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Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic

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Abstract Numerous species have adapted to the proximity of humans, and this feature is no clearer than among species that have invaded towns and cities. The characteristics of species that have successfully managed to expand their range into urban areas remain largely unexplored, although they are of general interest in a world that is increasingly urbanised. I hypothesised that widely distributed species with high dispersal abilities, species with a high rate of innovation, a high level of risk-taking, and a fast life history would have a selective advantage in habitats influenced by humans. Consistent with this hypothesis, in a comparative analysis of 39 independent evolutionary events of urbanisation of birds in the Western Palearctic (thus taking the fact that closely related species that have become urbanised are caused by common phylogenetic descent rather than convergent evolution), bird species that adapted to urban habitats were characterised by large breeding ranges, high propensity for dispersal, high rates of feeding innovation (novel ways of acquiring food), short flight distances when approached by a human, and a life history characterised by high annual fecundity and high adult survival rate. Urban species may be disproportionately resistant to parasitism and predation because they had disproportionately strong immune responses, as reflected by the size of the bursa of Fabricius, and a history of weak predation-mediated natural selection, as reflected by the force required to remove feathers from the rump. Urban species had high overall ecological success as indicated by large range size and population size and high population density. This suggests that a suite of ecological features providing them with general ecological success characterises species of birds that have successfully invaded urban environments.

Keywords Invasion · Life history · Parasitism · Risk-taking · Urbanisation

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Introduction

Large areas of natural habitats or farmland have been converted into urban areas during the last 50 years (Klausnitzer 1989; Marzluff et al. 2001; Shochat et al. 2006), and the rate of conversion is expected to increase dramatically during the next century. Urbanisation, defined as the conversion of natural habitats into areas partly covered by buildings, heavily fragmented and with a high level of edge effects, has caused dramatic increases in areas occupied by cities, and hence areas exposed to human proximity worldwide. For many, but not all, animal species, urbanisation has provided a high abundance of cover, nest sites and food. Such changes have forced animals and plants to either adapt or disappear.

Urbanisation has affected bird communities (and communities of other species) by decreasing species richness, and sometimes diversity, and by increasing total population density (summary in Klausnitzer 1989). Urbanisation may also have a homogenising effect on flora and fauna on a larger geographic scale (Clergeau et al. 2006). Surprisingly,

the characteristics of species that have adapted to urbanisation are relatively poorly known (Diamond 1986; Klausnitzer 1989). Early studies reviewed by Klausnitzer (1989) suggested many specific characteristics of urban species. For example, some of these studies suggested that urbanisation favours residency over migration (e.g. Lancaster and Rees 1979; Bezzel 1985), urbanisation favours nesting in holes and trees, whereas ground-nesters may suffer from urbanisation (Emlen 1974; Tomialojc 1970; Lancaster and Rees 1979; Luniak 1981; Gavareski 1976; Suhonen and Jokimäki 1988; Jokimäki 1999) and urbanisation favours omnivores (Dickman and Doncaster 1987a, b; Gilbert 1989) or species with broad environmental tolerance (Bonier et al. 2007). Others have suggested that humans feeding birds during winter may promote urbanisation (Pulliainen 1963), especially at northern latitudes with harsh conditions during winter (Jokimäki and Suhonen 1998). While these studies have highlighted the importance of different ecological factors, none of them have been based on formal comparative approaches that distinguish between similarity in phenotype among species due to common phylogenetic descent and convergent evolution. To the best of my knowledge there are no published studies comparing the ecological characteristics of urbanised species with closely related species that have not managed to colonise urban environments.

Urban life has a number of characteristics that facilitates colonisation by certain species over others. First, urbanisation is associated with the proximity of humans, and such presence is problematic for species with low thresholds for fear, long flight distances, and rapid and high corticosterone responses (Blumstein 2006; Wingfield and Ramenofsky 1999). Therefore, colonisation by a particular suite of species with high thresholds of fear and short flight distances is most likely. Whether colonisation then actually occurs will depend on the ability to colonise urban habitats and establish permanent populations that can become further adapted to urban environments. Second, urban environments often have a longer growing season due to high temperatures and precipitation (Klausnitzer 1989; Jokimäki et al. 1996). Thus, species with many reproductive events per year will be at a selective advantage in urban environments, suffering from fewer temporal constraints on reproduction than single-brooded species. Third, urban environments are characterised by high food abundance due to high primary productivity, a longer growing season and anthropogenic food due to feeding of birds and waste (Klausnitzer 1989; Stephan 1999; Jokimäki et al. 1996). In addition, humans often provide large amounts of food. Therefore, urban species generally have much higher population densities than rural populations. For example, population densities of common breeding birds in urban habitats are often two or more orders of magnitude higher

than densities in rural habitats (Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999). High densities will generally increase the rate of parasite transmission and predation rates (both predation of adults and nests). Species that are able to sustain these negative effects of high densities will be particularly successful in colonising urban areas (see also Anderies et al. 2007).

Successful colonisation and invasion are facilitated by a high propensity for dispersal because only individuals that eventually reach novel environments at a sufficient rate will be able to establish permanent populations (Clobert et al. 2001). A second prerequisite for successful colonisation of urban areas is that individuals start to probe such habitats and exploit available resources (Klausnitzer 1989), putting a premium on species with high rates of feeding innovation (ways of foraging that deviate from those commonly recognised for a species) that eventually may allow successful exploitation of environments dominated by human presence. Such a measure of the ability to cope with novel environmental conditions is the rate of feeding innovations, defined as the frequency of novel feeding behaviour adjusted for sampling effort (Garamszegi et al. 2005; Lefebvre et al. 1997; Reader and Laland 2002). Any species that regularly encounters urban environments, coupled with an ability to exploit those environments for resource acquisition and an ability to convert such resources into offspring, should have an elevated probability of establishment. Thus, successful colonisers should have elevated dispersal abilities and innovation rates.

The objectives of this study were to determine the characteristics of bird species that have managed to adapt to urban environments relative to those of species than have not managed to make this transition. More specifically, I tested (1) to what extent urban species had high rates of feeding innovations; and (2) whether urban species had a high propensity for dispersal that will facilitate colonisation of novel habitats such as urban environments. The assumed underlying mechanism is that individuals of species with a high degree of dispersal propensity would more often end up in novel environments, such as urban habitats, than individuals of species with a low likelihood of dispersal, and that this would facilitate colonisation of urban environments; (3) whether urban species were characterised by short flight distances; (4) whether urban species had high annual fecundity and high adult survival rate; and (5) whether species that had managed to establish urban populations had greater ecological success in terms of higher population size and density and larger breeding distributions. This latter prediction is based on the assumption that urbanised species have only a relatively small fraction of their total population breeding in urban environments. The test of differences in population density based on analysis of population size in the Western

Palearctic, adjusted for breeding range in the Western Palearctic, constitutes an especially conservative test of this prediction because the percentage of the Western Palearctic (west of the Urals) covered by urban habitats is less than 5%. I tested these predictions using information on urbanisation in the breeding birds of the Western Palearctic, exploiting the situation that adaptation to urban environments has occurred independently a large number of times.

Materials and methods

Choice of species

I defined urban areas as built-up areas with continuous houses or multi-storey buildings, with the only interspersed areas being roads and city parks. Rural areas had open farmland, forests, moors, lakes and other habitats with scattered houses and farms that were never continuous. This simple operational definition is in accordance with those adopted in other studies (e.g., Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999). I defined a species as being urbanised based on information in Cramp and Perrins (1977–1994) and Glutz von Blotzheim and Bauer (1966–1997). I relied on these standard handbooks because the information was collated in a similar and stringent manner, allowing comparison among species. I combined this with my personal experience with all the species considered, including information from colleagues interested in urbanisation of birds. A species being classified as urbanised had to fulfill the following two criteria: (1) breeding populations occur inside towns and cities, and (2) population densities in towns and cities are higher than in nearby rural habitats. Based on these criteria I made a list of 63 urbanised species of breeding birds out of the 521 species recorded in the Western Palearctic that fulfill the two criteria listed above. I note explicitly that many species are urbanised in some areas, but not in others because urbanisation is an ongoing process that starts initially in one area, followed by colonisation of urban areas in other parts of the continent. This list of species was subsequently reduced to 39 pairs of phylogenetically independent events of urbanisation of birds with information on urbanised species and their rural close relatives (see below for comparative analyses).

Ecological variables

Dispersal ability

I estimated maximum dispersal distance as the maximum distance from the mainland to an island with a permanent breeding population, using information from the distribution maps for 250 passerine bird species in Cramp and Perrins (1977–1994). I did that by considering the distance from the mainland to all islands closer than the most distant island to the mainland, even those that do not currently hold permanent populations. Therefore, the estimate of maximum dispersal distance was a minimum estimate because many populations on islands are likely not to have taken the shortest route from the mainland to an island, and because islands may have been colonised directly rather than by using intermediate islands as stepping-stones.

As a second estimate of dispersal ability I recorded the total number of subspecies in the entire range (Belliure et al. 2000), using Cramp and Perrins (1977–1994) as a source.

Feeding innovations

Garamszegi et al. (2007) published a list of feeding innovations in birds collated by Louis Lefebvre and his students from an exhaustive survey of 30 years (1970–2000) of the short note sections of 65 generalist ornithology journals covering six geographic areas of the world (Nicolakakis 2001). A feeding innovation was simply the total number of novel feeding behaviours reported in the literature. Here I used data from Europe only. I used an index of the relative frequency of feeding innovations as a measure of innovation ability, by controlling statistically for research effort because larger effort automatically would imply a greater estimate of innovations (Garamszegi et al. 2005). Because urban species may be studied more intensely than rural species, such control is essential in order not to draw biassed conclusions. Therefore, I estimated research effort by using the number of studies published since 1972 on each species as cited in the ISI Web of Science (http://isi1.newisiknowledge.com/) (see Garamszegi et al. 2007). To estimate relative feeding innovation independent of research effort, I used the number of publications as a covariate in the statistical models.

Flight distance

During March–August 2006 I estimated flight distances for birds, using a standard technique developed by Blumstein (2006). These recordings were made in Ile-de-France and Bretagne, France and Northern Jutland, Denmark. In brief, when an individual bird had been located while resting, foraging, preening or singing, I moved at a normal walking speed towards the individual, while recording the number of steps (which approximately equals the number of metres). The distance at which the individual took flight was recorded as the flight distance, while the distance

walked was the distance from where the observer started walking until the position of the bird. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest metre. While recording these distances, I also recorded habitat (urban, or rural), date and time of day, and the sex of the individual if external characteristics allowed sexing with binoculars. Flight distance was estimated as the square-root of the sum of the squared horizontal distance and the squared height (Blumstein 2006).

All recordings were made during the breeding season, when most individuals are sedentary, thus preventing the same individual from being recorded at different sites. Only adults were included to avoid problems caused by juveniles having short flight distances. If there was doubt about age, an individual was not recorded. I avoided pseudo-replication by recording only individuals of a given sex and species at a given site. I recorded 2,298 flight distances in total, and the present study of flight distance and urbanisation is based on data for 44 species for which I had information on flight distance for individuals from rural habitats. I excluded information from urban habitats because urban birds have shorter flight distances (Cooke 1980; Møller 2008).

I assessed the reliability of my estimates of flight distances in two different ways. First, I compared my estimates with those published by Blumstein (2006). For 13 species that were recorded in both data sets I found a strongly positive relationship between the two series of estimates [$F = 18.12$, $df = 1,11$, $r^2 = 0.62$, $P = 0.0013$, slope (SE) $= 0.89$ (0.21)], and the means were not significantly different (paired t-test, $t = 0.53$, $df = 13$, $P = 0.60$). Second, I compared my estimates from rural areas with those collected by an independent observer (Einar Flensted-Jensen) in rural areas in my Danish study area. The independent observer had been instructed how to estimate flight distances, but otherwise worked completely independently. Again, for 17 species I found a strongly positive relationship between the two series of estimates [$F = 12.86$, $df = 1,15$, $r^2 = 0.46$, $P = 0.0027$, slope (SE) $= 0.92$ (0.12)], and the means were not significantly different (paired t-test, $t = 0.04$, $df = 16$, $P = 0.99$). This provides evidence for reliability of the estimates.

Bursa of Fabricius

I used information on the mass of the bursa of Fabricius of juvenile birds from other studies (Garamszegi et al. 2007; Møller et al. 2005). The bursa of Fabricius is the most important immune organ in juvenile birds, as it synthesises antibodies, and is responsible for differentiation of the repertoire of B-cells (Glick 1983, 1994; Toivanen and Toivanen 1987). The relative size of this immune defence organ in birds may reflect the ability to respond to an infection (Glick 1983; John 1994; Rose 1981). For example, selection for increased and decreased immune response to an immune challenge by sheep red blood cells resulted in correlated response to selection for size of the bursa of Fabricius (Parmentier et al. 1995). In addition, relative bursa size has been found to relate to factors that involve high parasite pressure (Møller and Erritzøe 1996, 1998).

Life history

I obtained information on age at first reproduction (years), adult survival rate (%), mean clutch size, and maximum number of broods per year from Cramp and Perrins (1977–1994). If more than a single estimate was available, I used the first one reported.

Range size, population size and population density

I determined the global northernmost and southernmost latitude of the breeding and the wintering distributions, respectively, to the nearest tenth of a degree of all species from Cramp and Simmons (1977–1994). I estimated breeding range in the Western Palearctic and total breeding range size as the area of the shape bounded by the greatest span of latitude and longitude of each species' breeding range, as published in Cramp and Perrins (1977–1994). To take into account the curvature of the Earth (which was assumed to be spherical), this area was estimated by the equation

$$\text{Area} = R^2 \times (\text{Longitude}_1 - \text{Longitude}_2) \times (\sin(\text{Latitude}_1) - \sin(\text{Latitude}_2)),$$

where R is the radius of the Earth (6,366.2 km) and latitude and longitude are expressed in radians.

In widespread species, Old and New World ranges were calculated separately and subsequently summed. This method over-estimates true geographical range, but the error should be random with respect to the variables under test. Estimates of area were strongly positively correlated with geographical range size as calculated by counting 1° grid cells overlain on published distribution maps for a sample of 20 Palearctic and Nearctic bird species ($r = 0.87$, $P < 0.001$), and with range size as reported for a sample of 11 threatened species (Stattersfield and Capper 2000) ($r = 0.98$, $P < 0.001$, based on log-transformed data).

Population sizes were obtained from Hagemeijer and Blair (1997), who reported the total number of breeding pairs in the Western Palearctic west of the Ural Mountains, obtained in a consistent way from national bird census programs in all countries. I used the mean of the minimum and maximum estimates.

Body mass

I obtained body mass from Cramp and Perrins (1977–1994) or, if data were unavailable, from Dunning (1993).

Comparative analyses

I identified 39 independent events of urbanisation in birds, using extensive information on habitat use derived from handbooks, the primary literature and personal experience. This information was investigated in a phylogenetic context, relying on the phylogenetic relationships among species provided by Sibley and Ahlquist 1990), combined with information in Barker et al. (2004), Hackett et al. (2008) and other sources. These 39 urbanised species were matched with a close relative picked at random among congeners or, if congeners were missing, a close relative was picked at random among rural species in the same subfamily. If several urban species were found in a genus, I used the most urbanised species (the species with larger population density in urban habitats and a longer history of urbanisation) as a representative of the urban category of species and the less urbanised species as a representative of the rural category of species.

I used the paired species comparative approach (Møller and Birkhead 1992) because urbanisation can be considered a nominal variable that is not easily handled in standard comparative analyses, when several potentially confounding variables simultaneously have to be controlled. This approach has the advantage that not only known, but also unknown confounding variables are controlled automatically to a large extent because closely related species are by definition very similar in most respects (Møller and Birkhead 1992). The reason for this similarity is that almost their entire evolutionary history is shared, with only the time since divergence differing between pairs of species. I implemented the pairwise comparative approach in a repeated measures design using MANOVA by including each pair of observations as a repeated measure (JMP 2000). When controlling for confounding variables such as body size and distribution range in a given analysis, I used a repeated measures design in MANOVA by treating the two measures of a pair of species as the repeated measure and any potentially confounding variable as an additional variable in the model (JMP 2000).

Because the different variables analysed were not statistically independent, I used a MANOVA with all response variables entered as repeated measures, species pairs of urban and rural species as a categorical variable, and urbanisation as a factor (JMP 2000). The nine variables included were body mass, mean population size in the Western Palearctic, total breeding range, adult survival

rate, annual fecundity, residual force required to remove feathers from rump, flight distance, number of subspecies, and distance to the nearest mainland. I did not include feeding innovations and mass of bursa of Fabricius because this would have reduced sample size to such a level that an analysis would not have been meaningful. I tested all transformed variables for deviations from normality, and these tests were not significant after Bonferroni adjustment for multiple tests.

Given that urbanisation is a derived trait, the ancestral state must have been rural breeding. Therefore, phenotypic values for urban species were expressed relative to those of closely related rural species. As a measure of the magnitude of a difference between pairs of rural and urban species I calculated effect size as Pearson's product moment correlation coefficient because this is easily interpretable, as the squared value provides an estimate of the amount of variance explained. Cohen (1988) suggested that a small effect had an $r = 0.10$, accounting for 1% of the variance, an intermediate effect an $r = 0.30$, accounting for 9% of the variance, and a large effect an $r = 0.50$, accounting for 25% of the variance.

Results

Differences in ecological characteristics between urban and rural species

Urban species had significantly greater dispersal propensity than closely related rural species, when analysing the maximum distance of extant insular breeding populations from the mainland (Fig. 1; Table 1). Inclusion of body mass as a potentially confounding variable did not change
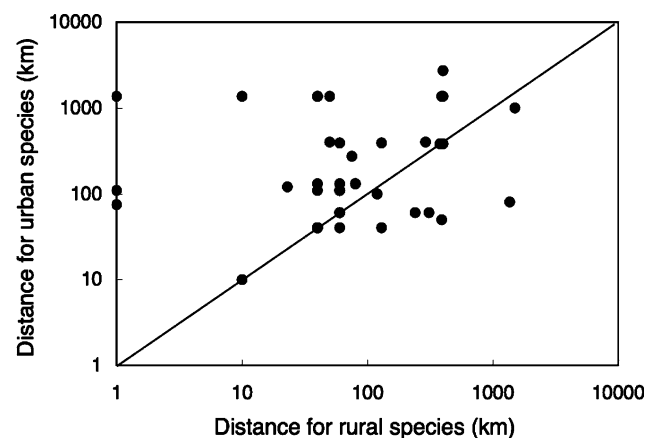

Fig. 1 Maximum distance of island breeding populations to the nearest mainland (km) for urban and rural species pairs of birds. The line is the $y = x$ line indicating similar distances for the two categories of species

Table 1 Summary statistics for differences in ecological variables between rural and urban species of birds

Variable	Mean	SE	F	df	P	Effect size
Dispersal						
Mainland distance	−0.434	0.140	9.55	38	0.0037	0.448
No. subspecies	−0.140	0.071	3.85	38	0.043	0.303
Innovation rate						
Innovation rate	−0.252	0.107	5.57	11	0.038	0.336
Flight distance						
Flight distance for rural birds	1.059	0.088	12.10	14	<0.0001	0.955
Parasitism and predation						
Mass of bursa of Fabricius	−0.183	0.060	9.36	10	0.012	0.696
Residual force required to remove rump feathers	−0.065	0.020	10.24	7	0.015	0.771
Life history						
Annual fecundity	−0.050	0.024	4.24	37	0.047	0.321
Adult survival	−0.053	0.020	7.29	14	0.017	0.585
Ecological success						
Total breeding range	−0.160	0.064	6.20	38	0.017	0.375
Western Palearctic breeding range	−0.179	0.042	17.89	38	0.0001	0.566
Population size	−0.828	0.153	29.27	38	<0.0001	0.660
Population density	−0.504	0.145	12.11	38	0.0013	0.492

The mean (SE) is the mean difference in phenotype between rural and urban species, with the test statistic for the difference deviating from the null expectation of zero. Effect size is Pearson's product–moment correlation coefficient. Sample size is $df + 1$

this conclusion. The effect size was intermediate-to-large (Table 1).

The high level of dispersal propensity of urban species was further supported by the finding that urban species had a relatively larger richness of subspecies than rural species, after inclusion of total distribution range as a variable in the analysis (Fig. 1; Table 1). Therefore, urban species generally had higher dispersal propensity than closely related rural species.

The two measures of dispersal propensity were not significantly related ($F = 1.81$, $df = 1,48$, $r^2 = 0.04$, $P = 0.18$).

The residual innovation rate of urban species, after accounting for research effort, was significantly larger than that of rural species, with an intermediate effect size (Table 1).

Urban species had significantly shorter flight distances in rural habitats than closely related rural species (Table 1). Inclusion of body mass as a potentially confounding variable did not change this conclusion.

Urban species had a larger bursa of Fabricius than rural species, with an effect size that was then larger (Fig. 2a; Table 1).

Urban species had less loose rump feathers as reflected by the greater force required to remove feathers from the rump relative to feathers from the back and the breast (Fig. 2b; Table 1), with seven of the eight species pairs having a larger value in the urban species. The effect size was large.

Urban species had significantly higher annual fecundity than rural species, the difference amounting to an intermediate effect size (Table 1).

Furthermore, urban species had higher adult survival rate than rural bird species (Fig. 3; Table 1).

Ecological success of urban species

Urban species had larger breeding distribution ranges than closely related rural species (Fig. 4a; Table 1). This was also the case when considering only the breeding distribution in the Western Palearctic (Table 1).

Urban bird species were more abundant than rural species, as reflected by their larger population sizes (Fig. 4b; Table 1). Furthermore, urban species had higher population densities than rural species when analysing total population size in the Western Palearctic, with breeding distribution range in the Western Palearctic as a covariate (Table 1). Therefore, urban bird species were more widespread and abundant than rural species, even in their breeding range.

Multivariate analysis of variance

The different factors associated with urbanisation were correlated, and I entered nine of these variables as repeated measures in a MANOVA. The overall model showed that the difference between species pairs differing in degree of urbanisation was not significant (Table 2). In contrast, there was a very large difference among factors, this difference
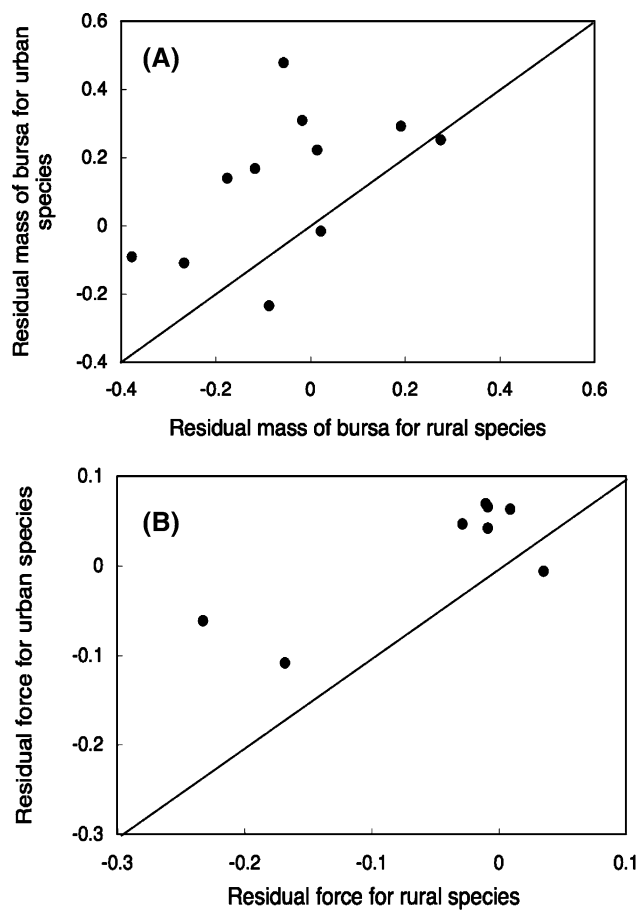
Fig. 2 **a** Residual mass of the bursa of Fabricius, after controlling for body mass, for urban and rural species pairs of birds. **b** Residual force required to loosen feathers from the rump, after adjusting for the force required to loosen feathers from the back and the breast, for urban and rural species pairs of birds. The lines are the $y = x$ lines indicating similar values for the two categories of species
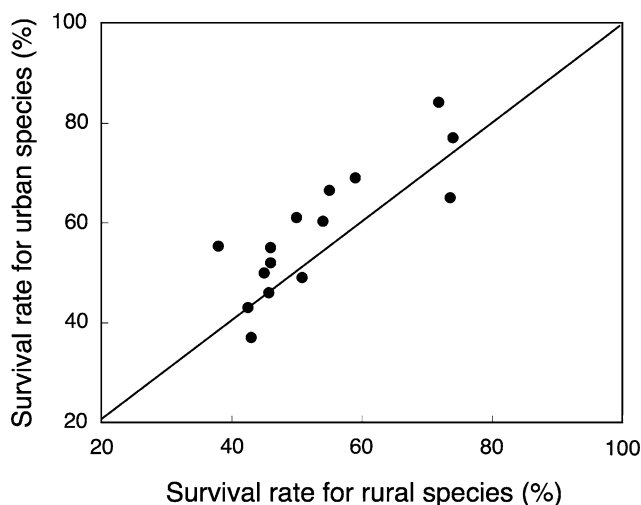

Fig. 3 Adult survival rate (%) for urban and rural species pairs of birds. The line is the $y = x$ lines indicating similar values for the two categories of species
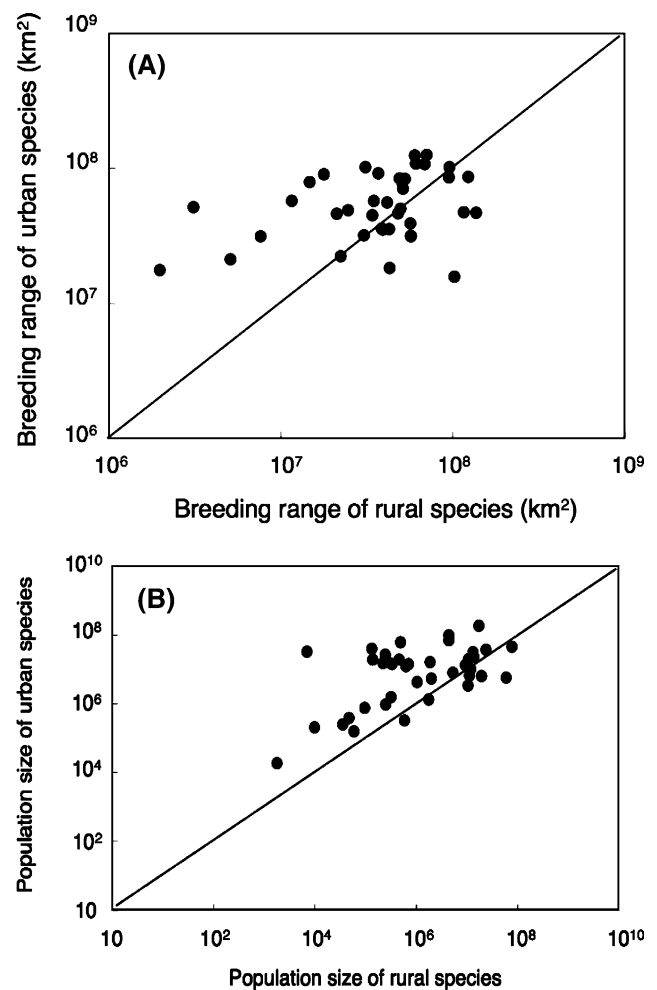

Fig. 4 **a** Breeding range size (km^2) and **b** breeding population size in the Western Palearctic (pairs) for urban and rural species pairs of birds. The lines are the $y = x$ lines indicating similar values for the two categories of species

interacted significantly with urbanisation, and this difference interacted strongly with species pair (Table 2). In other words, the difference between rural and urban species remained significant when correlations among variables were controlled statistically in a MANOVA.

Discussion

This first general study of the characteristics of urban species of birds compared with closely related rural species over a large geographic region identified a range of ecological differences, with the differences amounting to intermediate-to-large effect sizes. Urban bird species generally had elevated dispersal ability, elevated innovation rates, short flight distances, larger immune defence organs, required greater force to remove feathers from the rump, had higher annual fecundity and adult survival rate, and

Level	Factor	F	df	P
Between subjects		3.32	1,4	0.14
Within subjects	Ecological factors	4,558.36	8,32	<0.0001
	Ecological factors × urbanisation	2.47	8,32	0.033
	Ecological factors × species pair	3.82	168,32	<0.0001

larger breeding ranges and population sizes than closely related rural species. Given that the ancestral state in a phylogeny was rural breeding we can infer that these differences are associated with successful invasion of urban environments.

Invasion of any novel environment implies a certain degree of dispersal because otherwise a novel environment will not receive potential propagules that produce permanent settlement. Here I tested the assumption that bird species with a high dispersal propensity are disproportionately represented among species that have successfully colonised urban areas. First, I assumed that greater dispersal propensity as reflected by establishment of permanent breeding populations far from the nearest mainland indicated successful dispersal ability (Møller and Mousseau 2007). By definition, this direct measure of dispersal distance must reflect the ability of different species to regularly move long distances and there establish a breeding population, and hence reflect effective dispersal. Second, I used relative subspecies richness as a measure of effective dispersal ability. These two estimates of dispersal ability were statistically independent, and both independently predicted urbanisation of birds. These two findings in combination suggest that urban areas are more likely to become colonised by species with a high dispersal propensity.

Successful invasion of urban environments would require that individuals attempt to breed there, suggesting a history of innovations that would allow colonisation. A measure of the ability to cope with novel conditions is the rate of feeding innovations that has been shown to successfully predict a number of different ecological phenomena in both birds and primates (Garamszegi et al. 2005; Lefebvre et al. 1997; Reader and Laland 2002). Indeed, urban species had greater innovation rates than rural species after controlling statistically for research effort. Garamszegi et al. (2007) have shown that feeding

innovations in birds are more common in species with a large bursa of Fabricius, and that feeding innovations result in higher parasite-mediated selection. These results suggest that feeding innovations precede evolutionary changes in size of the bursa of Fabricius. If we assume that a large bursa of Fabricius for a given body size reflects a high level of resistance to parasites, then both innovations and resistance to parasites would favour invasion of urban environments. Interestingly, Yeh et al. (2007) have shown that colonisation of urban environments is associated with novel kinds of nesting behaviour, suggesting that innovation in domains other than feeding may favors urbanisation.

Urban birds are often 'tame', with short flight distances when approached by humans and other potential predators (Cooke 1980; Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999; Møller 2008). I emphasise that this comparison was based on flight distances of rural populations of urbanised and non-urbanised, closely related species, from which urbanised populations must have originated. While two studies have shown that urban populations generally have shorter flight distances than rural populations (Cooke 1980; Møller 2008), this is the first study to show that this difference already existed in rural populations before invasion of urban environments. Flight distance of an individual animal when approached by a potential predator like a human can be considered a standardised measure of the risk that this individual is willing to take (Blumstein 2006). Because individuals trade early flight against resource acquisition or rest, individuals should optimise flight distance to reflect the fitness costs and benefits of early flight. Therefore, flight distance can be considered a behavioural measure of risk-taking. Bird species that had successfully invaded urban areas had shorter flight distances in rural habitats than rural species, and this was also the case when body mass was entered as a potentially confounding variable. Therefore, species that have successfully invaded urban areas were, through their short flight distances, pre-adapted to urban environments with close proximity to humans.

Urban environments are often characterised by a release from predators and parasites (Klausnitzer 1989; Marzluff et al. 2001; Shochat et al. 2006; Møller 2008; this study). However, urbanised species of birds and other animals typically have very high population densities (Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999), implying that they would suffer disproportionately from parasite transmission and the functional responses of predators relative to their less abundant rural sister species. Here, I have shown that urban species may, on average, suffer less from parasitism and predation than their rural sister taxa, making these characteristic pre-adaptations to urbanisation. First, comparison of the mass of the bursa of Fabricius showed that this important immune defence organ is consistently

larger in urban than in rural species (Fig. 2a). The size of the bursa reflects investment in B-cell mediated immunity (Glick 1983, 1994; Toivanen and Toivanen 1987). For example, selection experiments in chickens for altered immune response to a challenge with sheep red blood cells resulted in a correlated response for size of the bursa of Fabricius (Parmentier et al. 1995). Furthermore, the relative size of the bursa relates to factors that involve intense selection from parasites such as hole nesting, colonial breeding and bird migration (Møller and Erritzøe 1996, 1998). Therefore, large relative size of the bursa in urban species would suggest that such species are resistant to a range of parasites compared to rural sister taxa. Second, the force required for removal of feathers from the rump relative to the back and the breast of urbanised bird species reflects an evolutionary history of low predation rates, because birds benefit from relatively loose rump feathers as a means of escaping predators (Møller et al. 2006). Therefore, bird species with relatively loose rump feathers would imply an evolutionary history of weak natural selection caused by predation (Møller et al. 2006). Such species with little impact of predation-mediated mortality would suffer less from increased levels of predation at high population densities in urban environments than their sister taxa in rural areas. This makes urban species of birds less affected by density-dependent predation rates than rural species. Møller (2008) has already shown that bird species with relatively large fractions of their total populations in urban areas are not particularly susceptible to predation by European sparrowhawks *Accipiter nisus*, as one would a priori expect from their large urban population densities.

Urban species of birds differed from their rural counterparts in terms of life history by having high annual fecundity and adult survival rate. Life history traits that increase the probability of successful colonisation of novel environments include high adult survival rate (Legendre et al. 1999). Therefore, urban bird species can be considered to be pre-adapted to invasion of novel environments. Low levels of parasite-mediated and predation-mediated natural selection in urban compared to rural species, as discussed above, will further increase the probability of successful colonisation.

Ecological success of urban and rural species of birds differed considerably. Urban species generally had larger breeding range size, population size and population density than urban species, even when controlling for potentially confounding variables like body size and similarity due to common descent. I can exclude the possibility that greater ecological success was a consequence rather than a cause of successful urbanisation because urbanisation is recent, with most cases having occurred during the last 200 years. Therefore, ecologically successful species are more likely to invade urban areas than less successful species.

The present study does not allow a test of whether differences between urban species are due to adaptation rather than to phenotypic plasticity. However, there is some evidence of adaptation to urban environments. For example, crosses between urban and rural populations of European blackbirds *Turdus merula* have suggested that urban populations have evolved slightly different annual cycles, with the reproductive season starting earlier and lasting for longer, a different degree of photo-sensitivity, and a change in life history including fecundity and survival (Partecke et al. 2004), although this requires confirmation from other urban and rural populations, because current knowledge is based on only a single comparison.

Urbanisation of birds can be considered a model system for invasion biology because numerous independent evolutionary events will allow statistical tests of the causes and consequences of urbanisation. Breeding experiments could identify the underlying genetic bases of differentiation and genetic correlations among apparent adaptations or pre-adaptations to urban life. Urbanisation of birds is associated with a number of known changes in selection pressures due to a scarcity of parasites and predators (Klausnitzer 1989; Møller 2008; this study), an increased population density and an elevated population density. Such factors would potentially be open to experimentation to test for the effects of ecological factors on life history in urban and rural species.

In conclusion, urbanisation has occurred successfully in a large number of independent evolutionary events, with urban species being characterised by a suite of phenotypic traits. These findings suggest that a specific subset of bird species with these particular ecological characteristics can be predicted to invade urban environments in the future.

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