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What makes an urban bird?

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Abstract

Urban development is increasing across the globe. This poses a major threat to biodiversity, which is often limited in towns and cities. Despite much interest in identifying species' traits that can predict their responses to environmental degradation this approach has seldom been employed to assess which species are particularly vulnerable to urban development. Here, we explore this issue, exploiting one of the best available datasets on species' responses to towns and cities in a highly urbanised region, comprising avian densities across approximately 3,000 British urban and rural 1km x 1km grid cells. We find that the manner in which species' responses to urbanisation is measured has a marked influence on the nature of associations between these responses and species' ecological and life history traits. We advocate that future studies should use continuous indices of responses that take relative urban and rural densities into account. Contrary to previous studies we find that urban development does not select against avian long-distance migrants and insectivores, or species with limited annual fecundity and dispersal capacity. There was no evidence that behavioural flexibility, as measured by relative brain size, influenced species' responses to urban environments. In Britain, generalist species, as measured by niche position rather than breadth, are favoured by urban development as are, albeit to a lesser extent, those that feed on plant material and nest above the ground. Our results suggest that avian biodiversity in towns and cities in urbanising regions will be promoted by providing additional resources that are currently scarce in urban areas, encouraging supplementary feeding, and developing suitable environments for ground-nesting species.

Key words: birds, brain size, cities, development, predation, specialist, species traits, urbanisation index

Introduction

Globally, urbanisation is amongst the fastest growing land uses (UN, 2008). This is partly due to human population growth, but also arises from socio-economic factors that result in people moving from rural to urban areas, a greater proportion of single person households, and elevated demand for low density housing (Liu *et al.*, 2003; UN, 2008). Increased urban development has a negative impact on biodiversity for three main reasons. First, urbanisation is most likely to occur in regions that contain large numbers of people; this results in conservation conflicts because, at broad spatial scales, human population density is positively correlated with species richness (Evans *et al.*, 2006, 2007; Luck, 2007). Second, the land selected for housing development is often more ecologically valuable than undeveloped areas (Bartlett *et al.*, 2000; Gonzalez-Abraham *et al.*, 2007; Radeloff *et al.* in press). Third, highly developed urban areas support fewer native species than the rural habitats which they replace; indeed, many species do not occur in urban areas despite being present in nearby rural habitats (Tratalos *et al.*, 2007; Grimm *et al.*, 2008). These reductions in biodiversity are increased because there is limited spatial turnover in the composition of urban assemblages, i.e. urbanisation promotes biotic homogenization (McKinney, 2006; Devictor *et al.*, 2007).

Urban development is thus a major threat to conservation (Czech *et al.*, 2000; McDonald *et al.*, 2008), and it is important to assess which ecological and life history traits predict species' responses to urbanisation. A small number of initial investigations have been conducted that classify species into two groups that differ in their response to urbanisation, such as those that occur or reproduce in cities and those that do not, and then assess how species' traits differ between the two groups (Bonier *et al.*, 2007; Kark *et al.*, 2007; Croci *et al.*, 2008; Møller, 2009). Such studies are severely limited because they assume that all species within a group have an equivalent response to urbanisation. This is highly unlikely to be valid as species vary in their urban densities, and the types of urban areas in which they occur (Tratalos *et al.*, 2007; Grimm *et al.*, 2008; Evans *et al.*, 2009). Here, we provide a rare assessment of associations between species' traits and responses to urban development. In notable improvements to previous studies we measure species' responses

using a continuous quantitative index, and assess how the nature of associations between species' traits and responses to urbanisation depend on the precise form of these urbanisation indices. We start, however, by assessing which ecological and life history traits are likely to influence a species' ability to thrive in urban areas; this will be determined by successful progression through each of the three phases of biotic urbanisation, i.e. arrival, adjustment and spread (Evans *et al.*, in press).

Species vary widely in their environmental tolerances, and generalists appear less vulnerable to habitat deterioration and loss (Owens & Bennett, 2000; Shultz *et al.*, 2005), including urban development (Bonier *et al.*, 2007; Kark *et al.*, 2007). Behavioural flexibility may also help species tolerate environmental change. Measurements of flexibility, such as the acquisition of new foraging techniques, are correlated with relative brain size (Lefebvre *et al.*, 1997, 1998; but see Healy & Rowe, 2007), which can predict the magnitude and direction of population trends in response to environmental degradation (Shultz *et al.*, 2005), and which species invade novel environments (Sol *et al.*, 2005, 2008). Therefore, urbanisation may also promote behaviourally flexible species with relatively larger brains.

Long distance migrants are declining more rapidly than residents, and may be more vulnerable or more exposed to environmental change (Sanderson *et al.*, 2006; Wilcove & Wikelski, 2008); they also appear to be scarcer in urban areas than residents (Friesen *et al.*, 1995; Rodewald & Bakermans, 2006). This may be because migrants are disadvantaged when competing for limited resources as they tend to arrive on breeding grounds after residents have established territories. Migrants also appear more susceptible to mismatches between the timing of breeding and peak food availability induced by climate change (Visser *et al.*, 2004; Post & Forchhammer, 2008); the urban heat island effect (Collier, 2006) may thus make developed areas less suitable for migrants.

Within urban areas green space is highly fragmented, thus dispersal may result in arrival in unsuitable environments more frequently than if individuals remained in their current habitat patch; reduced dispersal capacity can thus be advantageous in cities (Cheptou *et al.*, 2008). This advantage may also arise because frequent dispersal can generate sufficient gene flow between populations occupying contrasting environments to swamp locally evolving adaptive genotypes, thus preventing genetic adaptation to novel conditions, including those occurring in urban areas (Rasanen & Hendry, 2008; Rios *et al.*, 2008). In contrast, strong dispersal capacity increases the probability of a species colonising novel environments (Lloret *et al.*, 2005; Philips *et al.*, 2008), and recolonising previously occupied habitat patches following local extinction (Hanski, 2001). It is thus generally considered that, and despite the contrary hypotheses, species which have successfully colonised urban areas are likely to have strong dispersal abilities (Møller, 2009).

Adjustment to novel urban environments may require genetic change (Partecke *et al.*, 2006; Rios *et al.*, 2008). In sexually reproducing species the potential rate of such change is positively influenced by short generation times and the production of a large number of offspring, as these determine the number of meiosis events and thus the potential for DNA copying errors (i.e. mutations). These demographic traits also generate high intrinsic population growth rates which may enable rapid recovery from disturbance, and produce more potential colonists. These mechanisms may explain why fecund species appear less vulnerable to environmental degradation (Owens & Bennett, 2000; Purvis *et al.*, 2000).

Urban areas are often characterised by the provision of supplementary avian food, which predominantly consists of seeds or other plant material (Davies *et al.*, 2009). Therefore, species which can exploit such food sources may be more abundant in urban areas than those with alternative diets (Fuller *et al.*, 2008); indeed insectivorous species appear to be relatively scarce in urban areas (Chace & Walsh, 2006; Kark *et al.*, 2007).

Finally, predation risk may be greater in urban areas due to changes in habitat types (Riley *et al.*, 2005, Hamer & McDonnell, 2008), or higher densities of some predators such as domestic cats *Felis catus* and nest predating corvids (Sims *et al.*, 2008; Evans *et al.*, 2009). It is often suggested that bird species which nest on or close to the ground will be adversely impacted by urbanisation due to increased nest predation (Jokimäki & Huhta, 2000, Chace & Walsh, 2006, Croci *et al.*, 2008). In contrast, a recent review concludes that across those species which occur in towns and cities urbanisation does not consistently markedly alter avian nest predation rates (Chamberlain *et al.*, 2009). However, when considering a wider range of species it remains plausible that those which are vulnerable to predation because they nest on the ground will be adversely influenced by urbanisation.

Here we assess the hypotheses that avian species which have (i) broad ecological requirements; (ii) relatively large brains; (iii) resident populations, (iv) strong dispersal capacities, (v) high fecundity, (vi) a plant-based diet, and (vii) do not nest close to the ground are more likely to be urbanised than species which lack these traits. In so doing, we provide the first assessment of whether the nature of associations between species' traits and responses to urban areas varies with the form of urbanisation indices. Specifically, we compare indices constructed using different definitions of urban land, and which do and do not take species' rural abundances into account. We use the British avifauna as a case study for three reasons. First, the national Breeding Bird Survey (BBS) enables population densities to be calculated for specific habitat types. We can thus develop urbanisation indices along a continuous scale, a notable advance on previous studies that typically classify species on a binary, and somewhat subjective, scale as urbanised or not. Second, detailed data on the ecological and life history traits of British birds are available that enable more rigorous tests of associations between species' traits and urbanisation than previously possible. Finally, Britain has a long history of urban development and is now amongst the most highly urbanised regions (with

between 8% and 10% of the land area being urban, Haines-Young *et al.*, 2000; Fuller *et al*., 2002). Our analyses thus facilitate prediction of which species are likely to thrive, and which to be threatened, in regions that are currently less urbanised but are experiencing rapid urbanisation.

Methods

Urbanisation indices

For each of 88 commoner and accurately surveyed? native breeding bird species recorded in the 2006 BBS (Raven *et al.*, 2007) the urbanisation index was first calculated as the density in urban areas. Species may, however, occur at low densities in urban environments because their ecological characteristics are such that they have a large home range and thus always occur at low densities, irrespective of habitat type, rather than because urban environments are particularly unsuitable. We therefore also calculated another urbanisation index as the ratio of urban and rural densities. We used two definitions of urban areas that varied in the proportion of built up land in the focal area (see below), thus giving four different urbanisation indices.

A full description of the BBS survey methodology is provided in Appendix A. In brief, distance sampling was conducted along ten 200m transect sections in a randomly selected 1km x 1km square. The main habitat, such as human sites or woodland, in each section was recorded together with finer level habitat features (Crick, 1992). We defined urban BBS squares in two ways. First, those in which the primary habitat type in each of the ten transect sections was classified as urban or suburban; 153 of 3002 squares met this criterion. Second, those with at least six urban or suburban transect sections; 272 squares met this criterion. Urban squares are located throughout the focal region, and remaining squares were considered to be rural. The density of adult breeding birds was determined using the methodology of Newson *et al.* (2008).

Species traits

Data on species traits were obtained for British populations from Cramp *et al.* (1977-1994) unless otherwise stated (Appendix B). These data are typically derived from studies conducted in relatively natural environments. Annual fecundity was calculated as the mean number of clutches per year multiplied by the mean clutch size. Species were classified as nesting close to the ground if they typically nested on or just above the ground. We recorded whether invertebrates or plant material comprised major components of adult diets during the breeding season using two binary factors, thus omnivorous species were coded as using both food sources. Using Wernham *et al.* (2002), species were classified as long distance migrants if the majority of the population wintered south of the Sahara, and as residents if the majority wintered in Britain. Arithmetic mean natal dispersal distance of British birds was obtained for 61 species from Paradis *et al.* (1998). We used natal rather than breeding dispersal distance as the former was available for more species. Paradis *et al.* (1998) calculated both arithmetic and geometric mean dispersal distances, but the two are strongly correlated (Spearman rank correlation $r_s = 0.93$, n = 63, $P<0.0001$), and we arbitrarily decided to use the former. We logarithmically transformed natal dispersal distance to base ten to reduce the skew in its distribution.

Brain size can be measured as either endocranial volume or brain mass, and the two are very strongly correlated (Iwaniuk & Nelson, 2002). We obtained data on endocranial volume (mm^3) for 51 species that were obtained by filling the brain cavity, of unfractured skulls from apparently healthy adults, with a 50:50 mixture of sizes 10 and 11 lead shot, which yields highly repeatable measurements (Iwaniuk & Nelson, 2003; A. Iwaniuk, unpublished data). We also obtained brain mass data for 81 species from Mlíkovský (1989a-c, 1990). These data were converted to volumes using the widely accepted value of the density of fresh avian brain tissue (1.036 g/ml; Ebinger, 1995; Iwaniuk & Nelson, 2001). The resultant two data sets were strongly correlated ($r^2 = 0.987$, $P<0.0001$, n = 49; linear regression of data logarithmically transformed to base ten) and a paired t-test showed there were no significant differences between them ($T = -0.01$, $P = 0.989$, n = 49).

When brain size data were available from both sources we used the average value, but otherwise used information from a single source, thus providing data for 83 species. Brain size scales with body size and this allometric relationship must be taken into account when assessing the influence of brain size on species' ecological responses. The inclusion of both variables in the allometric relationship, i.e. brain size and body size, as predictors in a single multiple regression analysis provides the ideal method for assessing the influence of the focal variable, i.e. relative brain size (Freckleton, 2002). We adopted this approach using mean body mass data from the compilation in Gaston & Blackburn (2000) and logarithmically transformed both brain volume and body mass data, to base ten, to reduce the skew in their distributions. Previous studies have taken the allometry between brain and body size into account using residuals from a log-log regression of brain size against body size as a measure of relative brain size, but the use of such residuals as predictors in further analyses can generate biased parameter estimates and should be avoided (García-Berthou, 2001; Freckleton, 2002).

Due to the multi-dimensional nature of niche space we used two approaches to classify species along the continuum from specialists to generalists. First, geographic range size has previously been used as a measure of environmental tolerance under the assumption that possessing a large range requires adaptation to a wide variety of environmental conditions. This may not be valid in all situations, as a species may occur widely but use only a few habitat types within its range, but validity will be maximised when range size is measured as area of occupancy, rather than extent of occurrence, and will increase as spatial grain size becomes smaller (Gaston, 2003). Therefore, we calculated the number of European 50km x 50km grid cells occupied by each species during the breeding season from Hagemeijer & Blair (1997). Following Gregory *et al.* (1998) we excluded the far east of the surveyed region as survey coverage in these areas was typically limited. Hagemeijer & Blair (1997) do not distinguish between *Carduelis flammea* and *C. cabaret*. Only *C. cabaret*

breeds in Britain, and we estimated its range size from Hagemeijer & Blair (1997) using the description of its distribution in Clement *et al.* (1993).

Second, and in reflection of the multi-dimensional nature of niche space, we obtained data on niche breadth and niche position, which are two complementary measures of specialisation (Shugart & Patten 1972). Niche breadth measures a focal species' tolerance to contrasting environmental conditions. Niche position measures how typical the resource use of a particular species is relative to all other species and the resources available; species with a large niche position thus use less typical resources (Shugart & Patten 1972). Following the methodology of Gregory & Gaston (2000), who previously calculated niche breadth and position of British birds, we calculated niche breadth and position using a canonical correspondence analysis (CCA). The major change that we implemented compared to Gregory & Gaston (2000) was that we excluded environmental variables that described the magnitude of urbanisation from the calculations of niche metrics, thus leaving a total of 29 environmental variables (Table 1). We also implemented three further minor changes: (i) avian abundance data were from 2006, (ii) climatic data were updated to include more recent years, which required the use of cloud cover rather than sunshine hours, and (iii) land-cover classifications of 1km squares were updated. The standard deviation of each species' distribution of tolerance across each axis identified by the CCA provides estimates of niche breadth, and the root mean squared standard deviations across all four axes provides an overall estimate of niche breadth. Niche position is calculated as the distance of the centroid of a species from that of the whole assemblage, which is calculated as the mean of the coordinates of the species' centroids. Niche position was logarithmically transformed to base ten to reduce the skew in its distribution. The niche breadth and position data calculated by Gregory & Gaston (2000) were strongly correlated with our newly calculated data (niche breadth: $r = 0.900$, $P < 0.0001$; $\log_{10}$ niche position: $r = 0.842$, $P < 0.0001$; $n = 77$ in both cases).

Data analysis

Analyses were conducted in SAS vs 9.1. Whilst our four measures of urbanisation were strongly correlated (Table 2), initial analyses suggested that they may differ in the nature of their relationship with species traits. We thus assessed the relationship between species' urbanisation indices and traits using each of the four indices. Prior to analysis each index was logarithmically transformed to base ten, after adding 0.1 to all values (to ensure that indices of species that did not occur in urban areas could be transformed). For each continuous predictor we assessed if including the square term improved the fit, measured using AIC values, of a linear bivariate model. This was the case only for logarithmically transformed niche position, and its square term was thus included as an additional predictor.

We conducted multiple regression analyses and, following standard protocols, adopted the information theoretic approach to model simplification (Burnham & Anderson, 2002). All possible models given the set of predictor variables were constructed, models with lower AIC values are considered more parsimonious. We calculated model weights, the probability that a model provides the most parsimonious fit to the data, and then constructed the 95% confidence set of models as that with the smallest number of models whose cumulative weights summed to 0.95. We assessed the explanatory power of each predictor using model averaging over the 95% confidence set. For each response variable we first constructed multiple regression models for all 88 species but excluded the predictors for which data were missing for some species, i.e. relative brain size, natal dispersal, niche breadth and niche position (linear and quadratic terms), leaving six predictors and 63 possible models. We then constructed an additional set of models that used data for the 55 species for which data were available for all our predictors (11 predictors and 2047 models). For both sets of models the tolerance values of all predictors (analysis of all species, range 0.61 - 0.82; analysis of all predictors, range 0.29 - 0.74) were consistently above the threshold (0.1) at which colinearity becomes a major concern (Quinn & Keough, 2002).

Analyses were first conducted assuming that each species provided independent data. We then used phylogenetic generalised least squares (PGLS; Grafen, 1989; Martins, 1999; Garland & Ives, 2000) to test for non-independence arising from shared evolutionary history. PGLS explicitly incorporates the expected covariance among species into a statistical model fit. The correlations between error terms are thus altered to reflect the magnitude of phylogenetic relatedness amongst species. The PGLS approach was implemented in R, using the Analysis of Phylogenetics and Evolution (APE) package (Paradis *et al.*, 2004) and the phylogeny of Thomas (2008). This phylogeny excludes one of our focal species, coot *Fulica atra*, which was thus excluded from the PGLS analysis. PGLS generates a metric (λ) which varies from zero (no phylogenetic autocorrelation) to one (strong phylogenetic autocorrelation).

Results

Phylogenetic constraints

PGLS analyses demonstrated that λ was not significantly different from zero when modelling any of our response variables ($P > 0.6$ in all cases), and changes to parameter estimates were negligible. Phylogenetic correlation in these data is thus very low and analyses that treat species as independent data points are justified.

Urban densities

Analyses of species densities in urban environments, conducted across all focal species, generate remarkably consistent results whether those densities are calculated across highly urbanised squares (i.e. those in which each of the ten 200m transect sections are located in urban or suburban environments), or when moderately urbanised squares (i.e. those with six or more transect sections in urban or suburban environments) are included (Table 3a). Species' ecological and life history traits can explain almost 50% of the variation in species' urban densities (Table 3a). The predictor

with the largest explanatory capacity is European geographic range size, which correlates positively with urban density (model averaged partial r^2 = 0.23 for both density metrics; Table 3a, Fig. 1a). The explanatory capacity of two other predictor variables is greater or equal to 5%. Species have higher urban densities if they include plant material in their diet (model averaged partial r^2 = 0.08 and 0.07 when urban squares are respectively defined as moderately and highly urbanised ones), and if they are not long distance migrants (model averaged partial r^2 = 0.05 for both density metrics, Table 3a).

In analyses that focus on the 55 species for which data were available for all predictors, species traits can again explain approximately 50% of the variation in urban densities (Table 3b). In these models higher urban densities are associated with species that use resources which are common in the environment, i.e. have a low niche position (partial r^2 = 0.25 and 0.18 when urban squares are respectively defined as moderately or highly urbanised ones; Table 3b, Fig 2c). To a lesser extent high urban densities are also associated with species that feed on plant material (partial r^2 = 0.09 and 0.07 when urban squares are respectively defined as moderately or highly urbanised ones; Table 3b). The explanatory capacity of all other predictor variables was less than 5%.

Urban/rural density ratios

In analyses conducted across all species, ecological and life history traits can explain approximately 30% of the variation in the ratio of urban and rural densities; results are again consistent with regard to the definition of urban squares (Table 3a). The reduced explanatory power of the ratio indices does not appear to arise from reduced variation in the response variables as both response variables have similar coefficients of variation (moderately urbanised squares: density index, 2.55; ratio index, 2.38; highly urbanised squares: density index, 2.74; ratio index, 3.09). The traits associated with the ratio urbanisation index differ notably from those that explain variation in species' urban densities. The most marked difference is that the size of a species' European geographic range is no

longer strongly associated with urbanisation (partial r^2 is consistently < 0.01; Table 3a, Fig. 1b); the same also applies to migratory status (partial $r^2 \leq 0.01$; Table 3a). Species tend to have higher densities in urban areas than rural ones if they do not nest on or close to the ground (partial $r^2 = 0.08$ and 0.10 when urban squares are respectively defined as moderately or highly urbanised ones; Table 3a), and when their diet includes plant material (partial $r^2 = 0.10$ for both ratio indices; Table 3a).

In analyses conducted on the restricted set of species, their traits can explain approximately 40% of the variation in the ratio index of urbanisation (Table 3b). Species with higher urban to rural densities have lower niche positions (partial $r^2 = 0.20$ and 0.14 when urban squares are respectively defined as those with six and ten urban/suburban transect sections; Table 3b, Fig 1d), and tend to include plant material in their diet (partial $r^2 = 0.10$ and 0.09 respectively for moderately and highly urbanised squares; Table 3b). Partial r^2 values were less than 0.02 for all other predictors.

Discussion

The lack of phylogenetic signal in the urbanisation indices is not surprising given that a number of closely related avian species differ markedly in the extent to which they are urbanised in Britain. For example, turtle dove *Streptopelia turtur*, tree sparrow *Passer montanus* and rook *Corvus frugilegus* occur predominantly in rural areas, whilst congeneric species (collared dove *Streptopelia decaocto*, house sparrow *Passer domesticus*, and carrion crow *Corvus corone*) are highly urbanised (Evans *et al.*, 2009).

The species traits associated with urbanisation indices were consistent regardless of whether urban areas were defined as those that contained only highly developed areas, or when moderately developed areas were also included. In contrast, whether urbanisation indices were constructed using species' urban densities or the ratio of urban to rural densities had a marked influence on their

associations with species' traits, especially when analyses were conducted across all species. Urbanisation indices must thus be carefully designed to suit the aims of a particular study. We suggest that the ratio of urban and rural densities is generally the most appropriate metric for assessing responses to urban development. This is because associations between urban densities and species' traits may arise either because the traits influence a species' ability to cope with urbanisation, or because they are linked with traits that generally influence population density. Binary classifications of whether species are urbanised or not are commonly used, but they do not take relative rural and urban densities into account, and are further limited by their assumption that all species which occur in towns and cities have equivalent responses to urban development.

European range size provides a good example of how the nature of the urbanisation index alters relationships with species' traits. Whilst range size is positively associated with species' urban densities and the occurrence of species in urban areas (Table 4, as previously reported by Bonier *et al.*, 2007 and Møller, 2009), there is a negligible link between range size and the ratio of urban and rural densities. This contrast probably arises because species with large ranges are common in both urban and rural environments, as implied by the frequently documented positive interspecific abundance-range size relationship (Gaston *et al.*, 1998). Moreover, the finding that the ratio of urban to rural densities cannot be predicted by range size suggests that the latter provides relatively little information regarding how a species' density is likely to change in a rural area that subsequently becomes urbanised. This lends support to our suggestion that urban to rural density ratios provide a preferable metric of species' responses to urbanisation than either their urban densities in isolation or presence/absence in towns and cities.

Similarly, we find only limited evidence that long distance migrants have lower urban densities, and migratory status has a very negligible influence on the ratio of urban and rural densities. Whilst this appears to contradict previous suggestions that long-distance migration hinders a species' ability to

thrive in urban areas (Friesen *et al.*, 1995; Kark *et al.*, 2007; Croci *et al.*, 2008) it is partly a consequence of previous studies' use of binary indices of species responses to urban development. If we use an equivalent approach, species present in moderately urbanised squares are less likely to be long-distance migrants than expected by chance (χ^2 = 9.31, df = 1, P < 0.001), although migratory status does not influence occurrence in highly urbanised squares (χ^2 = 3.21, df = 1, P > 0.05).

Møller (2009) found that avian species occurring in European urban areas had greater dispersal ability than those absent from towns and cities; while we found no association between urbanisation indices and dispersal. However, it is difficult to compare the two studies directly due to differences in the conceptual approach (we used continuous indices of urbanisation rather than binary classifications), variation in the focal species, and in some cases differences in classification of species; for example, Møller (2009) classifies carrion crow *Corvus corone* and wren *Troglodytes troglodytes* as absent from European urban areas, but in Britain their mean urban densities are respectively 22.7 km^{-2} and 25.3 km^{-2} (Evans *et al.* 2009). Measures of dispersal also differed between the studies; we used data from intensive ringing studies, whilst Møller (2009) used surrogate measures, i.e. the number of described subspecies and maximum distance between a species' island and mainland populations. We removed the first of these differences by conducting bivariate analyses of differences in dispersal distances in species that did and did not occur in at least one of our focal urban BBS squares. The lack of association between dispersal ability and occurrence in highly urbanised areas remained, whilst species occurring in moderately urbanised areas tended to have shorter dispersal distances than non-urbanised species (Table 4), which is the opposite pattern to that found by Møller (2009). It thus appears that in highly urbanised parts of Europe, such as Britain, dispersal capacity has a limited influence on species' responses to urban development. Dispersal ability may play a more prominent role in promoting urban colonisation in

regions where development has occurred less frequently and more recently, thus reducing the number of potential sites and the time available for urban colonisation.

Annual fecundity was not associated with our urbanisation indices, even when classifying species as present/absent in urban areas (Table 4). This contrasts with previous studies reporting higher fecundity in urbanised species (Croci *et al.*, 2008; Møller, 2009), and the extent to which high fecundity generally promotes the establishment of urban populations is thus unclear.

We found strong evidence that specialists, as assessed by niche position, had lower urban densities and ratios of urban to rural densities than more generalist species. There was no association between urbanisation and niche breadth. Therefore, whilst other work suggests that urbanisation promotes generalist species, contributing to biotic homogenisation (McKinney, 2006; Bonier *et al.*, 2007; Kark *et al.*, 2007; Møller, 2009), our results indicate that such patterns depend on the precise definition of specialisation. Indeed, whilst niche breadth is a commonly used index of specialisation many studies find that niche position is a strong predictor of ecological patterns, and can be a better predictor than niche breadth (Gregory & Gaston, 2000; Shultz *et al.*, 2005; Hurlbert & White, 2007; Ranap *et al.*, 2009).

We found no evidence that relative brain size is associated with a species' ability to adapt to urban environments, thus concurring with Kark *et al.* (2007). An alternative measure of behavioural flexibility is the number of novel feeding behaviours documented for a species. This metric is sometimes positively associated with avian occurrence in urban areas (Møller, 2009; but see Kark *et al.*, 2007), but the causal nature of this relationship is uncertain as in urban areas birds may encounter more novel food sources, and thus have greater potential to exhibit novel feeding behaviours.

Urbanisation appears to select against insectivorous species (Chace & Walsh, 2006; Kark *et al.*, 2007), but we found no evidence that species which included invertebrates in their adult diet had lower urban densities, or lower ratios of urban and rural densities. It is possible that this contrast arises because we include species that feed on terrestrial invertebrates, such as earthworms (Lumbricidae), as insectivores. To test this we constructed full models (using the predictors retained in the 95% confidence set of models) in which insectivorous species were defined as those that gleaned invertebrates from vegetation, but such models still yielded little evidence that this trait was associated with urban densities or urban and rural density ratios (maximum partial r^2 value < 0.02). There was a tendency for species that included plant material in adult diets to have higher urban densities and urban to rural density ratios, than species which did not. This supports earlier work suggesting that urbanisation favours granivorous species (Chace & Walsh, 2006; Kark *et al.*, 2007), presumably because they benefit from supplementary feeding in urban areas (Jokimäki *et al.*, 2002; Fuller *et al.*, 2008).

In analyses conducted across all species, those that did not nest on or close to the ground tended to have higher urban to rural densities than ground-nesting species. Ground-nesting species tend to be open cup nesters, which typically experience higher predation rates than cavity nesting species (Martin & Li, 1992). In additional bivariate analyses we found no evidence that any of our urbanisation indices were associated with cavity nesting (partial r^2 < 0.01 for all urbanisation indices). Thus the association between ground-nesting and urbanisation in our data is not confounded with cavity nesting. Our results are comparable to the finding that ground nesting species are disadvantaged in French cities (Croci *et al.*, 2008). Whilst the reduced ability of ground-nesting bird species to thrive in urban areas may arise from increased predation risk, there is little evidence for a universal increase in predation risk in urban areas (Chamberlain *et al.*, 2009). Also, in analyses that take specialisation into account using niche metrics ground-nesting has no influence on species' urban to rural density ratios. We thus suggest that urbanisation may select against

ground-nesting species because it reduces the availability of their preferred habitat types in addition to altering predation rates.

Conclusions and implications

The total explanatory capacity of multiple regression models for the level of urbanisation of birds in Britain is higher (range of 28% to 56%) than that typically found in many ecological studies (Møller & Jennions, 2002), but is comparable to previous assessments of associations between species' traits and responses to other types of global change (Shultz *et al.*, 2005; Jiguet *et al.*, 2007; Seoane & Carrascal, 2008). The nature of associations between urbanisation indices and species' traits varies markedly with how responses to urbanisation are measured; future studies should pay close attention to this issue. We advocate that indices assessing relative urban and rural densities are preferable to the alternatives of using binary classifications of whether species are urbanised or not, which have been the focus of most other previous studies, or urban densities in isolation.

Britain has experienced profound habitat modification, but this has not resulted in marked alterations to the species composition of the regional avifauna during the last few centuries (Holloway, 1996; Stewart, 2004). Our results are thus unlikely to be biased by prior extinctions of species with certain ecological or life history traits. Britain is, however, amongst the most urbanised regions and the challenge remains of assessing how species' traits influence responses to urban development in non-avian taxa and in regions with divergent urban development patterns. Previous studies of avian species' responses to urban development have primarily been conducted in Europe and thus concern regions with similar levels of urbanisation to Britain. Despite this similarity our results differ markedly from these other studies as we find little evidence that urban development selected against insectivores, avian migrants, and species with low annual fecundity and limited dispersal ability. In some cases these differences probably arise, at least in part, due to differences in how urbanisation indices are calculated. We find support for the hypothesis that generalist

species are better adapted to urban areas than specialists, although this is dependent upon the precise definition of specialisation. Whilst explanatory power is more limited, our results also suggest that urbanisation favours species that feed on plant resources and that nest above the ground. In regions that are becoming highly urbanised, avian biodiversity in towns and cities may be increased by maximising the availability of scarce resources, encouragement of supplementary feeding, and increasing the suitability of urban areas for ground nesting species. The latter could necessitate both habitat creation, and management of predation risk.

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Table 1 Variables used to calculate niche breadth and niche position, adapted from the methodology of Gregory & Gaston (2000).

Variable	Description	Source
ALTH	Highest altitude (m)	ITE's land characteristics database from 10km x 10km squares (Ball *et al*., 1983)
ALTD	Difference between highest and lowest altitude (m)	"
RIVE	Frequency score of rivers (range 0 – 0.25) from a 5 x 5 grid overlay of square	"
RAIN	Average annual monthly rainfall (mm)	UKCP09 data for 5km x 5km squares for 2006 (http://ukclimateprojections.defra.gov.uk)
TEMP	Average annual daily temperature (°C)	"
CLOUD	Average annual hourly (or 3-hourly) total cloud cover (%)	As above but for 2003
CT01	Sea/estuary	CEH's LCM2000 data base, measured as percentage of 1km x 1km square (Fuller *et al*., 2002)
CT02	Inland waters	"
CT03	Beach/flats	"
CT04	Saltmarsh/seaweed	"
CT05	Lowland grass heaths	"
CT06	Pasture/amenity turf	"
CT07	Meadows, verges and semi-natural cropped swards	"
CT08	Marsh/rough grassland	"
CT09	Montane/hill grass	"
CT10	Dwarf shrub/grass moorland	"
CT11	Upland dwarf shrub moorland	"
CT12	Bracken	"
CT13	Lowland heath	"
CT14	Scrub/orchard	"
CT15	Deciduous wood	"
CT16	Evergreen wood	"
CT17	Upland bog	"
CT18	Arable land	"
CT19	Ruderal weeds	"
CT22	Bare ground	"
CT23	Felled forest	"
CT24	Lowland bog	"
CT25	Dwarf shrub/grass heath	"

Table 2 Pearson correlations between four urbanisation indices (logarithmically transformed to base ten) of 88 native British bird species. Indices are either the density within urban areas, or the ratio of urban and rural population densities. These indices are calculated when defining urban areas as those in which each of the ten transect sections are urban or suburban or when at least six sections met these criteria. $P<0.0001$ in all cases.

	$\log_{10}$ urban density_10 sections	$\log_{10}$ urban density_6 sections	$\log_{10}$ ratio urban to rural density_10 sections
$\log_{10}$ urban density_6 sections	0.978	_	_
$\log_{10}$ ratio urban to rural density_10 sections	0.896	0.846	_
$\log_{10}$ ratio urban to rural density_6 sections	0.853	0.859	0.938

Table 3 Multiple regression analyses of relationships between urbanisation indices of British birds and ecological and life history traits in analyses that restricted data to: (a) the six predictors that were available for all 88 species, and (b) the 55 species for which data were available for all ten predictors. For each of the two sets of analyses, model averaged partial r^2 values are presented when these are ≥ 0.01 for at least one response variable, together with model averaged parameter estimates. For categorical variables parameter estimates are reported for when the species lacks the focal trait and equal zero when a species exhibits the trait.

(a)

response	# models in 95% confidence set	model averaged total r^2	ground-nesting		diet_plants		diet_inverts		migrant		range	
			partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope
$\log_{10}$ density_6	9	0.471	0.001	+0.043	0.079	-0.643	0.006	-0.152	0.050	+0.584	0.233	+0.001
$\log_{10}$ density_10	9	0.452	0.002	+0.058	0.069	-0.618	0.003	-0.090	0.052	+0.616	0.225	+0.001
$\log_{10}$ ratio_6	6	0.318	0.103	+0.351	0.100	-0.360	0.001	-0.018	0.010	+0.097	0.000	0.000
$\log_{10}$ ratio_10	12	0.283	0.078	+0.319	0.106	-0.395	0.0002	-0.014	0.006	+0.078	0.003	+0.00002

(b)

response	# models in 95% confidence set	model averaged total r^2	ground-nesting		diet_plants		diet_inverts		migrant		$\log_{10}$dispersal		$\log_{10}$niche position		relative brain size	
			partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope	partial r^2	slope
$\log_{10}$ density_6	75	0.560	0.001	+0.034	0.089	-0.708	0.007	-0.170	0.003	+0.004	0.035	-0.584	0.253	lin. -3.617 sq. -2.095	0.009	$\log_{10}$ br_vol +0.042 $\log_{10}$ bo_size -0.131
$\log_{10}$ density_10	94	0.480	0.004	+0.107	0.070	-0.649	0.005	-0.152	0.001	+0.027	0.042	-0.680	0.184	lin. -2.179 sq. -2.179	0.004	$\log_{10}$ br_vol +0.038 $\log_{10}$ bo_size -0.079
$\log_{10}$ ratio_6	89	0.423	0.014	+0.099	0.095	-0.330	0.001	-0.024	0.007	+0.071	0.003	-0.055	0.201	lin. -1.893 sq. -1.394	0.002	$\log_{10}$ br_vol +0.020 $\log_{10}$ bo_size -0.004
$\log_{10}$ ratio_10	141	0.366	0.015	+0.111	0.086	-0.331	0.003	-0.048	0.006	+0.073	0.010	-0.122	0.135	lin. -1.744 sq. -1.401	0.004	$\log_{10}$ br_vol +0.014 $\log_{10}$ bo_size +0.009

Table 4 Variation in species' traits between British avian species that are present and absent in at least one urbanised 1km x 1km grid cell.

trait	urban definition	mean trait value		T - test
		species present	species absent	
range size (# of occupied 50km squares)	10 urban transect sections	1427 ±39, n = 56	1198 ±72, n = 32	t = -2.80, P = 0.007
"	6 urban transect sections	1377 ±40, n = 70	1215 ±97, n = 18	t = -1.54, P = 0.140
natal dispersal ($\log_{10}$)	10 urban transect sections	0.97 ±0.05, n = 43	1.24 ±0.08, n = 12	t = 2.41, P = 0.020
"	6 urban transect sections	1.02 ±0.05, n = 48	1.15 ±0.09, n = 7	t = 0.95, P = 0.350
annual fecundity	10 urban transect sections	7.63 ±0.44, n = 56	6.66 ±0.55, n = 32	t = 1.36, P = 0.170
"	6 urban transect sections	7.31 ±0.39, n = 70	7.11 ±0.71, n = 18	t = 0.24, P = 0.810
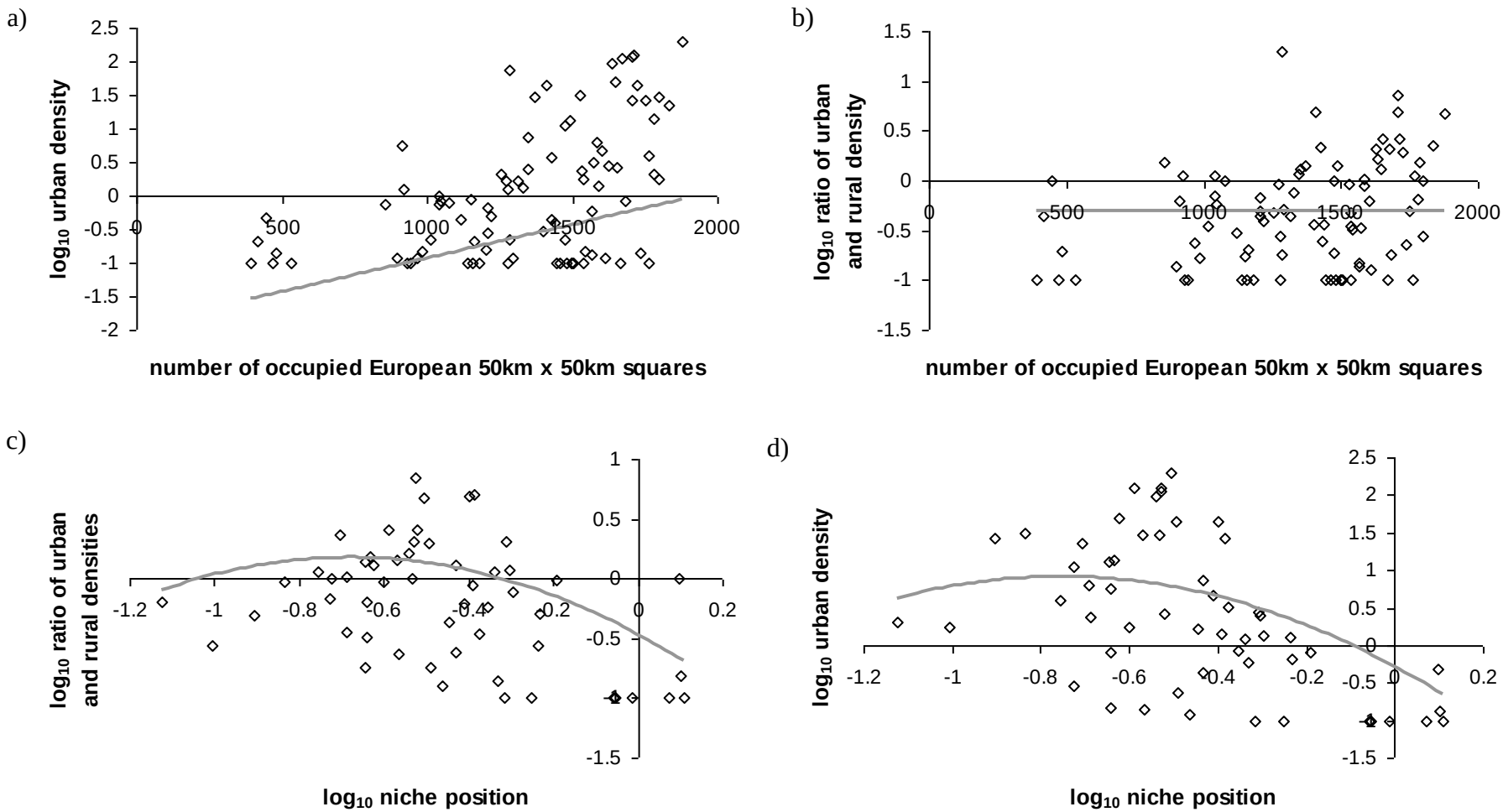
Figure 1. The relationships between: (a) European range size and urban density; (b) European range size and the ratio of urban and rural densities; (c) logarithmically transformed niche position and urban density; and (d) logarithmically transformed niche position and the ratio of urban and rural densities of British birds. Urban areas are defined as 1km x 1km squares in which at least six of the ten 200m transect sections are urban or suburban. Grey lines indicate the model averaged predicted values whilst holding other continuous variables at their mean values and categorical variables at their most frequently observed values. Defining urban areas as those squares in which each of the transect sections are urban or suburban does not substantially alter the results (Table 2).