muscicapa striata	0.243	.	Olomouc	4	11
Muscicapa striata	0	2010	Paris	0	0
Parus ater	0	.	Budapest	1	3
Parus ater	-0.1091	2010	Granada	7	6
Parus ater	-0.301	2010	Oslo	1	0
Parus ater	0.301	1990	Paris	0	3
Parus caeruleus	0.0414	1980	Brønderslev	9	14
Parus caeruleus	0.699	.	Budapest	4	17
Parus caeruleus	0.6021	.	Granada	5	5
Parus caeruleus	0.0896	.	Olomouc	29	51
Parus caeruleus	-0.0106	1980	Oslo	82	80
Parus caeruleus	-0.1001	1970	Paris	116	94
Parus caeruleus	0.0997	1973	Rovaniemi	18	23
Parus caeruleus	0.284	.	Toledo	22	34
Parus major	0.2969	1950	Brønderslev	58	106
Parus major	0.1701	1920	Budapest	78	218
Parus major	0.0782	.	Olomouc	66	70

Parus major	0.0173	1950	Oslo	73	76
Parus major	0.128	1950	Paris	114	145
Parus major	0.2523	1990	Poznan	26	36
Parus major	0.3104	1850	Rovaniemi	27	56
Parus major	-0.1461	.	Toledo	58	36
Parus palustris	-0.8451	2000	Paris	9	0
Passer domesticus	0.9542	1880	Brønderslev	0	5
Passer domesticus	-0.2218	.	Budapest	32	46
Passer domesticus	0.3916	1850	Granada	325	839
Passer domesticus	-0.8239	.	Olomouc	23	41
Passer domesticus	1.9191	1880	Oslo	0	82
Passer domesticus	1.3082	1850	Paris	7	208
Passer domesticus	0.5027	1900	Poznan	46	122
Passer domesticus	1.349	1919	Rovaniemi	3	80
Passer domesticus	0.7002	.	Toledo	54	666
Passer montanus	2.0212	1900	Brønderslev	0	86
Passer montanus	-0.6021	1901	Budapest	50	10

Passer montanus	-0.3358	2010	Olomouc	13	12
Passer montanus	1.5051	1950	Oslo	0	31
Passer montanus	-0.3181	.	Poznan	42	33
Passer montanus	1.2788	.	Rovaniemi	0	11
Passer montanus	0.6232	2010	Toledo	14	30
Phoenicurus ochruros	-0.4771	1937	Budapest	30	9
Phoenicurus ochruros	0.2596	.	Olomouc	16	21
Phoenicurus ochruros	1.2553	1850	Paris	1	24
Phoenicurus ochruros	0	1990	Poznan	18	5
Phoenicurus ochruros	0.6021	2010	Toledo	0	4
Phoenicurus phoenicurus	0	1990	Brønderslev	0	2
Phoenicurus phoenicurus	0.8451	.	Olomouc	2	14
Phoenicurus phoenicurus	-0.722	1967	Rovaniemi	34	6
Phylloscopus collybita	-0.2478	1990	Brønderslev	20	13

Phylloscopus collybita	-0.699	2010	Budapest	2	4
Phylloscopus collybita	0.7782	2010	Granada	0	0
Phylloscopus collybita	0.2218	2010	Olomouc	67	66
Phylloscopus collybita	-0.4771	1990	Paris	79	26
Phylloscopus collybita	-0.301	2010	Toledo	18	8
Pica pica	0.1326	1950	Brønderslev	15	18
Pica pica	-0.4424	2010	Budapest	67	30
Pica pica	-0.8033	2010	Granada	100	20
Pica pica	0.2553	.	Olomouc	2	7
Pica pica	0.6651	1950	Oslo	7	36
Pica pica	0.6368	1950	Paris	34	149
Pica pica	0.1102	.	Poznan	37	72
Pica pica	0.4973	.	Rovaniemi	12	39
Pica pica	0.1204	.	Toledo	92	94
Picus viridis	0	2010	Budapest	1	0
Picus viridis	-0.3212	1980	Paris	69	25
Picus viridis	-0.2218	2010	Poznan	1	5
Pyrrhula pyrrhula	0	2010	Brønderslev	0	0
Pyrrhula pyrrhula	0	2010	Paris	0	0
Regulus ignicapillus	0	2010	Granada	0	0

Regulus ignicapillus	0	2010	Paris	0	0
Regulus regulus	-0.6021	2010	Oslo	3	0
Regulus regulus	0.1139	1980	Paris	13	20
Serinus serinus	0.1217	1959	Granada	210	225
Serinus serinus	0.3559	.	Olomouc	11	33
Serinus serinus	-0.301	2010	Paris	2	0
Serinus serinus	0.1296	.	Toledo	68	78
Sitta europaea	0	.	Budapest	0	2
Sitta europaea	-0.0348	2010	Olomouc	8	7
Sitta europaea	-0.7782	1980	Oslo	17	2
Sitta europaea	-0.4771	1950	Paris	5	3
Streptopelia decaocto	1.3979	1950	Brønderslev	1	59
Streptopelia decaocto	1.1399	.	Granada	11	120
Streptopelia decaocto	0.3287	.	Olomouc	17	56
Streptopelia decaocto	0.976	1950	Paris	10	204
Streptopelia decaocto	0.4175	.	Poznan	10	27
Streptopelia decaocto	0.9542	.	Toledo	4	46
Sturnus unicolor	0.1754	1989	Granada	254	333

Sturnus unicolor	-0.0161	.	Toledo	74	202
Sturnus vulgaris	1.2304	1900	Brønderslev	0	9
Sturnus vulgaris	-0.8373	1923	Budapest	23	16
Sturnus vulgaris	-0.7036	2010	Olomouc	67	18
Sturnus vulgaris	0	1900	Oslo	11	11
Sturnus vulgaris	0.2932	1850	Paris	51	90
Sturnus vulgaris	-0.7817	1900	Poznan	120	46
Sylvia atricapilla	0.1513	1990	Brønderslev	11	11
Sylvia atricapilla	-0.2109	2010	Budapest	20	28
Sylvia atricapilla	0.0322	.	Granada	11	17
Sylvia atricapilla	-0.0766	2010	Olomouc	97	95
Sylvia atricapilla	-0.1271	1950	Paris	124	99
Sylvia atricapilla	0.9031	.	Toledo	6	58
Sylvia communis	-0.7179	2010	Brønderslev	40	7

Sylvia communis	-0.3802	2010	Olomouc	8	4
Sylvia curruca	0.4771	1960	Brønderslev	3	6
Sylvia curruca	0	.	Budapest	1	10
Sylvia curruca	0.9031	.	Olomouc	3	9
Sylvia melanocephala	-0.6672	2010	Granada	100	9
Sylvia melanocephala	-0.5563	2010	Toledo	20	6
Troglodytes troglodytes	0.0941	1930	Brønderslev	36	47
Troglodytes troglodytes	0	1930	Oslo	0	0
Troglodytes troglodytes	-0.1491	1950	Paris	188	143
Turdus iliacus	-0.9031	2010	Olomouc	0	0
Turdus iliacus	-0.4821	1967	Rovaniemi	52	17
Turdus merula	0.4386	1900	Brønderslev	97	170
Turdus merula	0.649	1893	Budapest	24	212
Turdus merula	0.7016	1959	Granada	50	159
Turdus merula	0.7435	.	Olomouc	29	196
Turdus merula	0.1082	1900	Oslo	52	67
Turdus merula	0.0803	1880	Paris	243	279
Turdus merula	-0.2218	1904	Poznan	22	21
Turdus merula	0.8337	.	Toledo	6	76
Turdus philomelos	0.2648	.	Olomouc	21	31
Turdus	-0.3493	1950	Paris	57	25

philomelos					
Turdus philomelos	-0.3802	1920	Poznan	8	4
Turdus pilaris	0	2010	Brønderslev	0	0
Turdus pilaris	-0.9542	2010	Olomouc	38	12
Turdus pilaris	0.1293	1980	Oslo	97	131
Turdus pilaris	1.0414	.	Poznan	1	22
Turdus pilaris	-0.15	.	Rovaniemi	53	37
Turdus viscivorus	-0.4771	2010	Brønderslev	4	0
Turdus viscivorus	0.2218	1990	Paris	3	4