

Bird densities are associated with household densities

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Abstract

Increasing housing density is an important component of global land transformation, with major impacts on patterns of biodiversity. However, while there have been many studies of the changes in biodiversity across rural–urban gradients, which are influenced in large part by housing densities, how biodiversity changes across the full range of regional variation in housing density remains poorly understood. Here, we explore these relationships for the richness and abundance of breeding birds across Britain. Total richness, and that of 27 urban indicator species, increased from low to moderate household densities and then declined at greater household densities. The richness of all species increased initially faster with household density than did that of the urban indicator species, but nonurban indicator species richness declined consistently after peaking at a very low housing density. Avian abundance showed a rather different pattern. Total abundance and that summed across all urban indicator species increased over a wide range of household densities, and declined only at the highest household densities. The abundance of individual urban indicator species generally exhibited a hump-shaped relationship with housing density. While there was marked intraspecific variation in the form of such relationships, almost invariably avian abundance declined at housing densities below that at which the UK government requires new developments to be built. Our data highlight the difficulties of maintaining biodiversity while minimising land take for new development. High-density housing developments are associated with declines in many of those species otherwise best able to exploit urban environments, and those components of native biodiversity with which human populations are often most familiar.

Keywords: assemblage structure, bird density, habitat diversity, housing density, urban planning

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Introduction

The global human population passed 6.5 billion in 2005, and is expected to reach 7.7–10.6 billion by 2050 (United Nations, 2004). The resulting demand for housing exerts enormous pressures on landscapes, and brings about major changes in ecosystems. It contributes substantially to the 4.7 million km² (ca. 4%) of global land area (UNDP *et al.*, 2000) that are covered by urban areas (characterized by high human population densities or significant commercial or industrial infrastructure), and to the fact that urban areas (particularly suburban) are growing proportionally faster than any other forms of land cover, that the largest cities are becoming yet

larger, and that the number of large cities is growing (Meyer & Turner, 1992; McKinney, 2002). It has been predicted that by 2007 more than half of the global human population will live in urban areas (United Nations, 2004). However, in many developed nations that proportion is already much higher (Pickett *et al.*, 2001; Antrop, 2004). For example, since the late 1940s there has been substantial growth in the urbanization of the United Kingdom, with ca. 7% of the land presently comprising built-up areas (from a full count of cover based on a 25 m grid; Fuller *et al.*, 2002), and ca. 90% of the human population being suburban/urban (ODPM, 2001), with a large proportion distributed among London, the major conurbations (e.g. Birmingham, Manchester), and the larger cities (DETR, 2000).

This said, the impacts of housing are much more widespread than those derived simply from levels of

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urbanization, with housing developments shaping patterns of land cover over much of the nonurban landscape, potentially even when housing occurs at rather low densities. Moreover, in many developed regions, human population growth is no longer the sole primary driver of housing demand. The human population in England alone, already high by European standards, is projected to grow by a further 7% on the 49 million of 1998 to 52.4 million in 2021 (DETR, 2000). However, social changes mean that more people are living alone and for longer, such that around 3.8 million additional houses may be required before 2021 (DETR, 2000). There has been much debate and discussion of the need for 'compact cities' and densification of housing to limit the resultant footprint (e.g. Breheny, 1997; Burgess, 2000; Schoon, 2001; Jim, 2004). Indeed, in order to protect greenfield sites, the government target for England is that 60% of new houses must be built on brownfield sites or in place of existing buildings (DETR, 2000), and housing planning guidelines, therefore, recommend an increase in the current density of new housing from 2000–2500 to 3000–5000 houses km⁻² (ODPM, 2002). In 2004, 72% of new dwellings were built on previously developed land, at an average density of 4000 dwellings km⁻² (ODPM, 2006).

The broad scale implications for biodiversity of spatial variation in housing density have been surprisingly little explored. Large numbers of empirical studies have examined changes in the size and composition of species assemblages along rural–urban gradients (e.g. Blair, 1996; Blair & Launer, 1997; Germaine & Wakeling, 2001; Marzluff, 2001; Niemelä *et al.*, 2002; Green & Baker, 2003; Crooks *et al.*, 2004; Riley *et al.*, 2005; Zquette *et al.*, 2005). While much has been learnt from these, they have typically comprised comparisons among rural, suburban and heavily urbanized study plots around and within individual towns and cities. However, in the absence of an understanding of the full shape of relationships between, for example, species richness or abundance and housing density, across a sufficient range of variation in housing density, limited inferences can be made about the consequences for biodiversity of continued densification.

In this paper, we examine the relationship between bird species richness and abundance and household density across a full continuous range of the latter and across the whole of Britain.

Materials and methods

Avian data

Analyses were based on BTO/RSPB/JNCC Breeding Bird Survey (BBS) data for 2000. Full field methods of

the BBS are given in Raven *et al.* (2005). Squares of 1 km × 1 km were selected across Britain (the United Kingdom excluding Northern Ireland), according to a stratified random design, stratification being based on the availability of observers. Two bird-recording visits were made by volunteers to each square, the first between early April and mid-May and the second between mid-May and late June. Birds were recorded within 200 m sections along two 1 km transects in one of three distance bands (0–25, 25–100, 100 m or more), estimated at right angles to the transect line. Counts began at 06:00–07:00 hours where possible. Flying birds not actively using resources in a square were excluded from counts, and observers were asked not to include juvenile birds in their counts (the BBS aims to monitor the number of breeding individuals). All other birds were assigned to the distance band in which they were first located. To reduce further the probability of including immature birds we only used data from the first visit for the earlier breeding residents, and to maximize the probability that all migrants that would arrive at a site were included we only used data from late visits for such species. We, thus, only included squares for which two visits were made. Habitat within each 200 m transect section was recorded according to a four-level hierarchical coding system describing the main habitat type, together with data on finer level habitat features (Crick, 1992).

Detectability must be taken into account when converting count data into densities, otherwise the latter will be underestimated. This was achieved using distance sampling software (PROGRAM DISTANCE, version 4.1 Release 2; Buckland *et al.*, 2001; Thomas *et al.*, 2004) to model the decline in detectability with distance from the transect line. Birds recorded in the final distance band (100 m or more) were excluded from the analyses, because counts within an unbounded category are difficult to interpret. Because the vast majority of species tend not to form flocks during the breeding season, we assume here that counts were a collection of individual birds rather than attempt to model the detectability of flocks.

Habitat types differ in vegetation structure and are, thus, likely to influence detectability in different ways. Region may also influence detectability (e.g. the structure of a single main habitat type, such as broadleaved woodland, may exhibit geographical variation). We took into account heterogeneity in detectability arising from variation in habitat type and region by incorporating the effect of multiple covariates into the estimation procedure using a conditional likelihood approach (Marques & Buckland, 2003). We fitted half-normal and hazard-rate key functions, as other key functions available in DISTANCE either do not allow the inclusion of

covariates (uniform key) or have an implausible shape (exponential key). We identified nine main habitat types (broadleaved woodland, coniferous woodland, mixed woodland, scrub, semi-natural grassland, heath and bog, farmland, human sites and water bodies) based on Crick (1992), and 11 regions (nine English Government Office Regions, Wales, and Scotland) and adopted the following stepwise approach. For each species we estimated $f(0)$ (i.e. the value of the probability density function of perpendicular distances at zero distance) without including habitat or region covariates to both half-normal and hazard-rate models. We then added a single covariate habitat or region and established whether the model fit was improved, defined as a reduction in the Akaike Information Criterion (AIC), and identified the best-fitting model. We then fitted a model with both habitat and region as covariates and used AIC to see whether the relative fit of the model improved. If there was no improvement in model fit (i.e. no decrease in the AIC value was observed), the best-fitting model with a single covariate was regarded as that which best explained heterogeneity in detectability. Once this best-fitting model had been chosen for a species, it was applied to the encounters from surveyed squares to produce an estimate of the number of individuals of that species within each square.

We calculated the following, assemblage level, response variables (i) species richness, (ii) total bird density, and (iii) an abundance index (akin to those used in many biodiversity indicators). Abundance indices were calculated for each species by dividing the density in each square by the total density of that species summed across all squares. Abundance indices for assemblages were then calculated by summing the indices across each species in the assemblage and dividing by the number of species in the assemblage; this value was then rescaled by multiplying by 100.

The UK government has five urban biodiversity indicators, one of which is based on 'UK populations of birds in towns and gardens' (indicator T3: DEFRA, 2002; indicator T1: DEFRA, 2003), 'to ensure that urban areas contribute fully to the goals of biodiversity conservation and enhance the quality of life of people who live there by maintaining town and garden bird populations' (DEFRA, 2002). The indicator is based on 27 species that occur in urban/suburban areas to a greater degree than would be expected based on their national population estimates, with four of these species being identified as urban specialists as at least 15% of their national population occurs in urban areas (Table 1). Given the major contribution of housing densities to urbanization, at least in Britain, we explicitly analysed the relationship between housing density and the density of each of these species for two reasons. First, these

Table 1 The 27 urban indicator species with a greater proportion of their national population occurring in urban areas than expected by chance (Defra, 2002, 2003)

Blackbird <i>Turdus merula</i>
Blackcap <i>Sylvia atricapilla</i>
Blue tit <i>Parus caeruleus</i>
Carrion crow <i>Corvus corone</i>
Chaffinch <i>Fringilla coelebs</i>
Collared dove <i>Streptopelia decaocto</i> *
Dunnock <i>Prunella modularis</i>
Goldfinch <i>Carduelis carduelis</i>
Great tit <i>Parus major</i>
Green woodpecker <i>Picus viridis</i>
Greenfinch <i>Carduelis chloris</i>
House martin <i>Delichon urbicum</i> *
House sparrow <i>Passer domesticus</i> *
Jackdaw <i>Corvus monedula</i>
Jay <i>Garrulus glandarius</i>
Long-tailed tit <i>Aegithalos caudatus</i>
Magpie <i>Pica pica</i>
Mallard <i>Anas platyrhynchos</i>
Mistle thrush <i>Turdus viscivorus</i>
Pied wagtail <i>Motacilla alba</i>
Robin <i>Erithacus rubecula</i>
Song thrush <i>Turdus philomelos</i>
Sparrowhawk <i>Accipiter nisus</i>
Starling <i>Sturnus vulgaris</i>
Swift <i>Apus apus</i> *
Woodpigeon <i>Columba palumbus</i>
Wren <i>Troglodytes troglodytes</i>

*Species with more than 15% of their national population occurring in urban areas are considered urban specialists.

are species which are known to be able to thrive in areas with at least some housing, and are therefore, more likely to show effects of specific housing densities on their abundance, rather than merely effects due to changes from nonresidential to residential habitat types. Second, these species are the ones most likely to be encountered by the majority of the human population, and therefore, have the largest effects on their quality of life.

Household data

Household density in each BBS square was obtained from the 2001 UK census (Boyle & Dorling, 2004). The country is divided into output areas, each of which contains approximately 100 households. For each census output area sharing at least part of its location with one of the BBS squares, the number of households for the output area was obtained, and its value multiplied by the proportion of the output area lying within the BBS square. The values obtained by this process were

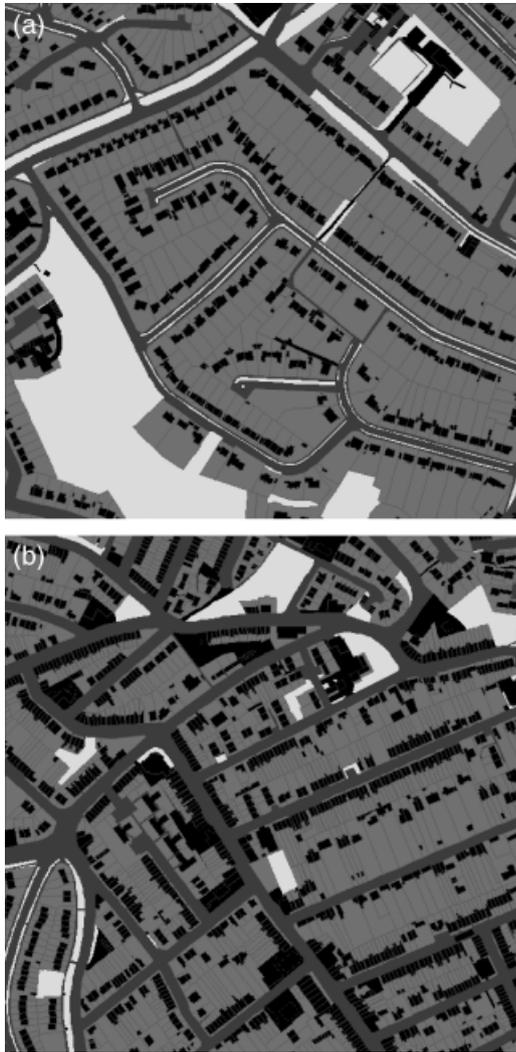


Fig. 1 Examples of two different types of areas with high housing densities. (a) A suburban residential development comprising mainly semi-detached and detached houses set within a 1 km square containing an estimated 1082 households and (b) comprises mainly terraced housing set within a 1 km square containing an estimated 3781 households. Progressively lighter shading indicates buildings, impervious surface, gardens and vegetated surface, respectively. Each map covers an area of 500 m × 500 m. Mapping from Ordnance Survey MasterMap data (Ordnance Survey © Crown Copyright. All rights reserved).

summed for each grid square, to obtain an estimate of the density of households in each square (Fig. 1).

Analyses

Regression models of the relationships between household density and the structure of avian assemblages and the densities of individual species were constructed in SAS version 9.1 (SAS Institute Inc., 2001). For the

models of the assemblage variables, all six of which were approximately normally distributed after appropriate transformations, the PROC MIXED procedure was used. Total avian density estimates were square-root transformed and the mean species abundance index was \log_e transformed after adding 0.01 to allow transformation of zero values. There was no need to transform the species richness variables. For the individual species models we used the PROC GLIMMIX version 1.0 add-in to construct Poisson regression models due to the high proportion of zero and low values. In order to reduce the skew in the distribution of household density the latter was also \log_e transformed after adding 1. Square terms of household density were included in order to detect simple nonlinear relationships.

We first constructed independent error models. However, spatial autocorrelation may invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests misleading (Cressie, 1991; Lennon, 2000; Legendre *et al.*, 2002). To avoid this, analyses were also conducted that implemented spatial correlation models that fit a spatial covariance matrix to the data and use this to adjust test statistics accordingly (Littell *et al.*, 1996). The choice of the exponential, over other spatial covariance structures, was based on inspection of semi-variograms of independent error model residuals. Spatial models fitted the maximum geographic distance or range parameter (ρ) over which spatial autocorrelation in equivalent independent errors model residuals was observed to occur. This involved estimating ρ from the semi-variograms that included the relevant combination of predictors. In all cases, forward stepwise model-building procedures were used to determine minimum adequate models. Estimates of variance explained (i.e. r^2 values), cannot be derived from either of the spatial model types, or from independent error Poisson models, but are provided for independent error normal models. To show the relationships graphically, the household density data were \log_e transformed after adding 1, and split into 10 equal interval groups. The cut-off point for the final group was lowered so as to ensure there were at least 20 observations in the group, thus facilitating the comparison of standard error bars.

Results

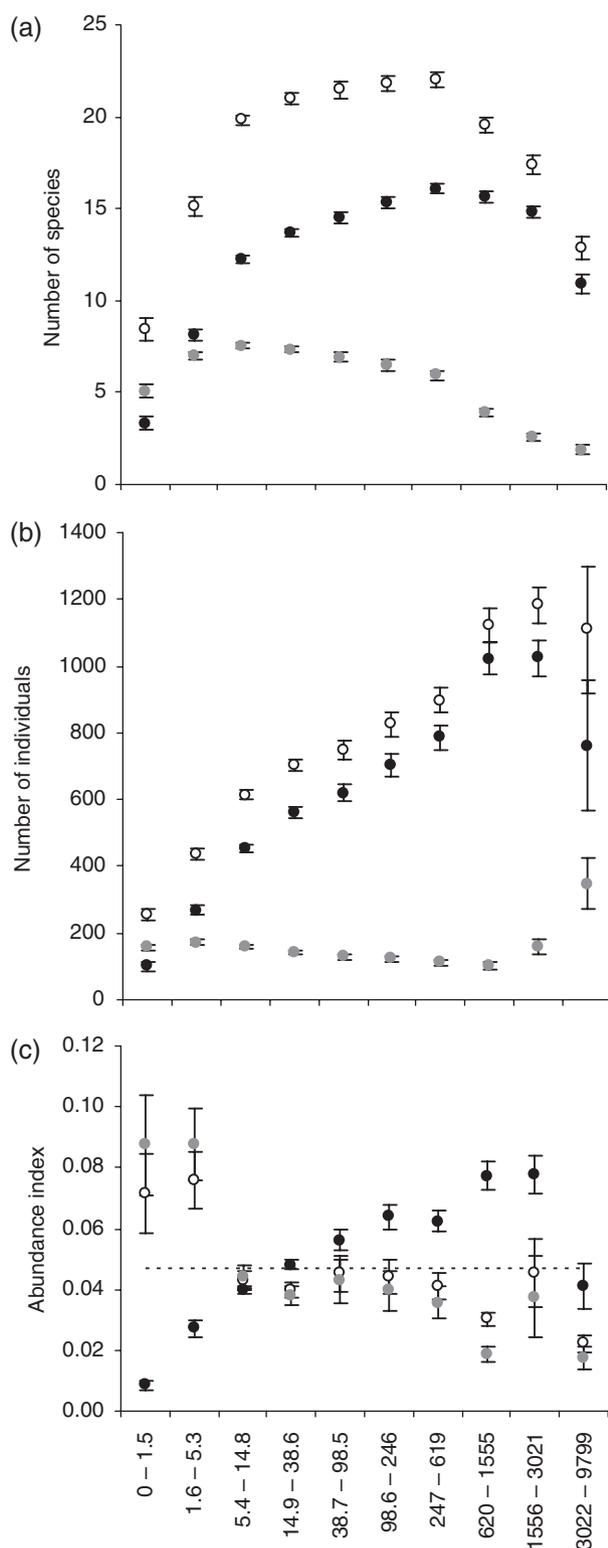
Assemblage patterns

The species richness of all recorded bird species, and of the 27 urban indicator species, increased from low to moderate household densities and then declined at greater household densities (Fig. 2a and Table 2). The

richness of all species increased initially faster with household density than did that of the urban indicator species, but nonurban indicator species richness declined consistently after peaking at a very low housing

density (Fig. 2a). These patterns in species richness were evident in both spatial and nonspatial models (Table 2). Avian abundance showed a rather different pattern, increasing for all species and for urban indicator species over a wide range of household densities, and apparently declining only at the highest household densities (Fig. 2b). Feral pigeon *Columba livia* was not included in the DEFRA list of urban indicator species, and its elevated abundance in highly urbanized areas (Fig. 3) is solely responsible for an apparent rise in abundance of nonurban indicator species at the highest household densities (Fig. 2b). Nonspatial models had a statistically significant negative squared log household density term, indicating that the increase in avian abundance was at least slowing with increasing household density if not actually declining at the highest household densities (Table 2), although sample sizes at these high densities were too small formally to distinguish the two possibilities. Spatial models had no significant squared log household density term (Table 2). The relationships between abundance and household density were similar for all bird species and for just the urban indicator species, although any decline in abundance at high household densities may be more pronounced for the latter (Fig. 2b).

By contrast, the relationship between the abundance index and housing density differed substantially between all species and urban indicator species (Fig. 2c). Using a nonspatial model, the abundance index for all species declined with household density, although explanatory power was extremely low, while using a spatial model there was no significant relationship (Table 2). For urban indicator species, there was a hump-shaped relationship, with a pronounced decline in the abundance index at the highest household densities (Fig. 2c), supported by both nonspatial and spatial models (Table 2).



Intraspecific patterns

The relationships between household density and the abundances of each of the 27 urban indicator species were highly variable (Fig. 3). However, with two excep-

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Fig. 2 Relationships between housing density in 2132 1 km × 1 km squares across Britain and (a) mean number of species, (b) mean number of individuals, and (c) abundance index. Housing density (households per square kilometre) has been binned into equal interval classes based on \log_e -transformed data (see 'Materials and methods'). Open circles are for all species, black circles for the 27 urban indicator species, and grey circles for the remaining species. Error bars are ± 1 SE. Broken line indicates the average abundance index for all species across all squares.

Table 2 Results of spatial and nonspatial mixed models of the relationships between six measures of avian assemblage structure and housing density in 2132 1 km × 1 km squares across Britain

	Nonspatial models				Spatial models				Household density at maximum response variable
	Housing <i>F</i>	Housing ² <i>F</i>	<i>r</i> ²	Household density at model turning point	Housing <i>F</i>	Housing ² <i>F</i>	AIC (ΔAIC)	Household density at model turning point	
Species richness (all species)	515.3 +++	436.0 ----	0.201	108	86.9 +++	86.9 ----	14 677.1 (79.6)	100	247–619
Species richness (urban indicator species)	673.2 +++	422.3 ----	0.326	233	113.3 +++	67.1 ----	12 830.9 (180.5)	395	247–619
Species richness (nonurban indicator species)	86.3 +++	161.8 ----	0.130	22	40.4 +++	85.7 ----	11 645.2 (179.4)	21	5.4–14.8
Number of individuals (all species)	140.2 +++	35.2 ----	0.236	5542	249.0 +++		15 151.9 (256.6)		1556–3021
Number of individuals (urban indicator species)	307.6 +++	115.1 ----	0.314	1169	344.6 +++		15 294.0 (295.4)		1556–3021
Number of individuals (nonurban indicator species)	18.4 ----	7.5 ++	0.023		41.4 ----		13 234.9 (37.7)		3022–9799
Abundance index (all species)	5.5–		0.002						1.6–5.3
Abundance index (urban indicator species)	324.1 +++	162.1 ----	0.248	450	21.6 +++	5.0–	4457.8 (328.3)	*	1556–3021
Abundance index (nonurban indicator species)	138.4 ----		0.061						1.6–5.3

*Housing' is log_e (1 + number of houses km⁻²).

Avian abundance variables are square-root transformed and the 'all species index', 'urban indicator species index' and 'non urban indicator species index' are log_e transformed after adding 0.001, 0.01 and 0.001, respectively. Symbols after *F* values indicate the direction of the effect and the significance level ($P < 0.05$, $P < 0.01$, $P < 0.001$ for one, two and three symbols, respectively). Degrees of freedom were 1, 2130 where both housing terms were included in the final model and 1, 2129 where only term was included. In cases where one of the predictors was nonsignificant in the full model, the model was rerun using only 'housing', and only the results from this model, where significant, are shown in the table. *R*² values cannot be calculated for the spatial models, so the Akaike Information Criteria (AIC) of the final model is shown, together with ΔAIC, the reduction in AIC from the null model (i.e. a model with no predictor variables) to the final model. For a given response variable models with lower AIC values provide a better fit to the data. In all cases the Akaike weight of the final model, which is the probability that this model provides a better fit to the data than the null model, is > 0.999. For models with a significant negative square term, household density at the turning point (indicating the maximum predicted value of the response variable) is shown.

*Cases where the turning point exceeded the maximum observed household density. Finally, the household density band corresponding to the highest observed value of the response variable is shown.

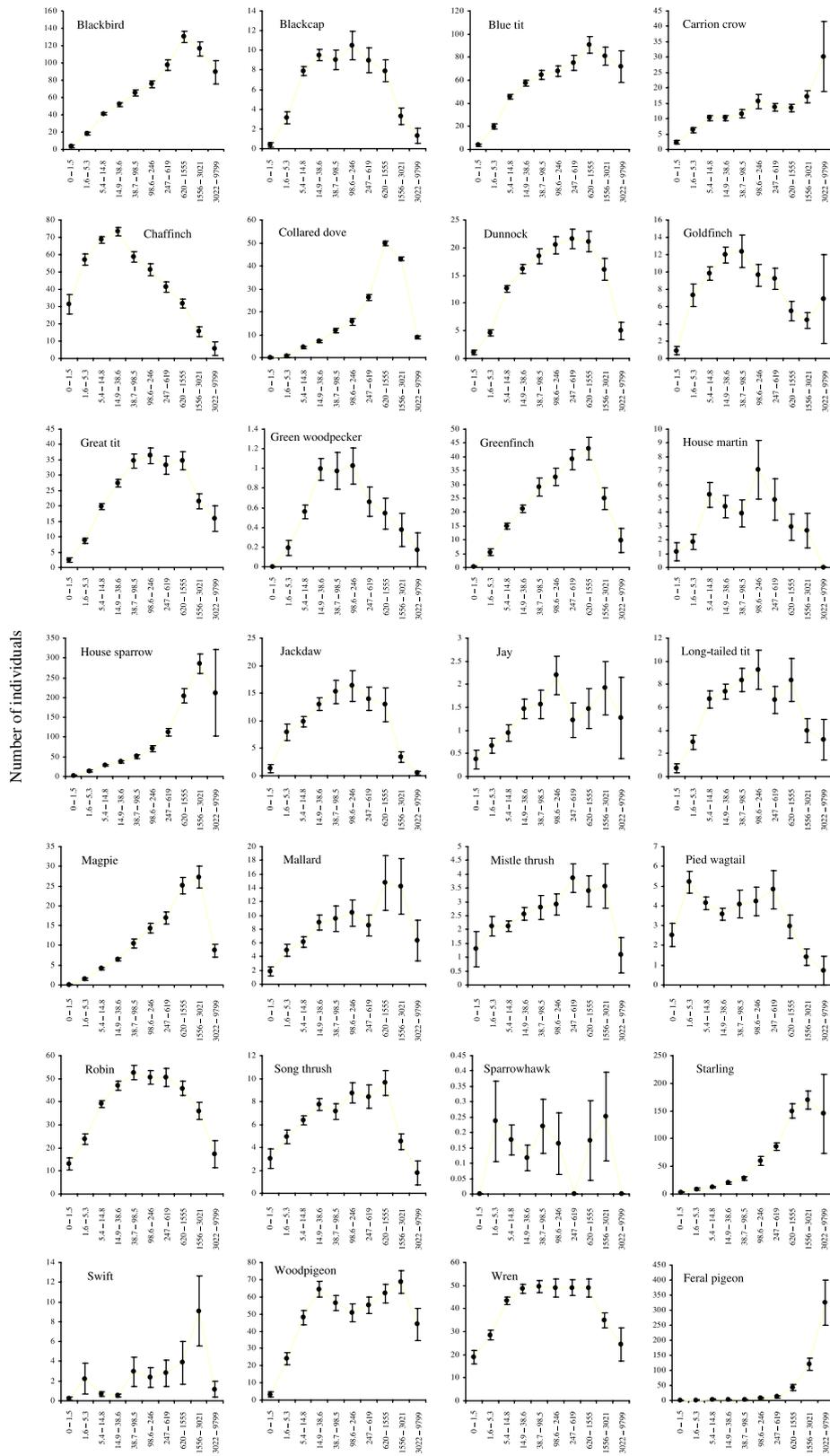


Fig. 3 Relationships between number of individuals (km^{-2}) and housing density for each of the 27 urban indicator species, and feral pigeon (final plot). Housing density (km^{-2}) has been binned into equal interval classes based on \log_e -transformed data (see 'Materials and methods'). Error bars are ± 1 SE.

Table 3 Poisson regression models of the relationships between the density of 27 urban indicator bird species and the density of households in 2132 1 km × 1 km squares across the UK

	Nonspatial models				Spatial models			
	Housing <i>F</i>	Housing ² <i>F</i>	AIC (ΔAIC)	Household density at turning point	Housing <i>F</i>	Housing ² <i>F</i>	Household density at turning point	Household density at max. bird density
Blackbird	8117.6 +++	3478.5 ----	81 951.0 (34 979.39)	1487	27.85 +++			620–1555
Blackcap	1953.7 +++	1781.1 ----	35 784.0 (2395.25)	19	47.43 +++	42.74 ----	94	98.6–246
Blue tit	7290.3 +++	4169.6 ----	114 308.4 (18 158.6)	455	19.40 +++			620–1555
Carriion crow	406.5 +++	126.7 ----	46 232.5 (2033.68)	3716			16	3022–9799
Chaffinch	4594.2 +++	6748.8 ----	94 925.1 (11 727.52)	25	8.07 ++	18.43 ----	*	14.9–38.6
Collared dove [†]	3399.4 +++	1358.9 ----	48 659.7 (22 995.98)	3524	36.97 +++	7.06 --		620–1555
Dunnoek	3508.6 +++	2631.6 ----	42 139.9 (5528.79)	190	29.07 +++	17.41 ----	516	247–619
Goldfinch	1597.4 +++	1640.2 ----	55 471.39 (1975.59)	62	34.08 +++	34.23 ----	65	38.7–98.5
Great tit	6151.7 +++	4688.1 ----	61 340.16 (9471.41)	180	44.41 +++	37.10 ----	152	98.6–246
Green woodpecker	256.5 +++	231.8 ----	66 74.40 (333.8)	93	39.35 +++	35.81 ----	88	98.6–246
Greenfinch	6410.1 +++	4376.6 ----	78 351.5 (13 210.38)	292	12.65 +++	6.42 --	5084	620–1555
House martin [†]	570.6 +++	556.7 ----	47 388.59 (653.77)	74				98.6–246
House sparrow [†]	4849.0 +++	151.0 ----	200 170.3 (107 423.9)	*	73.50 +++			1556–3021
Jackdaw	2096.9 +++	1897.7 ----	71 846.98 (2479.11)	94	11.97 +++	9.35 --	270	98.6–246
Jay	158.1 +++	104.3 ----	13 226.17 (284.94)	266	5.21 +	4.91 --	82	98.6–246
Long-tailed tit	1324.8 +++	1145.1 ----	45 878.25 (1625.78)	110				98.6–246
Magpie	2190.6 +++	956.7 ----	31 282.7 (11 459.58)	1937	126.82 +++	55.73 ----	1828	1556–3021
Mallard	571.0 +++	253.4 ----	60 708.89 (1969.66)	1010	8.98 ++	4.07 --	914	620–1555
Mistle thrush	74.0 +++	32.7 ----	18 417.17 (224.36)	863	13.98 +++			247–619
Pied wagtail	28.5 +++	63.0 ----	25 645.41 (160.34)	15	5.18 --			1.6–5.3
Robin	5243.0 +++	4299.4 ----	81 026.2 (6513.43)	129	35.41 +++	32.29 ----	1099	38.7–98.5
Song thrush	485.6 +++	386.2 ----	30 873.5 (596.24)	137	8.17 ++	4.19 --	819	620–1555
Sparrowhawk								1556–3021
Starling	5975.4 +++	943.8 ----	125 719.5 (86 086.3)	*	28.30 +++	3.85 --	*	1556–3021
Swift [†]	5.0 +	40.9 +++	27 751.29 (1757.93)		11.06 +++			1556–3021
Woodpigeon	6738.8 +++	4980.0 ----	168 834.5 (9946.3)	182				1556–3021
Wren	3102.1 +++	2621.8 ----	81 993.45 (3569.89)	114	13.47 +++	12.58 ----	106	38.7–98.5

For more details see the legend to Table 2. For each of the nonspatial models the model weight, the probability that the fitted model provides a better fit to the data than a null model, is >0.999. AIC values cannot be calculated for spatial Poisson regression models. For long-tailed tit and swift, both housing terms were nonsignificant in the full model, although the linear term was significant in the reduced model when it was the sole predictor.

*Cases where the turning point exceeded the maximum observed household density.

[†]Urban specialists.

tions, using nonspatial models all species had significant positive parameter values for log household density, and significant negative parameter values for the square term (Table 3), and in most cases these were indicative of hump-shaped relationships (Fig. 3). Spatial models generally supported this conclusion, although for five species both household density terms were nonsignificant, and for another five the log household density term was positive and significant but the squared term was not significant (Table 3).

These urban indicator species exhibited marked variation in the housing densities at which they reached their maximum abundance. Broadly speaking there were three types of avian–housing density relationships: (i) avian density peaks at low housing densities (chaffinch), (ii) avian density peaks at high, although typically not the highest, housing densities (carrion crow, collared dove, greenfinch, house sparrow, mallard, swift and feral pigeon), and (iii) avian density peaks at intermediate housing densities (all other species). House martin densities peaked at much lower housing densities than the other three urban specialist species. Moreover, it is noticeable that the only species whose densities peaked at the highest housing densities, carrion crow and feral pigeon, are not considered to be urban specialists. In the case of the former species this is because its urban population is <15% of its national population size, while feral pigeon is not considered by DEFRA (2003).

Discussion

Avian species richness and abundance respond markedly to spatial variation in household densities, presumably both through the direct impacts of the latter on the availability of land for other uses and through the associated changes in habitat and other resource availabilities.

The positive relationship between species richness and household density over much of the range of variation in the latter (Fig. 2a) is consistent with previous demonstrations of a broadly positive relationship between bird species richness and human population density in Britain (Evans & Gaston, 2005; Evans *et al.*, 2007) and elsewhere (Balmford *et al.*, 2001; Araújo, 2003; for a review see Gaston, 2005). This pattern in part arises from species richness and human density responding in similar ways to environmental gradients, reflected in the high richness and high density in southern Britain (Evans & Gaston, 2005). In part it might also arise from an increase in habitat diversity over much of the range of variation in human densities across the region (Fig. 4); bird species richness and habitat diversity are generally positively correlated across Britain

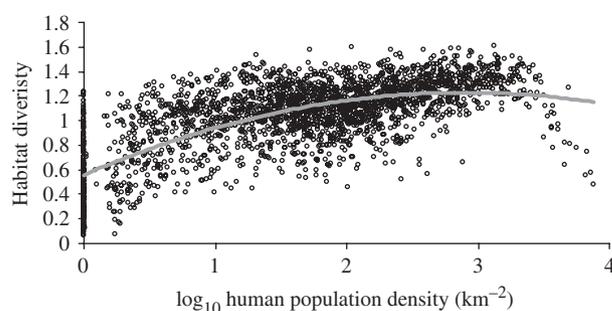


Fig. 4 Relationship between $\log(1 + \text{human population density})$ and habitat diversity, in $10 \text{ km} \times 10 \text{ km}$ squares across Britain. The latter is expressed as a Shannon–Wiener information index and is based on broad habitat types (inland water, coastal, moor/heathland/bog, woodland, built environments, grassland and tilled land) sampled using remote sensing (Fuller *et al.*, 1994). Human population density data are from the 1991 population census (Martin & Tate, 1997). Quadratic regression outperformed higher order polynomial regression in describing the relationship between the variables, and the result of this model is shown as a best-fit line.

(Lennon *et al.*, 2000). The decline in the richness both of all bird species and of urban indicator species sets in at much lower household densities than current planning guidelines recommend ($3000\text{--}5000 \text{ houses km}^{-2}$), and the decline does not abate (Fig. 2a), suggesting that as housing is built at progressively higher densities the richness of birds will become progressively poorer.

The summed abundance of the urban indicator bird species, and of almost all of the individual species increase over a wide span of household densities (Figs 2b and 3), generally substantiating their choice as urban indicators. Using nonspatial models, the only species not showing a significant positive relationship between abundance and log household density is the sparrowhawk (Table 3), the abundance estimates of which are highly variable across all household densities, and for which individual estimates doubtless have large associated variances (because of the large home ranges of adults). Using spatial models, the other species that do not show a significant positive log household density term are carrion crow, house martin (an urban specialist species, see ‘Materials and methods’), long-tailed tit, pied wagtail and woodpigeon (Table 3). It is not obvious that any particular trait unites these.

The majority of the urban indicator species also had significant negative squared log household density terms, both for nonspatial and spatial models (Table 3). In some cases this could be indicative of a slowing rate of increase in abundance with increasing household density (suggested by a turning point in the relationship that lies beyond the highest observed

household density; Table 3). However, in most it is plainly indicative of a hump-shaped relationship, with abundance declining towards higher densities of households (Fig. 3). This decline sets in at different household densities for different species, as shown by the turning points of the relationships (Table 3), and the housing density category in which the highest value of the response variable was recorded (Fig. 3). However, regardless of which measure is used, the decline typically also sets in at much lower household densities than current planning guidelines recommend, and does not abate.

Determining the precise relationship between bird abundance and the recommendations of housing planning guidelines is complicated by the scale dependency of measures of household density. Readily available measures of housing density, and those used here, are of gross density (in ecological terms, 'crude density'), the numbers of households in a 1 km × 1 km grid cell. However, plainly this can hide much heterogeneity. Current housing developments are typically (though not invariably) much smaller in extent, and planning guidelines focus on the density within their bounds (excluding major roads, schools, large open spaces and landscape buffer strips; in ecological terms, 'effective density'). This means that the household density as documented here that is of concern with regard to present planning guidelines is likely to be lower than that specified in the guidelines. Nonetheless, net densities are not measured consistently in published national and local government statistics, with the guidelines being interpreted in different ways, and given the heterogeneity in urban form, it is not possible to apply a simple correction factor to gross densities to obtain net densities (ODPM, 2004). However, the abundances of many of the urban indicator species plainly start to decline at household densities that are much lower than any realistic difference between crude and effective housing densities.

In sum, the relationships between the abundances of bird species and household density suggest a substantial conflict between maintaining biodiversity and minimising land area conversion for new development. In the United Kingdom at least, our results suggest that building new developments at intermediate housing densities over a larger area of land will result in higher overall avian abundance than building housing at the very high densities suggested by current guidelines. This is especially true when it comes to the densities of the urban indicator species, a stated formal indicator of urban development. These species appear to thrive in areas occupied by housing, but show lower abundance both in relatively undeveloped areas and areas of very high housing density.

Our study indicates the need to understand more precisely the drivers of the relationships between avian abundance and housing density shown in this study. These could relate to how the management and the extent of green space affects habitat, the degree to which specific types of housing provide suitable nest sites, the effects of housing density and housing type on the tendency of the human population to provide food and habitat for birds, the effects of human disturbance, and the disturbance and mortality caused by domestic cats.

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