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Changes in breeding bird populations due to housing development based on bird densities and assemblages along urban-rural gradients

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1. EXECUTIVE SUMMARY

1. To date there has been no quantification of net levels of change in biodiversity due to housing expansion into rural areas. This prevents objective and tiered assessments of risk to landscapes, from those supporting high biodiversity to those holding less significant bird communities or populations.

2. This report combines existing bird data for 2000, from the long-term BTO/RSPB/JNCC Breeding Bird Survey (Noble *et al.* 2006) with ITE/CEH Land Cover Map data for 2000 to quantify and assesses broad-scale differences between suburban and rural bird communities (species composition and abundance of breeding birds), along urban-rural gradients, on a regional basis.

3. Land cover data were used to define squares into suburban and suburban-adjacent rural squares. The results suggest that those rural squares adjacent to suburban areas have less arable agriculture, and may also be less intensively managed, than rural squares 'isolated' in the wider countryside (as suggested by the area of set-aside grass). The finding that broadleaved woodlands cover a greater area in those rural squares that are adjacent to suburban areas is important where the potential for urban expansion exists. Analysis by region showed that these patterns were genuine and not caused by large-scale geographic biases in the data.

4. Bird species richness, diversity and individual species density were analysed in two ways in relation to land cover. First, regression analysis was performed on bird data in relation to continuous land cover variables: suburban, urban, woodland and farmland cover. Second, bird data were compared between suburban and 'rural' (as defined above) squares using ANOVA. A key focus was the species used in the England Biodiversity Strategy Indicator on wild birds and species on the individual urban specialists House Sparrow, Swift and House Martin.

5. Species richness, diversity and individual species density showed a significant non-linear response to a suburban land cover gradient in most cases, where there was a peak at intermediate levels of suburban cover. This was not the case, however, for several farmland and woodland indicator species. The explanatory power of the models (as measured by adjusted R^2) was very low for all species except Collared Dove, Blackbird, Starling and House Sparrow. When other cover variables, apart from 'urban', were included in the model, there were marked improvements in adjusted R^2 suggesting that the majority of species respond most strongly to woodland and/or farmland cover.

6. For all bird species combined, bird species diversity and richness were both significantly *higher on rural squares* than suburban squares. For the 27 urban species there was no significant difference in species diversity between rural squares and suburban squares, and species richness was expectedly *higher on suburban squares* than on rural squares. For individual woodland species, nine occurred at higher density on rural squares than suburban squares and three showed the opposite pattern. Respective figures for farmland species were eight and two, and for urban species, two and 10.

7. Overall, the results indicate a net loss on species richness and diversity when substituting rural habitats for suburban habitats, particularly in the south and east of England. In the Eastern region, there were over eight more species on average in rural than suburban squares for all species and just under five for indicator species. Differences may be particularly pronounced in Eastern England, with high species richness and significant proportions of several species, such as Turtle Dove, Lesser Spotted Woodpecker, Lesser Whitethroat, Nightingale and Yellow Wagtail. This analysis suggests that such species are likely to be at

risk from urban expansion, and is particularly important given that the Eastern region is one that is especially likely to be targeted for further housing development.

8. In terms of possible mitigation, it may be that 'mature' greenspace is a critical factor that can increase the value of urban developments, although at the same time, occupy more space. We could provide no assessment of the average 'quality' of suburban land cover in this analysis and whether this average could be improved upon on a large scale, in order to reduce the impact of urban expansion into rural areas. It is likely that in some cases, mature suburban and rural gardens and parks are able to support 'acceptable' populations of several woodland indicator species. However, developments should probably avoid areas of countryside where relatively high populations of farmland and some woodland specialists exist, or where a high potential exists for such habitats to improve in future (due to their proximity to species–rich areas).

9. Further research: Much greater detail, and finer assessments of the impact of urban expansion on rural bird communities are now possible using existing data along with BBS volunteer support. The BTO, in collaboration with Central Science Laboratories (CSL), can derive densities and areas of buildings, greenspace etc., using *Mastermap.* In addition, CSL access to 'Defra aerial photographs' would allow an assessment of habitat 'composition'. The two data sources, together with the Breeding Bird Survey data would provide a powerful, spatially-linked analysis of urban impact, at a finer resolution than 1-km squares (e.g. 200 m BBS transect sections), incorporating also measures of habitat condition. BBS volunteer support would be available to 'ground-truth' electronic data where necessary, while also collecting new bird data. Such a project would provide a strong evaluation of the suburban 'habitat', and of variation in and therefore potential for suburban habitats to support or affect bird assemblages. These data would provide more reliable and quantifiable estimates of impact on rural bird assemblages. At the time of writing, a planned programme of research and timed framework was being developed between BTO and CSL.

10. In addition to these data sources, a further Land cover map survey is scheduled for 2007 and if compatibility with LCM2000 is good, then the BTO proposes to use such data to identify impact, through temporal change, for example, in areas that had become developed between survey years.

2. INTRODUCTION

Rates of urban expansion and road development depend on three main factors: the policy context, the state of the general economy and demographic trends. Over the last two decades, these factors contributed to a period of rapid growth: in rural areas in Great Britain, the cover of developed land has increased by about 4% (92,000 ha) since 1990 (in less than 10 years). Economic and demographic pressures are likely to remain for the foreseeable future.

Continued housing development on farmland and semi-natural habitats has enormous implications for the composition of biodiversity in "green-belt" areas, with potential impacts on sensitive wildlife "amenities", such as river corridors, heathlands, woodlands and coastal strips. However, with age, housing could benefit some bird species (e.g. Song Thrush – Mason 2000) or communities, and even exceed some measures of biodiversity in poorer landscapes such as intensive open farmland (e.g. O'Connell *et al.* 1998). Urban expansion represents one of the biggest single changes in land-use to occur outside of farming, but with more permanent consequences. The subject is topical - house-building on flood plains and in green belt areas of the south-east has raised questions about the way building programs can proceed, sometimes, apparently without exhaustive environmental assessment.

To date there is no way of quantifying net levels of change in biodiversity due to housing expansion into rural areas. This prevents objective and tiered assessments of risk to landscapes, from those supporting high biodiversity to those holding less significant bird communities or populations. With respect to birds, some environmental costs of house building may be pre-supposed (e.g. loss of farmland specialists), but some long-term benefits of suburban "succession", where vegetation development over time in suburban green spaces (including gardens) may provide some quality habitats for certain species, are possibly under-estimated.

This report combines existing bird data for 2000, from the long-term BTO/RSPB/JNCC Breeding Bird Survey (Noble *et al.* 2006) with ITE/CEH Land Cover Map data for 2000 (LCM2000) to quantify, and assesses broad-scale differences between suburban and rural bird communities (species composition and abundance of breeding birds), along urban-rural gradients, on a regional basis. It examines data from rural areas adjacent to existing suburban areas and so provides some guiding information for housing developments in order to avoid major effects on woodland and farmland birds. The analysis determines how bird diversity and the density of individual species vary according to continuous measures of suburban development (and other land cover types). The bird community is likely to change markedly from highly urbanised town/city centres to rural areas with low housing density (e.g. Blair 1996, Chamberlain *et al*. 2004). Understanding how key individual species and the bird community as a whole responds to such urban-rural gradients will enable an assessment of how urbanisation may effect overall bird community composition.

- *Objective 1.* For bird counts, at the 1-km square level, to be analysed in relation to land cover data derived from LCM2000. In order that the LCM2000 adequately represents cover in BBS squares, only bird data from a single year (2000) was considered.
- *Objective 2*. To compare bird communities of suburban landscapes with immediately adjacent rural landscapes. This analysis will take a simple approach, comparing classes of 1-km square ('suburban' and 'suburban-adjacent rural') in order to identify potential impacts or 'risk' to undeveloped land. The analysis will be repeated on a regional basis, according to Government Office Regions (or where sample sizes are too small, adjacent regions may be combined) and will determine whether patterns of bird abundance and community composition on urban-rural gradients are consistent in different parts of the country.
- *Objective 3*. The report will identify and evaluate spatially referenced datasets in terms of their costs, easy of access, quality and usefulness for future research into bird/habitat relationships in urban/rural transition zones and multi-year analyses.
- *Objective 4*. To assess the broad impacts of any future housing development scenarios on suites of species used in the England Biodiversity Strategy, and to identify possible mitigation

strategies. The analysis will differentiate between the impacts on birds of ‘Woodland’ ‘Farmland’ and ‘Towns & Gardens’ with particular reference to woodland, farmland and urban specialists.

3. METHODS

In this report various descriptions, terminology and abbreviations are used to describe elements of the data or the source of data used in the analysis. The following is a summary of the terminology used:

Table 1 Terminological summary for the present report.

Terms used	Definition (see also Fig. 1)
Isolated rural squares	Rural squares that were not adjacent to suburban squares
Suburban-adjacent	Rural squares lying adjacent to suburban squares.
Rural adjacent	Suburban squares lying adjacent to rural squares.
Landcover variables	Percentage cover for different landscape features contained within the Land Cover Map 2000 (LCM2000) data base.
Predictor variables	Variables added to analytical models that may explain some of the variation present in the subject variable (the number or density of birds counted or the number of species counted (species richness))

3.1 Data Sources and Defining Sample Squares

The analysis combined two large, existing sources of data:

1. The cover of various land use types at a 1-km square level is available through a professional survey, the ITE/CEH Land Cover Map data for 2000 (LCM2000: Fuller *et al*. 2002), which includes urban land cover and suburban land cover for every 1-km square in Great Britain, but only lowland squares from England were used for this report (by omitting any squares classed as English/Welsh Uplands by Haines-Young *et al*. 2000). LCM2000 data were analysed in two ways. First, data were expressed as continuous variables, where five percentage cover types were considered (suburban, urban, pastoral farmland, arable farmland and woodland). Second, LCM2000 data were used to assign 1-km squares as *rural-adjacent* suburban or *suburban-adjacent* rural squares ('rural') that were adjacent to suburban classes (Fig. 1; Table 1). Large urban areas (i.e. city centres), defined as 1-km squares with >50% cover of LCM2000 cover type 25 (continuous urban) were excluded (Fig.1 – black squares). For the remaining sample of BBS squares, two land cover classes were defined: suburban (>= 25% cover of LCM2000 cover types 24 [suburban/rural development] and type 25 combined), and, rural (all other 1-km squares). The selection procedure ensured that any given square selected was adjacent to at least one square of the other class (i.e. every rural square was adjacent to a suburban square and vice-versa). This is illustrated in Figure 1.

2. Breeding bird data was extracted from the BTO/JNCC/RSPB Breeding Bird Survey (BBS). This is an annual volunteer-based survey that has been running since 1994. BBS survey sites are 1-km squares (based on the national grid) that are randomly selected within regions stratified according to human population size. The distribution of survey squares is therefore biased towards more urbanized regions with higher human populations. A large number of squares are surveyed annually. For example, there were 1700 squares surveyed in England in 2000 and 332 of these had at least 25% combined urban+suburban land cover. Each BBS square is divided into two parallel transects of 1-km length, which are in turn divided into 200 m transect sections. Volunteers are required each year to undertake counts of all bird species seen or heard within each section of each transect. Two visits are made per year, the first

between late March and mid-May and the second between mid-May and the end of June. In addition, volunteers are required to undertake a habitat survey when they are first allocated a square, using a specially designed habitat coding system (Crick 1992) that assigns habitat types to each transect section (including habitat types describing the built environment). Any habitat changes on subsequent visits are also recorded. The distance of each registration from the transect line is recorded in BBS (into distance categories). This allows the decline in detection probability to be modelled and bird density estimates to be adjusted accordingly. Importantly, this also allows the fitting of different detection functions in different habitats, as detectability is likely to vary between habitats of differing structure. In this way, relative densities derived from different habitats can be regarded as comparable. The density estimates used in this report have been derived by incorporating different density functions for different broad habitat types at the transect section level as used in the BBS habitat recording system (including 'human habitat'). Therefore, density estimates used in this report should be comparable across habitat types that may differ in detectability (e.g. suburban vs rural). The validity of this technique can be found in Newson *et al.* (submitted).

There were 675 BBS squares in the analytical sample: 396 rural and 279 suburban. Although habitat data are collected as described, during BBS, it was decided to classify BBS squares on the basis of the independent data set LCM2000. However, there was good agreement between measures of human development across the two data sets: A pre-analysis showed a significant difference in the proportion of BBS 'human habitats' (with urban, suburban or rural development) between LCM2000 suburban and rural classes: the number of BBS transect sections classed as human habitat out of the total number of transects visited per BBS square was significantly higher in squares classed as suburban (mean ratio ± sd = 0.64 ± 0.33, n = 265[1]) than those classed as rural (0.17 ± 0.22, n = 369) according to LCM2000 (logistic regression $\chi^2_1 = 392$, $P < 0.0001$).

3.2 Comparing Habitat Composition Between Suburban-Adjacent Rural Squares and 'Isolated' Rural Squares (BBS Squares)

The mean percentage cover for each of the 27 land cover types defined by LCM2000 was calculated separately for suburban and rural 1-km squares. Of particular interest was the habitat composition of rural squares and how they compared to other rural squares that were *not* adjacent to suburban habitats. Therefore, a third classification of squares was made: rural squares that were not adjacent to suburban squares, termed 'isolated rural squares'. The sample was not restricted to those that were also BBS squares as the typicality of rural squares in the context of the whole of lowland England was of interest. A comparison of percentage cover for each land cover type was made between rural squares and isolated rural squares (considering those landscape types that occurred in at least 20% of rural squares) using a two-sample Wilcoxon test for ranked data. In order to eliminate potential biases caused by large-scale gradients in land cover types and in the distribution of the defined land classes, these comparative analyses of percentage land cover were repeated for separate English regions, using Regional Development Agency regions (RDAs - http://www.defra.gov.uk/funding/rda.htm; Fig. 2).

3.2.1 Comparing habitat composition between suburban-adjacent rural squares and 'isolated' rural squares (national squares).

The above analyses compare the BBS sample of squares classified in 'suburban or 'rural' against a national sample of 'isolated rural' squares. This enables the analyses of BBS data (see below) to be put into context of the wider landscape. However, a similar approach can also be taken to compare land cover between those squares assumed to be at most risk of development (i.e. 'rural' squares) and other 'isolated rural' squares at a national level, irrespective of the BBS sample. We therefore extended the same analyses outlined above to a national (i.e. English) sample of squares.

[1] Some BBS squares were missing habitat data, hence these sample sizes differ from the total squares in the classification.

3.3 Bird Data: The Relationship Between Breeding Bird Species Composition and Densities and Land Cover Between Rural, Suburban and Urban Squares

3.3.1 Selecting best models for species analysis of densities

The species densities, the species richness (analysed as the log of number of species seen per 1-km square) and species diversity (expressed through Shannon indices; Magurran 2004) was analysed in relation to suburban and urban land cover per 1-km square using Generalized Linear Models (GLMs). Initially, univariate models, considering only measures describing the cover of developed land, were made. So, for example, the effect of (arcsine-transformed) percentage suburban-cover was calculated for species richness and species density for different groups of species (urban indicator species, farmland indicator species and woodland indicators species or all three indicator groups combined). Then, other land cover variables (%arable, %pastoral farmland and %woodland) were added to the models to see which combinations were the strongest predictors of the species parameters. This analysis was repeated to look for non-linear relationships (Appendix 2). A key focus was the species used in the England Biodiversity Strategy Indicator on wild birds and species on the individual urban specialists House Sparrow, Swift and House Martin.

3.3.2 Species diversity and richness

Bird species diversity (Shannon index) and species richness were calculated and compared by analysis of variance (ANOVA), between suburban and rural BBS squares. These categories were defined according to the BBS/LCM2000 method in section 3.1 (point 2) above. The whole analysis was repeated for English RDA regions (see 3.2).

3.3.3 Species densities

Bird density values were also calculated by regression analysis for 27 urban species, 19 farmland species and 33 woodland species (not necessarily mutually exclusive), using the full model for %farmland, %woodland, %suburban and %urban predictor variables. Densities were compared between 'suburban' and 'rural' BBS squares, for the three indicator groups (according to the BBS/LCM2000 method in section 3.1 (point 2) above).

4. RESULTS

4.1 Analysis of Habitat Composition: Comparing Suburban-Adjacent Rural Squares to 'Isolated' Rural Squares

The mean percentage cover for each of the 27 land cover types defined by LCM2000, as calculated separately for rural-*adjacent* suburban and *suburban-adjacent* rural 1-km BBS squares and '*isolated* rural squares', are given in Appendix 1.

The results of a comparison of percentage cover for each land cover type between *suburban-adjacent* rural squares and *isolated* rural squares (two-sample Wilcoxon test for ranked data), are shown for the BBS sample in Table 2(a). There was significantly greater cover of broadleaved woodland, neutral grassland, set-aside grassland, suburban and urban habitat; and significantly lower cover of arable cereals and arable horticulture in rural compared to isolated rural squares. The results therefore suggest that those rural squares that are closest to suburban areas have less arable agriculture and may also be less intensively managed, than in the wider countryside (as suggested by the area of set-aside grass). The finding that broadleaved woodlands cover was greater in those landscapes with *suburban-adjacent* rural squares is potentially important if these areas are at some risk to urban 'sprawl'. There remains, however, a possibility that this is in some way reflective of regional biases in suburban landscapes and in the distribution of broadleaved woodland. Note also that for all of the results in Table 2(a), the absolute differences in means were small (<5%).

4.1.1 Regional biases

Regional bias was examined by analysis of easting and northing expressed as continuous variables (both were approximately normally distributed). Predominantly suburban squares were, on average, further north than predominantly rural squares (t_{673} = 2.23, P < 0.026; mean rural = 241.7 ± 104.9, mean suburban = 260.9 ± 117.0). Rural squares tended to be further east, although the difference was not quite significant (t_{673} = 1.83, P < 0.07; mean rural = 459.5 ± 86.3, mean suburban = 447.6 ± 78.0). Broadleaved woodland cover decreased significantly with northing in *suburban-adjacent* rural squares only (linear regression $F_{1, 394}$ = 5.40, P < 0.021). Thus, rural squares adjacent to suburban areas in the south of England have proportionately more broadleaved woodland.

In order to eliminate potential biases caused by large-scale gradients in land cover types and in the distribution of the defined land classes, the analyses in Table 2(a) were repeated for separate English regions using RDAs (Table 2(b-e). When using all nine separate RDAs (Fig. 2), sample sizes were sometimes small. In order to increase sample sizes, RDAs were combined into four regions as follows: South = RDA 7 and 8; East = RDA 5 and 9; Midlands = RDA 4 and 6; North = RDA 1, 2 and 3 (Fig. 2). The mean cover for each land cover type that was present in at least 20% of the sample of *suburban-adjacent* rural squares and that differed significantly from the cover in *isolated* rural squares is shown in Table 2 (b-e). Although the land cover types showing significant differences varied between regions, the results were in close agreement with Table 2(a), suggesting that differences in land cover types between *suburban-adjacent* rural and *isolated* rural squares were genuine and not caused by large-scale geographic bias in the data.

Repeat analyses were carried out at the national level (i.e. using all squares rather than just BBS squares) according to the four defined regions. Results are shown in Table 3. Patterns were in general agreement with the BBS sample of rural squares (Table 2), where grassland areas tended to be higher in rural squares and arable areas tended to be higher in isolated rural squares. Broadleaved woodland cover was significantly higher in the national sample of *suburban-adjacent* rural squares compared to *isolated* rural squares (Table 3), but the differences were not as marked as they were in the BBS sample (Table 2).

4.2 Bird Data: Breeding Bird Species Composition and Abundance in Urban, Suburban and Rural Classified BBS Squares

4.2.1 Analysing the effects of continuous land cover variables on species densities

Initial analyses of continuous land cover simply considered how species diversity, richness and density varied in relation to suburban land cover, considering both linear and quadratic terms in the model. There were significant non-linear associations between suburban land cover and species diversity and richness for all species, indicator species and urban indicator species (Appendix 2). This suggests that intermediate levels of suburban cover support a more diverse bird community than either wholly rural or wholly suburban landscapes. However, it should be noted that the amount of variation explained by these models was typically very low, with most adjusted R^2 values being below 0.1 (Appendix 3), therefore the models' predictive power is likely to be low.

Similar analyses were carried out for individual species' density (Appendix 2(b-d)). For urban indicator species (Appendix 2b), most (23 out of 27) also showed a significant non-linear relationship between density and suburban cover. Exceptions were Blackbird and Magpie, which showed linear increases in density with suburban cover and Sparrowhawk that showed no significant association with either variable. Adjusted R^2 values were typically very low, exceptions being Blackbird, Collared Dove, House Sparrow and Starling ($R^2 > 0.20$). For woodland indicator species, there were relatively few significant associations (Appendix 2c), although there were non-linear effects of suburban cover in nine species, two of these showing a negative linear and a positive quadratic parameter estimate (i.e. with peak numbers associated with intermediate levels of suburban cover more so than high or low values). For farmland indicator species, there were very few significant effects (Appendix 2d). Skylark showed a linear decrease, Turtle Dove a non-linear decrease and Whitethroat a quadratic relationship. For both woodland farmland indicator species, adjusted R^2 values were extremely small, all being < 0.04, therefore these associations can be regarded as weak.

A series of results from regression analyses including additional land cover variables of farmland, woodland and urban cover, that were used to select the best model fit to describe bird diversity and richness (on the basis of the highest adjusted R^2 value), are shown in Appendix 3. In each case the strongest model effect on bird species richness or species diversity was provided by the full or near full linear model (that is a combined effect of %suburban + %farmland + %woodland – sometimes with %urban). With a few exceptions, the explanatory power of models that included measures of rural land cover was far greater than those models that considered only suburban cover (Appendix 2). Although suburban cover on its own was significantly related to species richness and the density of several species, the low R^2 values for these analyses show that these relationships are actually quite weak. Additional habitat variables are therefore needed in order to describe more accurately how bird species respond to gradients in suburban land cover. The full linear model including the %urban category was therefore taken forward and used to identify continuous land cover effects on the densities of 'urban' 'farmland' and 'woodland' bird species.

For the majority (20) of the 27 urban indicator species, the effect on density (i.e. the magnitude of the parameter estimates) was higher for %suburban compared to %farmland habitat (opposite for Pied Wagtail, Goldfinch and Chaffinch) (Appendix 4a). For woodland, the densities of Green Woodpecker, Robin, Wren, Blackcap, Long-tailed Tit, Jay and Chaffinch densities were very much more (by at least two fold) strongly associated with woodland than the %suburban habitats, and even the density of Song Thrush (a species of high conservation concern and, often associated with suburban gardens) was around 50% higher in woodland than suburban habitat. This suggests that the distribution of these species between adjacent suburban and rural squares (c.f. Table 4) was mainly an effect of the relative woodland component of the habitat (these species are also woodland indicator species) and all were more strongly associated with the rural squares.

The densities of Collared Dove, House Martin, Magpie, Blackbird, Starling, House Sparrow and Greenfinch were most strongly associated with (at over twice the rate of increase) %suburban habitats compared to %woodland or %farmland. This difference was particularly strong for Blackbird, Starling, House Sparrow and Dunnock and suggests that the distribution of these species between *rural-adjacent* suburban squares and *suburban-adjacent* rural squares (c.f. Table 4) was an effect of a specifically suburban component (an affiliation with houses and gardens). Blackbird and Dunnock are also woodland indicator species but for Dunnock, farmland rather than woodland was the next most important factor.

4.2.2 Analysing the effects of 'class' variables on species diversity & richness

Using 'analysis of variance (ANOVA), bird species diversity and richness were both significantly *higher on suburban-adjacent rural squares* than *rural-adjacent* suburban squares when the model was run for all species, and for the 61 indicator species (farmland, woodland and urban species combined). Bird species diversity and richness were both significantly higher on the same rural squares than suburban squares. However, when the model was run for just the 27 urban species there was no significant difference in species diversity between the same rural squares and suburban squares, and species richness was expectedly higher on these suburban squares than on rural squares (Table 5).

Across regions, species richness and diversity for all species and all indicator species were consistently higher on rural squares, including the Midlands where the difference was non-significant (Table 5). The effect was particularly strong in the South and in the East, probably because of a higher occurrence and quality of woodland in rural squares, particularly in the south of England (see 4.1.1). For urban indicator species, the results were equivocal and although, generally, species richness and diversity was higher in suburban squares, the differences were non-significant except in the Midlands (as well as, again, for species richness over all regions combined). *Overall the results would indicate a net loss of species richness and diversity when substituting rural habitats for suburban habitats, particularly in the south and east of England.* The current analysis takes no account of habitat quantity or quality either of suburban green spaces or of the adjacent rural environment (see section 5).

4.2.3 Analysing the effects of 'class' variables on species densities

Across all indicator categories, using the full linear model, seven species that occurred in higher densities on the 'opposite' habitat category to their indicator definition (as urban, farmland or woodland) are all species that are not mutually exclusive to their categories but are used in two different indicator groups. For example, Blackcap and Chaffinch are both used in the urban indicator as well as the woodland indicator. For each indicator group:

1. Twelve of the 33 woodland indicator species had significantly different densities on rural and suburban squares (Table 4). *Nine occurred at higher density on rural squares* than suburban, (21 of the 33 species for all species combined), but Blackbird, Blue Tit and Dunnock occurred at a higher density on suburban squares – implying that suburban expansion into woodland rural squares would cause a net loss in bird density for this indicator group (Table 4).

2. Ten of the 19 farmland indicator species had a significantly different density on rural and suburban squares. *Eight occurred at a higher density on suburban-adjacent* rural squares than *rural-adjacent* suburban squares and generally, for all 19 species, densities were two to three times higher on farmland. Only Greenfinch and Starling occurred at significantly higher density on the suburban squares. The results imply that suburban expansion into farmland rural squares would cause a net loss in bird density for this indicator group – causing at least 50% declines for most species (Table 4).

3. Twelve of the 27 urban bird species had significantly different densities between *suburban-adjacent* rural and *rural-adjacent* suburban squares (Table 4a). *Ten occurred at higher density* on the same suburban squares than rural, but Blackcap and Chaffinch occurred at a higher density on rural squares – due their stronger affiliation to woodland and for Chaffinch to

woodland and farmland (Appendix 4a). Interestingly, when comparing between suburban and urban categories, 23 of the 27 species were more strongly associated with the %suburban than %urban component of squares (Appendix 4a). Only Mallard, Pied Wagtail and Carrion Crow showed the opposite trend, and only Mallard and Carrion Crow were recorded at their highest densities in association with the urban habitat. Possibly this 'attraction' to suburban squares or the suburban components of squares (Table 4) lies in the availability and quality of greenspace mosaic (parks and gardens) for providing nest sites and food for birds in summer, although proximity to rural populations may also be important. Overall, for urban species there was and apparent trade-off between species benefiting most from woodland and those being associated more closely with suburban habitats (itself a woodland/urban mosaic), with Blackbird, House Sparrow and Starling being particularly dependent upon the latter. Table 6, and Figure 3, however suggest a significant loss of 'rural' species to urban expansion for woodland and farmland bird species due to a low frequency of occurrence in urban-related squares.

5. DISCUSSION, LIMITATIONS & FURTHER WORK

5.1 Discussion

The results suggest that those rural squares that lie close to suburban areas, where the potential for urban expansion may exist, contain less arable agriculture and may be less intensively managed than those in the wider countryside and have greater broadleaved woodland cover (the effect being more acute in the south of England; *Objective 1*). Generally, bird species diversity and richness were both significantly *higher* on these same rural squares than suburban squares, so that a net, negative change on birds would be expected overall, from urban expansion. Even for the urban-indicator bird species, where species richness and densities were expectedly higher on suburban squares than on rural squares, the data suggest a strong, probably crucial association for most species with woodland and/or 'suburban' habitats (as opposed to the urban component, per se; *Objective 2*). Thus, the short-term impact on species in rural squares, of new developments, without mature greenspaces or woodland, is undoubtedly negative for virtually all urban indicator species (and therefore most species in general), except possibly Carrion Crow and Mallard (*Objective 4*). Over time, maturing gardens and greenspaces could ameliorate some of the worst effects of development, with some species, such as Blackbird, Collared Dove, Starling and House Sparrow benefiting from the long-term provision of maturating 'green' areas within urban developments. For this study, however, such effects are assumed and implied, as the quality and quality of greenspaces could not be measured and accounted for in the analysis. A more accurate assessment of the impact of urban expansion into nearby rural areas would depend on knowledge of species/habitat relationships in suburban (and village) 'landscapes' (see 5.2.3 below; *Objective 3*).

From this study, based on a 1-km scale of analysis, we would predict that urban expansion into nearby rural areas would cause significant net losses in bird species richness and density (*Objective 4*). This change would be particularly acute in the south and east of England where the differences in species composition and density were highest between suburban and rural squares (or in response to the rural/urban gradient). This reflects both the likely 'quality' of the rural habitat and the occurrence of species that are least likely to be associated with an urban or suburban environment. For species densities, almost all woodland and farmland indicator species were higher in rural than suburban squares, the difference being greater for farmland species. Although the densities of farmland species (eg. Grey Partridge, Lapwing, Skylark and buntings – all species of conservation concern) may be considered poor on farmland, most of these species were not in anyway associated with suburban landscapes, and would generally 'avoid' areas of urban land or urban expansion. Of course there is much greater potential for contiguous areas of species-poor open arable or pastoral farmland to support stronger populations of farmland-related species than they currently do, but on average farmland habitat in its own right is relatively impoverished compared to 'average' suburban habitats. In species-poor areas of farmland, where the more important species, above, are rare or absent than the net impact of urban expansion may be minimal and quite possibly strongly positive in some instances over the long term, though permanent.

For woodland species, the situation probably depends more on the quality of the suburban and woodland habitat discussed above. The differences in species densities between *rural-adjacent* suburban and *suburban-adjacent* rural squares for the woodland indicator species, though generally higher in rural squares, were not as extreme as for farmland species (*Objective 4*). Also, several woodland species occur as urban indicator species too – so are already identified with both suburban and woodland habitats. Under these circumstances, the expansion of urban areas into rural squares may not necessarily cause a replacement of species, but mainly affect the relative densities of species. Some species occurred at very much higher densities in association with suburban covers than woodland cover (again, Blackbird, Starling and House Sparrow). But perhaps surprisingly, the densities of Robin, Wren and even Song Thrush were higher in association with woodland cover than suburban cover, despite strong populations in suburban areas. This suggests that the suburban 'habitat', on average, is not necessarily optimal for these species. Other common species, such as Treecreeper, Blackcap and other warblers, are still relatively rare in the 'average' suburban context, in contrast to Tawny Owl and Dunnock, for example. Overall, for woodland and urban indicator species, this study would predict a net negative impact of urban expansion into rural squares, on the 'biodiversity' (abundance & species richness values) of common species (*Objective 4*). Clearly then, the impact would be even more acute for habitats supporting specialist species that are unlikely to adapt to a suburban environment (eg., heathland or riparian birds).

In addition, in some circumstances, the transition zone between suburban and rural habitat may be relatively species rich, where open, hedgerow (eg., Dunnock & Whitethroat) and woodland species lie adjacent to each other. However, disturbance and habitat deterioration due to excessive exposure to human activities could be problematic (eg., Liley & Clarke 2003) and reduce bird populations in suburban-rural transition zones to below their potential. Statutory monitoring of several species of high conservation concern in the UK, such as Cirl Bunting (Wotton *et al.* 2000) Nightjar (Conway *et al*. 2007) and Woodlark (Conway *et al*. in prep) helps to assess such effects on population change at a local level. On the other hand, some benefits may be accrued where suburban birds are able to gather food for broods in summer, from nearby rural habitats, or vice versa, where rural bird populations access suburban food sources in either summer or winter. The significance of urban/rural exchange by bird requires further study, together with currently unknown relative differences in brood productivity warrant serious investigation (see 5.2 below) is reproductive.

Across regions, species richness and diversity for all species and all indicator species were consistently higher on rural squares, including the Midlands where the difference was non-significant (*Objective 2*). The effect was particularly strong in the South and in the East, probably because of a higher occurrence and quality of woodland in rural squares, particularly in the south of England (Table 2). The current analysis is relatively crude in this respect in that it make no account of habitat quantity or quality either of suburban green spaces or of the adjacent rural environment (see section 5). For urban indicator species the results were equivocal and although, generally, species richness and diversity was higher in suburban squares the differences were non-significant except in the Midlands (as well as, again, for species richness over all regions combined). *Overall the results would indicate a net loss on species richness and diversity when substituting rural habitats for suburban habitats, particularly in the south and east of England.*

Absolute differences in species richness between suburban and rural classes were typically between two and three species on average (where significant). A notable exception was in the Eastern region, where there were over eight more species on average in rural than suburban squares for all species and just under five for indicator species. Differences may be particularly pronounced in Eastern England as this region has high species richness and holds significant proportions of several species that occur more sparsely in other parts of England, such as Turtle Dove, Lesser Spotted Woodpecker, Lesser Whitethroat, Nightingale and Yellow Wagtail. This analysis suggests that such species are likely to be at risk. *This is particularly important given that the Eastern region is one that is especially likely to be subject to further housing development.*

For mitigation, it may be that 'mature' greenspace is a critical factor that can increase the value of urban developments, although at the same time, occupy more space. We could provide no assessment of the average 'quality' of suburban land cover in this analysis and whether this average could be improved upon on a large scale, in order to reduce the impact of urban expansion into rural areas. It is likely that in some cases, mature suburban and rural gardens and parks are able to support 'acceptable' populations of several woodland indicators species. However, developments should probably avoid areas of countryside where relatively high populations of farmland and some woodland specialists exist, or where a high potential exists for such habitats improve in future (due to their proximity species–rich areas).

In Summary:

- *Objective 1*. Bird counts, at the 1-km square level, were analysed in relation to land cover data derived from LCM2000, using BBS bird data from a 2000.
- *Objective 2*. Bird communities of suburban landscapes and immediately adjacent rural landscapes were compared using classes of 1-km square ('suburban' and 'suburban-adjacent rural') in order to identify potential impacts or 'risk' to un-developed land. The analysis was repeated on a regional basis, based on Government Office Regions. The data were used to determine that patterns of bird abundance and community composition on urban-rural gradients were broadly consistent in different parts of the country.
- *Objective 3*. The report identifies (in section 5.2.3) spatially referenced datasets in terms of their costs, easy of access, quality and usefulness for future research into bird/habitat relationships in urban/rural transition zones and multi-year analyses.
- *Objective 4*. The report assesses the broad impacts of any future housing development scenarios on suites of bird species used in the England Biodiversity Strategy, and identifies possible mitigation strategies. The analysis differentiates between the impacts on birds of 'Woodland' 'Farmland' and 'Towns & Gardens' with particular reference to woodland, farmland and urban specialists.

5.2 Further Research and Development to Assess the Impact of Housing Development on Breeding Bird Populations

5.2.1 Limitations to the present study

This study is effective in assessing bird communities, their composition and relative abundance, in relation to broad landscape components, at a 1-km square scale. It assesses the study sample of squares and quantifies relative proportions of landscape/habitat components in order to understand and account for sampling biases. It nevertheless relies on broad supposition to predict the impact of urbanisation on rural bird communities, without precise knowledge of the quantity and quality of some habitat factors that will influence the use of urban areas by breeding birds.

Also, in this report, we have used the species lists in the published England Biodiversity Strategy indicators to derive various measures of species richness and diversity. The species composition of these indicators was constrained by data availability (scarcer species are excluded) and the need to categorise species by habitats. This might be refined in future work by using existing BBS data to quantify species use of habitats (suburban, woodland, farmland, etc) in different regions, and carrying out analyses on a broader suite of species including those already relatively scarce near suburban areas.

The scale of analysis is this study is relatively crude since 1-km squares can contain many habitat components, of which some may be relatively small in area (over looked) but important in influence (eg, small bodies of water, patches of scrub or woodland). Furthermore, there are additional key elements, not included in this study, that are likely to be important determinants of bird communities across urban-rural gradients that are not available from LCM2000 or BBS habitat data. In particular, vegetation development over time within urban-developed areas is likely to have significant effects on the bird community: a new housing development is likely to have a substantially different avifauna to one that is long-established.

5.2.2 Limited urban data sources

One potential source of urban data is Census 2001. This contains information on the number of households and house types in 'output areas'. Crucially, however, in the context of bird-habitat relationships, it does not include information on greenspace/private gardens and is therefore of limited use. For example, it would not be possible to derive an *accurate* measure of housing density from this data source (eg. Tratalos *et al*. in press). Using this Census 2001 data Tratalos *et al*. (in press) analysed BBS data in relation to 'housing density' where the data are summarised into output areas of approximately 100 households. These output areas vary in size and shape and do not match up with national grid squares (as used in the Breeding Bird Survey). Rough approximations were therefore needed to estimate 'housing density' within in BBS squares. 'Housing density' used in this way should correctly be termed an index, but it should nevertheless be strongly correlated with 'true' housing density. Crucially, however, there is no measure of the key habitat effects that dictate bird diversity/abundance in urban areas within the Census 2001 data, such as private gardens or parks. The Census 2001 data does include housing type (e.g. flats, terrace, semi-detached) and it should have been possible to build this into the analysis of Tratalos *et al*. (in press) and possibly make some assumptions about the approximate area of garden associated with each housing type. However, we believe that Census 2001 data are limited in giving insights into effects of urban expansion or ways in which to ameliorate the effects of such expansion by sympathetic planning. These data offer very limited scope for identifying detailed effects on birds that relate to habitat quality.

There exists, however, spatially referenced datasets that contain relevant information (e.g. housing age, garden area, housing type, rural land ear-marked for development) that could be analysed with respect to Breeding Bird Survey data for example within a GIS framework. There is scope for primary research, and not just the use of existing data sets, to investigate topics of habitat quality and use by birds, not least by using BBS volunteers to provide additional information, as would be necessary to fully determine impacts of housing development into the rural environment (see 5.2.3 below).

5.2.3 New scope and opportunities for informative additional studies

- *In collaboration with Central Science Laboratories (CSL)*, and using BBS data, we can derive densities and areas of buildings, greenspace and other land use types for urban areas, using *Mastermap* (for which CSL have a public sector licence). *Mastermap* can categorise polygons at selected scales (such as the BBS 200m transect section scale), using the General Land Use Database, as follows: Domestic buildings, Domestic gardens, Non-domestic buildings, Roads, Paths, Rail, Greenspace, Water and Other land uses. The BBS data itself is collected at the 200 m transect section level (the first two distance bands essentially constitute a 200 m by 200 m square) and good quality route maps will be available for all surveyed squares after the 2007 breeding season. Analyses of the transect section data would allow exploration of the impact of finer spatial differences in habitat and provide proper density estimates for habitats at a finer resolution than the present analysis. *This would allow quantification of positive or negative impacts of housing developments on bird numbers given relative change to the area of availability of specific housing/greenspace, woodland or farmland habitats*. In doing so, it would also be possible to extend the spatial scale, or even consider the role of corridors by quantifying the habitat composition of larger areas than the 3 km by 3 km blocks used in this report here to separate 'suburban' from 'rural' BBS squares.

  In addition, CSL have access to 'Defra aerial photographs' (that are autocorrelated to correct for topography and upgraded on a rolling basis so the data are five or less years old), which have sufficient resolution to allow an assessment, for example, of greenspace 'composition' for a selected area. These three data sources (Mastermap, BBS and aerial images) provide a powerful spatially linked background for analysing bird 'biodiversity' measures at finer spatial scales than in the present report. Quite possibly, some of the electronic data would require ground calibration, but this in itself is feasible through the BBS volunteer network (after summer 2007), by using volunteers to gather targeted categorical information (relating to housing age or greenspace 'composition'). Without the Defra aerial photography, volunteers could still be used to gather the same information from their survey squares, but probably with less consistency (and therefore more 'noise') than with photography. Nevertheless, subtle differences in habitat composition may still require volunteer involvement. Ultimately, these 'desk-based' analyses should be linked to targeted observational studies that would quantify birds' reliance on adjacent habitats at the urban/rural interface.

This research would provide more reliable and quantifiable estimates of impact on rural bird assemblages. At the time of writing, a planned programme of research and timed framework was being developed between BTO and CSL.

Additional studies

- *Other scope:* Local authorities may hold relevant spatially-referenced databases that could be used in conjunction with bird data to assess impacts of urban expansion. The availability of such data and their format is likely to vary between individual local authorities, making use of such data logistically difficult at regional or national scales. Colleagues at BTO Scotland have considered assessing possible impacts of urban expansion on biodiversity by using such local authority data by using case studies, rather than collating national (in this case Scottish) level data. Specifically, the Glasgow and Clyde Valley Urban Greenspace Mapping project is being used as a case study and data from other local authorities (Falkirk and Edinburgh) are being sought. A **case study** approach such as this may be the only practical option in using local authority data, although work on the ongoing project in Scotland should provide further information on these types of data sets in the near future.
- *CEH Land cover* – LCM2000 data (Fuller *et al*. 2002), as used in this report, provide a useful measure of suburban, urban and other land uses at a scale appropriate to BBS. These classes were also determined for the 1990 Land Cover map (Fuller & Parsell 1990), but due to differences in methodology, it is not possible to directly compare the two data sources to determine land use change (e.g. to measure rates of urban expansion). *A further land cover map is planned in 2007* that will use (hopefully) identical methodology to LCM2000 (G. Smith pers. comm.). Once these data are available, there will be an opportunity to model the impact of urban expansion on bird communities (change through time).
- *Comparing reproductive success between urban and rural populations of birds*. In addition to spatial and or temporal studies of bird distributions and assemblages connected to changes between urban and rural environments, there is considerable scope for observational work to target patterns of habitats use within and between these environments. Such studies could compare seasonal use of habitats, particularly in transition zones where urban and rural habitats lie adjacent to one another. Two parallel approaches are possible:

1**)** Nest record data**:** *Comparing reproductive success between urban and rural populations of birds*

Numbers (and diversity) of birds can apparently be higher in urban and, particularly, suburban areas (Mason 2000), particularly those with greenspace or high garden diversity (Mason 2006). However, little is known about whether urban bird populations are potential sources or sinks with respect to populations in the surrounding or peri-urban countryside. Individuals inhabiting such areas can have extremely low reproductive success, leading to such habitats being termed 'ecological traps' (Harris 1988). Reductions in reproductive success are often associated with increased nest predation (Schmidt & Whelan 2001, Vierling 2000), but may also be attributable to poor food availability (Crick *et al.* 2002). Urban development can thus not only reduce the original bird community present by removing habitat, but also continually draw birds in to (apparently) attractive habitat where they have little chance of reproducing successfully. However, certain types of garden or green-space may provide increased resources, or prolonged nesting opportunities (due perhaps to urban warming effects or artificial watering) creating ecological sources, supporting populations in the surrounding countryside. Thus it is important to quantify the relative nesting success of birds along urban/rural habitat gradients to accurately assess the impact of new developments.

The data to address such questions are available through data already gathered by the Nest Record Scheme. There are currently more than one million records held by the BTO, of which c. 35% are computerised, covering about 100 species, which can provide estimates of laying dates, clutch size, brood sizes and nest survival rates (Crick *et al.* 2003). Some additional computerisation of data would be required, particularly of detailed habitat data associated with each nesting attempt, to allow these analyses; the data (being geo-referenced) could also be linked with other habitat datasets (such as Land Cover). Specifically we will address, for a suite of indicator species:

1. Does nesting success vary between urban/suburban habitats and the wider countryside?
2. Within urban catchments, is there a gradient in nesting success along an urban/rural axis?
3. Within urban areas, are particular habitat features associated with higher nesting success?
4. Is the urban nesting season prolonged relative to that of the wider countryside?
5. Are there regional variations in these relationships?

This will determine whether urban areas provide better or worse habitat than the wider countryside (1 and 4), in particular whether they have the potential to act as source or sink habitats; whether spreading development around current urban centres will affect bird's reproductive performance (2) and whether guidance can be provided on features to mitigate any adverse impacts (3). They will also address the fact that the extent of housing development is likely to vary regionally, and so whether bird populations in some areas will be affected disproportionately (5). These questions would be addressed using a small range of species common across the urban rural gradient but with differing ecologies (e.g. Blackbird, Robin, Blackcap, Chaffinch, Blue Tit, House Sparrow) to represent the range of impacts likely.

2). *Observational studies*

Observational studies of bird use of adjacent rural/urban environments, particularly for pairs nesting in and around houses and gardens: how far do they travel when provisioning young, where to they travel too, how often (parent use of habitats and work rates), chick development and fledging parameters. This kind of data should be gathered over more than one year, and could also incorporate summer and winter seasonal studies. Their scope would suite a focused case-study along the lines of a Ph.D or professional research project(s).

Table A A summary of sources of data and their potential use and cost for future studies of urban/rural gradients. The information here is indicative rather than definitive.

Data source	Access	Requirement	Task cost	Coverage	Quality	Use
Breeding Bird Survey (BBS)	Immediate: Via BTO	Bird density data for 600 to 1000 1-km squares in the UK, and up to 10,000, 200m sub sections.	Digitising 200m sub-sections to give grid-ref ID: £5000-£9000	UK and UK regions	Relative values for bird densities / 200m^2, with detectability adjustments	Spatial and temporal data.
Master Map	Immediate: via CSL licenced user	Analysis of 10,000 200m x 200m BBS transect sub-sections including greenspace.	*Minimum* cost around £5,000 (CSL).	UK and UK regions	Densities & areas of buildings & greenspace.	Spatial data for 'habitat' coverage.
Defra aerial photography	Immediate	Classifying habitat types of 200m BBS transect sub-sections.	Manual task see *. At 1-hour per photo - possibly £34,000 (CSL)	England and English regions	Assessing	2-D evaluation of habitats and the quality of greenspace
Volunteer based data	2008/2009	Classifying habitat types of 200m BBS transect sub-sections.	Mailing, handling correspondence, designing forms inputting. 20-30 days Probably £6,000 to £9,000.	BBS distribution; UK	Ground-evidence of habitat quality of greenspace or urban /rural habitats	3D evaluation, housing age, habitats and the quality of greenspace
Overall analysis and modelling using the combined data sources above. eg. for 2007/2008			Data handling analysis and reporting. Estimated 20-40-days: £6,000-£12,000.			
LCM2007	Planned but currently unknown level of availability now or in the near future.	Changes in bird distribution with changes in Land class data between 2000 and 2007.	Currently unknown	UK	Percentage cover values for land classes.	1-km scale spatial data.
Observational studies.	2008 onwards.	Targeted studies of bird use of habitats, provisioning data, nest data	Full research theme yet to be developed	Identified study area.	Detailed activity data from sample of target nests territories. Parent time budgets and nest data.	Bird use of adjacent urban and rural habitats.
Nest Record Data (BTO)			Indicative Costs: Data Collation c £8,500 + VAT Data Analysis c£13,000+ VAT			

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Table 2. A regional-level comparison of land cover between 1-km squares defined as either rural (*adjacent to suburban land* from the BBS sample) or *isolated* rural squares. Regions were defined according to RDA (see Fig. 2). Only significant differences are shown.

(a) East *suburban-adjacent* rural = 84; *isolated* rural squares = 17960

	Rural			Isolated		|Z|
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	11.20	11.46		6.50	9.40	4.69***
Improved grassland	8.96	11.57		5.97	8.93	2.49*
Set-aside grass	4.12	5.93		3.27	5.88	2.08*
Calcareous grass	6.07	9.19		4.66	8.99	2.18*
Arable cereals	24.79	20.62		34.01	21.68	3.83***
Arable horticulture	26.99	17.17		32.02	18.68	2.45*
Suburban	5.93	6.08		2.86	4.59	5.50***
Urban	2.35	3.55		1.15	2.68	3.16***

(b) Midlands *suburban-adjacent* rural = 76; *isolated* rural squares = 21448

	Rural			Isolated		|Z|
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Neutral grass	3.01	5.06		1.81	4.82	3.13***
Arable cereals	7.98	13.13		17.07	19.08	4.84***
Suburban	6.21	6.31		3.20	4.67	5.20***
Urban	2.53	3.97		1.31	2.99	3.67***

(c) **North *suburban-adjacent* rural = 59; *isolated* rural squares = 21304**

	Rural			Isolated		|Z|
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	12.57	16.76		6.88	9.42	2.18*
Neutral grass	5.21	8.66		3.24	8.31	3.71***
Arable horticulture	19.51	24.01		28.61	26.92	2.64**
Suburban	6.54	5.99		3.01	4.62	6.38***
Urban	3.70	5.37		1.32	2.88	5.27***

(d) South *suburban-adjacent* rural = 175; *isolated* rural squares = 38329

	Rural			Isolated		|Z|
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Set-aside grass	2.66	5.83		1.44	3.73	4.65***
Arable cereals	14.14	15.05		16.31	16.17	2.17*
Arable horticulture	14.78	12.95		17.40	14.84	2.18*
Suburban	7.24	6.38		3.31	4.66	9.95***
Urban	1.97	3.22		1.05	2.43	6.15***

Table 3. A regional-level comparison of land cover between 1-km squares defined as either rural (*adjacent to suburban land* from the whole LCM2000 database for lowland England) or *isolated* rural squares. Regions were defined according to RDA (see Fig. 2). Z statistics calculated from a two-sample z-test for comparing means of two large samples (Fowler & Cohen 1986).

(a) East *suburban-adjacent* rural = 4543; *isolated* rural squares = 17960

	Rural			**Isolated**		**|Z|**
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	7.78	10.95		6.10	8.80	9.34***
Improved grassland	8.05	10.48		5.29	8.25	16.13***
Neutral grassland	2.79	7.44		2.09	6.85	2.64**
Set-aside grassland	4.42	6.63		2.89	5.55	13.93***
Calcareous grass	5.26	8.80		4.47	9.05	5.19***
Arable cereals	27.98	20.46		35.97	21.73	22.42***
Arable horticulture	28.60	17.76		33.13	18.83	14.64***
Suburban	5.15	5.88		2.11	3.81	32.66***
Urban	2.04	3.55		0.86	2.25	21.12***

(b) Midlands *suburban-adjacent* rural = 5547; *isolated* rural squares = 21448

	Rural			**Isolated**		**|Z|**
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	7.54	9.37		7.23	9.33	2.11*
Coniferous woodland	1.45	5.15		1.71	5.93	3.01**
Neutral grassland	2.33	5.44		1.63	4.57	8.55***
Set-aside grassland	1.54	3.64		1.34	3.19	3.56***
Calcareous grass	6.96	8.64		6.07	8.15	6.70***
Arable cereals	12.63	16.28		18.55	19.72	22.05***
Suburban	5.84	6.02		2.31	3.75	41.03***
Urban	2.38	4.01		0.95	2.47	25.00***

(c) North *suburban-adjacent* rural = 5958; *isolated* rural squares = 21304

	Rural			**Isolated**		**|Z|**
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	8.27	10.41		6.25	8.84	13.36***
Coniferous woodland	0.91	3.18		2.51	8.94	19.85***
Improved grassland	22.74	21.79		30.58	25.95	22.64***
Neutral grassland	3.67	7.96		3.08	8.38	4.89***
Calcareous grass	7.68	9.46		5.83	7.93	13.49***
Arable cereals	13.80	16.49		12.16	17.18	6.52***
Arable horticulture	26.63	24.70		28.65	27.12	5.29***
Suburban	5.94	6.01		1.80	3.30	50.55***
Urban	2.59	3.92		0.79	2.13	33.75***

(d) South *suburban-adjacent* rural = 9198; *isolated* rural squares = 38329

	Rural			**Isolated**		**|Z|**
Cover type	**Mean**	**SD**		**Mean**	**SD**	
Broadleaved woodland	12.94	14.09		11.99	13.39	5.71***
Coniferous woodland	2.55	8.26		2.20	6.67	3.71***
Improved grassland	27.77	19.57		32.75	21.99	20.66***
Set-aside grassland	1.92	4.44		1.29	3.48	12.44***
Calcareous grass	6.38	8.24		6.06	9.23	3.10**
Arable cereals	13.99	15.39		17.02	16.33	16.26***
Arable horticulture	15.96	13.79		17.83	15.12	11.07***
Suburban	6.18	6.10		2.44	3.73	55.67***
Urban	1.86	3.23		0.81	2.07	29.35***
Inland bare ground	0.98	3.13		1.18	4.42	4.72***

Table 4 Mean species densities by *rural-adjacent* suburban (n=272) and *suburban-adjacent* rural (n=376) land classifications. Significance probabilities (where Prob F < 0.05 (also denoted*)) show differences between the two land classifications for each bird species.

(a) for 27 urban indicator species.

Species	Suburban Mean (n)	Rural Mean (n=376)	Sum of Squares	Mean Square	F Value	Prob F
Blackbird*	113.92	61.88	427470.27	427470.27	120.04	<0.0001
Blackcap*	7.92	10.21	829.46	829.46	4.10	0.0433
Blue Tit*	83.64	65.42	52399.54	52399.54	12.48	0.0004
Carrion Crow	12.63	11.37	251.08	251.08	0.77	0.3802
Collared Dove*	42.14	10.64	156586.40	156586.40	143.85	<0.0001
Chaffinch*	36.49	57.58	70228.19	70228.19	39.20	<0.0001
Dunnock*	22.58	16.96	4978.31	4978.31	14.42	0.0002
Green Woodpecker	0.78	0.83	0.37	0.37	0.09	0.7684
Goldfinch	8.06	9.09	166.33	166.33	0.52	0.4693
Greenfinch*	40.18	23.97	41455.14	41455.14	27.53	<0.0001
Great Tit	34.10	32.07	652.78	652.78	0.63	0.4291
House Martin	5.09	4.02	183.06	183.06	0.53	0.4649
House Sparrow*	176.25	45.01	2718166.73	2718166.73	163.72	<0.0001
Jay	1.45	1.93	36.23	36.23	1.51	0.2190
Jackdaw	8.92	10.13	230.94	230.94	0.41	0.5198
Long-tailed Tit	7.68	8.28	56.30	56.30	0.21	0.6431
Mistle Thrush*	3.69	2.80	125.34	125.34	3.90	0.0486
Mallard	11.67	10.23	327.24	327.24	0.41	0.5234
Magpie*	22.42	10.90	20948.67	20948.67	61.31	<0.0001
Pied Wagtail	3.33	3.77	30.34	30.34	0.44	0.5066
Robin	48.91	48.02	125.55	125.55	0.09	0.7696
Starling*	115.33	36.74	974707.57	974707.57	106.24	<0.0001
Sparrowhawk	0.13	0.19	0.52	0.52	0.47	0.4934
Swift*	5.35	1.21	2697.31	2697.31	8.80	0.0031
Song Thrush	8.12	7.45	69.43	69.43	0.67	0.4148
Woodpigeon	61.33	65.18	2341.23	2341.23	0.41	0.5246
Wren	47.83	47.27	49.46	49.46	0.03	0.8666

(b) for 19 farmland indicator species.

Species	Suburban Mean	Rural Mean	Sum of Squares	Mean Square	F Value	Prob F
Corn Bunting	0.28	0.93	66.53	66.53	3.76	0.0529
Goldfinch	8.06	9.09	166.33	166.33	0.52	0.4693
Greenfinch*	40.18	23.97	41455.14	41455.14	27.53	<0.0001
Jackdaw	8.92	10.13	230.94	230.94	0.41	0.5198
Kestrel	0.45	0.40	0.38	0.38	0.03	0.8617
Lapwing	0.67	1.11	31.68	31.68	0.97	0.3252
Linnet*	6.01	12.03	5737.97	5737.97	10.86	0.0010
Pheasant*	0.44	1.35	132.46	132.46	5.50	0.0193
Reed Bunting*	0.79	1.73	140.53	140.53	5.37	0.0208
Rook	4.67	6.27	402.40	402.40	0.69	0.4066
Skylark*	2.63	8.60	5621.10	5621.10	35.78	<0.0001
Stock Dove	1.06	1.52	33.41	33.41	1.46	0.2270
Starling*	115.33	36.74	974707.57	974707.57	106.24	<0.0001
Turtle Dove*	0.08	0.74	67.11	67.11	11.47	0.0008
Tree Sparrow	0.43	1.05	60.99	60.99	2.61	0.1067
Whitethroat*	7.92	15.52	9114.08	9114.08	21.10	<0.0001
Woodpigeon	61.33	65.18	2341.23	2341.23	0.41	0.5246
Yellowhammer*	3.82	12.14	10917.31	10917.31	39.01	<0.0001
Yellow Wagtail*	0.29	1.17	122.33	122.33	4.67	0.0311

(c) for 33 woodland indicator species.

Species	Suburban Mean	Rural Mean	Sum of Squares	Mean Square	F Value	Prob F
Blackbird*	113.92	61.88	427470.27	427470.27	120.04	<0.0001
Blackcap*	7.92	10.21	829.46	829.46	4.10	0.0433
Bullfinch	1.77	2.50	84.95	84.95	1.68	0.1948
Blue Tit*	83.64	65.42	52399.54	52399.54	12.48	0.0004
Chiffchaff	2.91	3.85	141.81	141.81	3.24	0.0724
Chaffinch*	36.49	57.58	70228.19	70228.19	39.20	<0.0001
Coal Tit	1.82	2.60	94.59	94.59	1.18	0.2784
Dunnock*	22.58	16.96	4978.31	4978.31	14.42	0.0002
Green Woodpecker	0.78	0.83	0.37	0.37	0.09	0.7684
Goldcrest*	0.00	0.43	29.58	29.58	4.16	0.0418
Great Spotted Woodpecker	1.02	1.50	36.58	36.58	2.96	0.0858
Great Tit	34.10	32.07	652.78	652.78	0.63	0.4291
Garden Warbler*	0.66	1.44	95.41	95.41	7.38	0.0068
Hawfinch	0.00	0.00	0.00	0.00		
Jay	1.45	1.93	36.23	36.23	1.51	0.2190
Lesser Redpoll	0.03	0.09	0.55	0.55	0.45	0.5020
Lesser Spotted Woodpecker	0.04	0.01	0.08	0.08	0.75	0.3859
Long-tailed Tit	7.68	8.28	56.30	56.30	0.21	0.6431
Lesser Whitethroat*	0.26	0.72	32.85	32.85	5.62	0.0180
Marsh Tit*	0.03	0.33	14.07	14.07	4.88	0.0275
Nightingale	0.05	0.03	0.03	0.03	0.11	0.7447
Nuthatch	0.62	1.00	23.31	23.31	1.98	0.1595
Robin	48.91	48.02	125.55	125.55	0.09	0.7696
Redstart	0.00	0.08	0.96	0.96	1.94	0.1645
Spotted Flycatcher*	0.18	0.88	78.39	78.39	6.98	0.0085
Sparrowhawk	0.13	0.19	0.52	0.52	0.47	0.4934
Song Thrush	8.12	7.45	69.43	69.43	0.67	0.4148
Treecreeper*	0.21	1.15	140.12	140.12	11.36	0.0008
Tawny Owl	0.08	0.06	0.07	0.07	0.12	0.7297
Tree Pipit	0.06	0.21	3.55	3.55	1.65	0.1995
Wren	47.83	47.27	49.46	49.46	0.03	0.8666
Willow Tit	0.26	0.22	0.26	0.26	0.05	0.8178
Willow Warbler*	3.64	5.15	358.35	358.35	3.97	0.0468

Table 5 Species diversity and richness mean values on BBS squares defined as 'suburban' (*rural-adjacent*) and 'rural' (*suburban-adjacent*) for (a) England and for (b-e) English combined RDA regions. Differences between the suburban and rural squares are shown as F values with associated probabilities of significance Prob F (where α = 0.05). Note that species richness was log-transformed prior to analysis to satisfy the requirements of normally distributed data for the analysis. Untransformed ('raw') mean species richness values are also presented.

(a) England	**Suburban Mean (n=272)**	**Rural Mean (n=376)**	**Sum of Squares**	**Mean Square**	**F Value**	**Prob F**
All species						
Species diversity	2.75	2.93	5.30	5.30	50.67	<0.0001
Species richness (log)	3.35	3.48	2.86	2.86	44.26	<0.0001
Species richness (raw)	28.5	32.5				
Indicator species (61)						
Species diversity	2.63	2.75	2.39	2.39	22.80	<0.0001
Species richness (log)	3.19	3.28	1.24	1.24	20.74	<0.0001
Species richness (raw)	24.3	26.6				
Urban species (27)						
Species diversity	2.48	2.48	0.00	0.00	0.00	0.9713
Species richness (log)	2.97	2.94	0.22	0.22	4.59	0.0326
Species richness (raw)	19.5	18.9				

(b) North	**Suburban Mean (n=76)**	**Rural Mean (n=59)**	**Sum of Squares**	**Mean Square**	**F Value**	**Prob F**
All species						
Species diversity	2.76	2.97	1.51	1.51	11.23	0.0010
Species richness (log)	3.38	3.48	0.34	0.34	4.53	0.0351
Species richness (raw)	29.4	32.5				
Indicator species (61)						
Species diversity	2.62	2.77	0.72	0.72	5.93	0.0162
Species richness (log)	3.19	3.25	0.13	0.13	1.94	0.1658
Species richness (raw)	24.3	25.8				
Urban species (27)						
Species diversity	2.46	2.51	0.07	0.07	0.75	0.3884
Species richness (log)	2.96	2.92	0.06	0.06	1.41	0.2366
Species richness (raw)	19.3	18.5				

(c) Midlands	**Suburban Mean (n=52)**	**Rural Mean (n=77)**	**Sum of Squares**	**Mean Square**	**F Value**	**Prob F**
All species						
Species diversity	2.86	2.90	0.05	0.05	0.57	0.4519
Species richness (log)	3.41	3.44	0.03	0.03	0.39	0.5320
Species richness (raw)	30.3	31.2				
Indicator species (61)						

Species diversity	2.74	2.72	0.01	0.01	0.12	0.7248
Species richness (log)	3.26	3.23	0.02	0.02	0.34	0.5618
Species richness (raw)	26.0	25.3				
Urban species (27)						
Species diversity	2.56	2.44	0.46	0.46	5.39	0.0218
Species richness (log)	3.01	2.90	0.38	0.38	7.38	0.0075
Species richness (raw)	20.3	18.2				

(d) East Anglia	**Suburban Mean (n=53)**	**Rural Mean (n=85)**	**Sum of Squares**	**Mean Square**	**F Value**	**Prob F**
All species						
Species diversity	2.58	2.94	4.19	4.19	33.02	<0.0001
Species richness (log)	3.26	3.53	2.37	2.37	32.22	<0.0001
Species richness (raw)	26.0	34.1				
Indicator species (61)						
Species diversity	2.46	2.74	2.52	2.52	22.03	<0.0001
Species richness (log)	3.12	3.31	1.24	1.24	20.80	<0.0001
Species richness (raw)	22.6	27.4				
Urban species (27)						
Species diversity	2.34	2.44	0.34	0.34	2.85	0.0935
Species richness (log)	2.94	2.96	0.02	0.02	0.42	0.5196
Species richness (log)	18.9	19.3				

(e) South	**Suburban Mean (n=98)**	**Rural Mean (n=175)**	**Sum of Squares**	**Mean Square**	**F Value**	**Prob F**
All species						
Species diversity	2.78	2.93	1.37	1.37	17.75	<0.0001
Species richness (log)	3.34	3.47	1.13	1.13	23.24	<0.0001
Species richness (log)	28.2	32.1				
Indicator species (61)						
Species diversity	2.68	2.77	0.56	0.56	6.21	0.0133
Species richness (log)	3.20	3.29	0.57	0.57	10.66	0.0012
Species richness (log)	24.5	26.8				
Urban species (27)						
Species diversity	2.54	2.52	0.03	0.03	0.31	0.5791
Species richness (log)	2.99	2.95	0.08	0.08	1.75	0.1868
Species richness (log)	19.9	19.1				

Table 6 Presence/absence of woodland and farmland species in urban BBS squares. Here urban squares comprise at least 25% urban (suburban plus urban) and less than 25% of either woodland or farmland cover. Seven species from the woodland and farmland indicators do not occur at all on these squares and many species occur on less than 5% of the 142 urban squares.

Species	Absent on all urban squares	Present on less than 5% of urban squares	Present on less than 10% of urban squares
Woodland species			
Blackbird			
Blackcap			
Bullfinch			
Blue Tit			
Chiffchaff			
Chaffinch			
Coal Tit			
Dunnock			
Green Woodpecker			
Goldcrest			
Great Spotted Woodpecker			
Great Tit			
Garden Warbler		X	X
Hawfinch	X	X	X
Jay			
Lesser Redpoll		X	X
Lesser Spotted Woodpecker	X	X	X
Long-tailed Tit			
Lesser Whitethroat		X	X
Marsh Tit		X	X
Nightingale		X	X
Nuthatch			X
Robin			
Redstart	X	X	X
Spotted Flycatcher		X	X
Sparrowhawk			
Song Thrush			
Treecreeper	X	X	X
Tawny Owl	X	X	X
Tree Pipit		X	X
Wren			
Willow Tit		X	X
Willow Warbler			
Farmland species			
Corn Bunting	X	X	X
Goldfinch			
Greenfinch			
Jackdaw			
Kestrel			
Lapwing		X	X
Linnet			
Grey Partridge		X	X
Reed Bunting		X	X
Rook			
Skylark			X
Stock Dove			X
Starling			
Turtle Dove		X	X
Tree Sparrow		X	X
Whitethroat			
Woodpigeon			
Yellowhammer		X	X
Yellow Wagtail	X	X	X

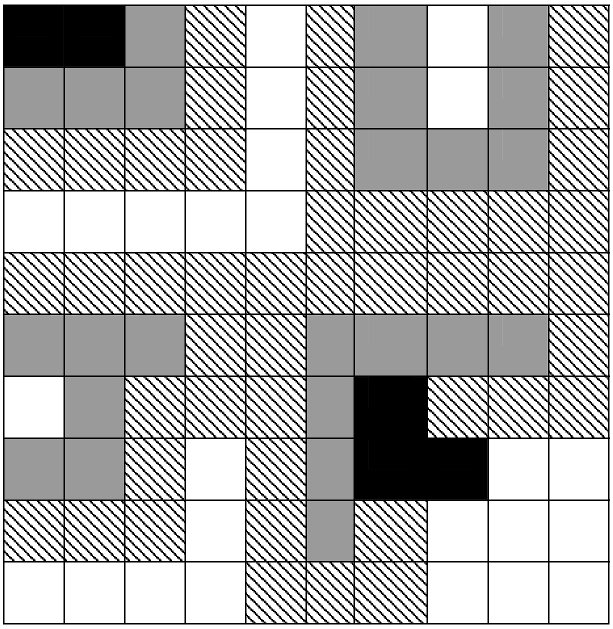

Figure 1 A hypothetical example of the classification of 1-km squares into *rural-adjacent* suburban and *suburban-adjacent* rural habitat classes (LCM2000). Grey squares are classed as suburban and diagonal shading as rural. Squares that were predominantly continuous urban (black squares) and squares that were adjacent (or diagonally adjacent) only to squares of the same class or urban (white squares) were not included in the analysis.

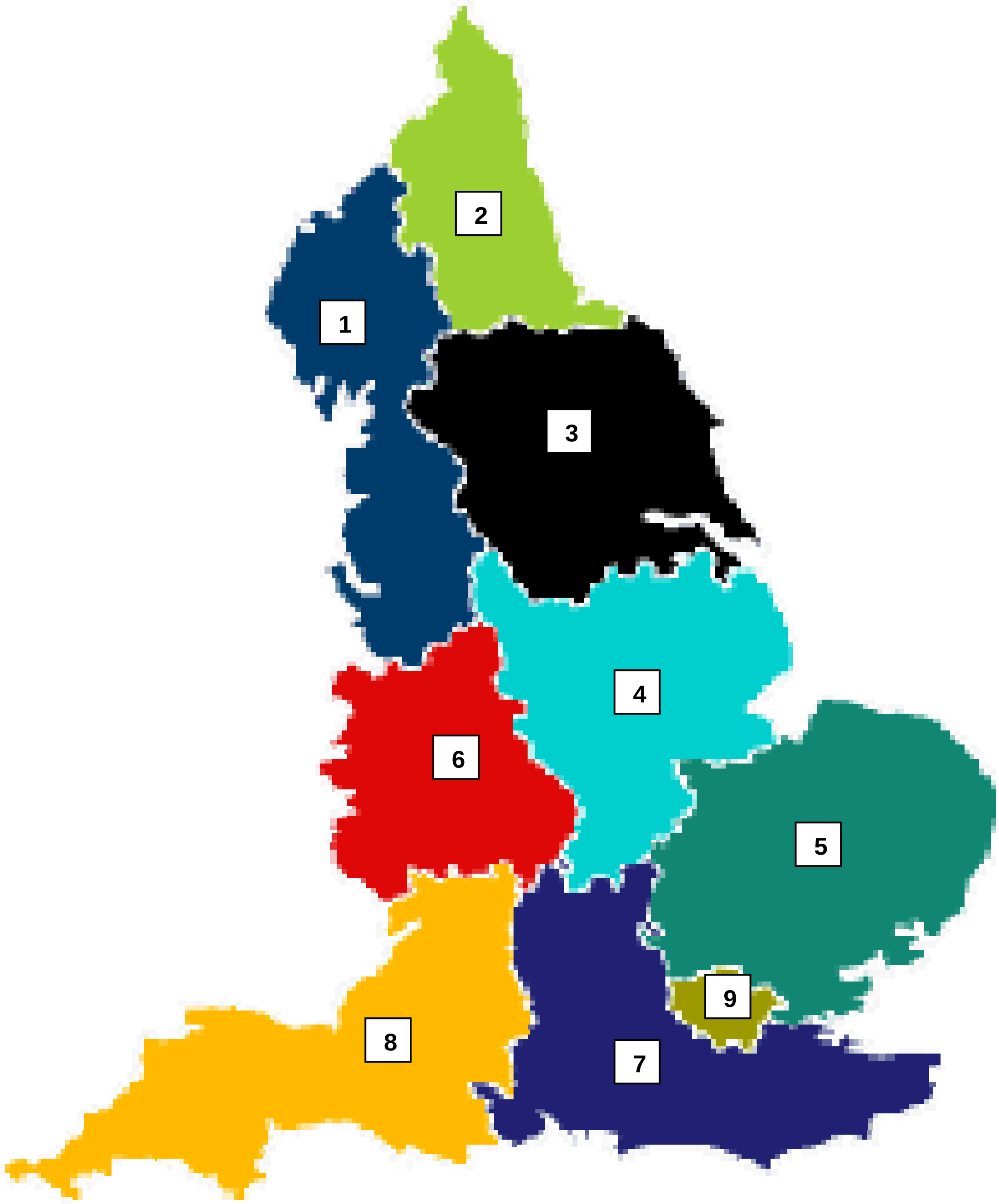

Figure 2 Regional Development Agency regions (RDAs) of England. For the purposes of the analysis, RDAs were combined as follows: South = RDA 7 and 8; East = RDA 5 and 9; Midlands = RDA 4 and 6; North = RDA 1, 2 and 3.

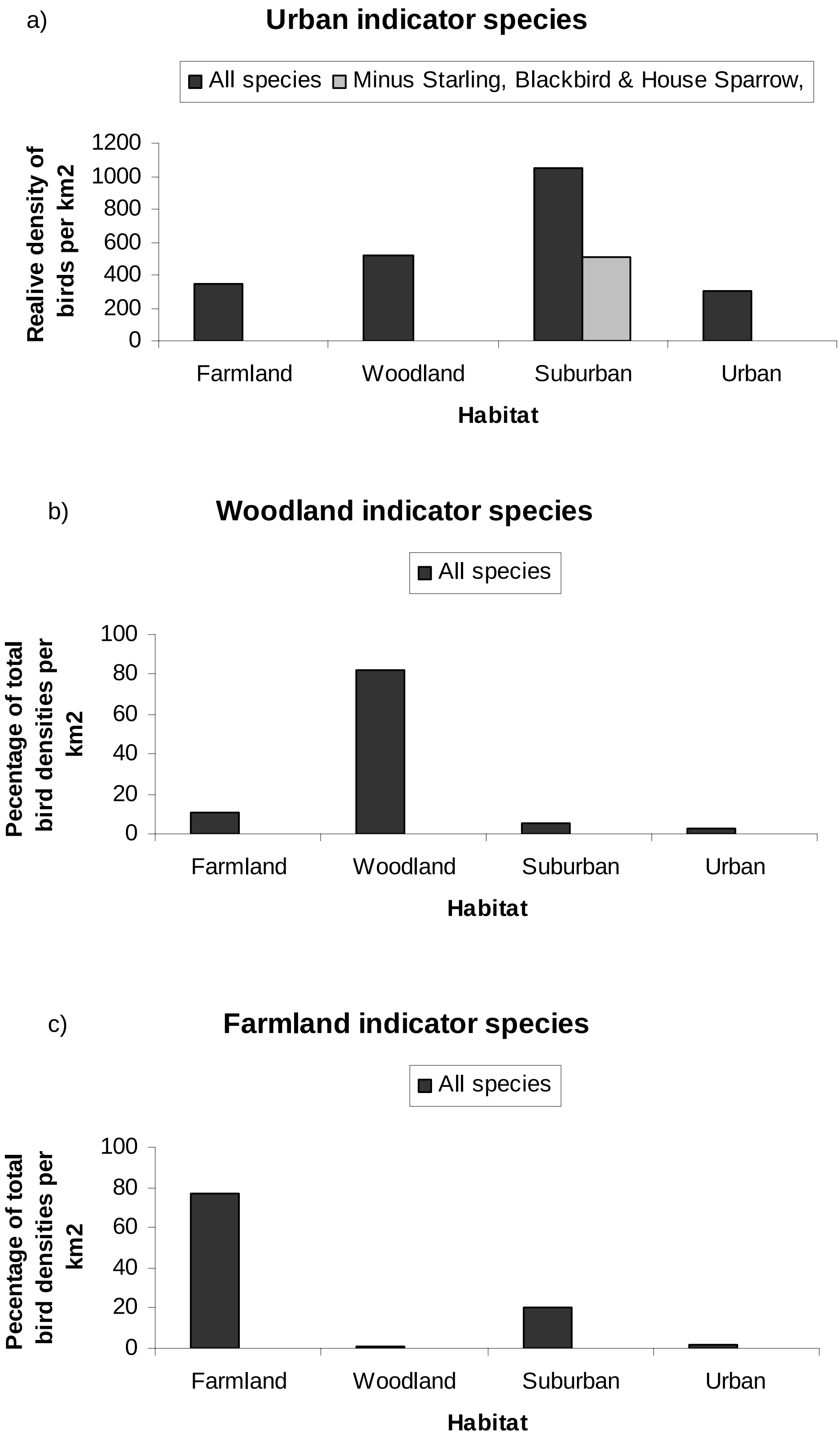

Figure 3 The proportional distribution of bird densities in relation to the percentage cover of farmland, woodland, suburban and urban habitat for (a) Urban, (b) Woodland and (c) Farmland indicator species. For the Urban indicators (a), around 50% of the total bird density associated with suburban habitats comprised Blackbird, Starling and House Sparrow.

Appendix 1 Mean % cover per 1-km square for 27 land cover types derived from LCM2000 (Fuller *et al*. 2002), for squares classed as suburban (*rural-adjacent*), rural (*suburban-adjacent*)(BBS sample) or *isolated* rural squares (national level). Sample sizes: suburban = 279, rural = 394, isolated rural squares = 99041.

	Suburban		**Rural**		**Isolated**	
Cover type	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Sea / Estuary	0.69	5.60	0.24	2.52	1.41	9.69
Water (inland)	0.36	1.57	0.92	5.45	0.39	3.05
Littoral rock	0.00	0.00	0.00	0.00	0.01	0.29
Littoral sediment	0.13	1.17	0.72	6.06	0.73	5.99
Saltmarsh	0.03	0.27	0.18	1.92	0.30	3.48
Supra-littoral rock	0.00	0.00	0.00	0.00	0.00	0.05
Supra-littoral sediment	0.08	0.74	0.00	0.00	0.10	1.77
Bog (deep peat)	0.04	0.69	0.00	0.00	0.06	1.18
Dense dwarf shrub heath	0.15	1.22	0.29	2.74	0.25	2.76
Open dwarf shrub heath	0.08	0.67	0.14	1.20	0.22	2.28
Montane habitats	0.00	0.00	0.00	0.00	0.00	0.00
Broad-leaved / mixed woodland	7.79	9.29	12.08	13.96	8.97	11.48
Coniferous woodland	0.97	3.73	2.34	8.83	1.96	7.16
Improved grassland	12.75	11.62	23.57	20.64	24.71	22.68
Neutral grass	3.59	6.70	2.60	5.83	1.92	6.19
Setaside grass	1.47	3.29	2.31	5.03	1.52	3.94
Bracken	0.00	0.00	0.06	0.82	0.10	1.33
Calcareous grass	4.25	6.48	6.33	8.14	5.98	8.75
Acid grassland	0.46	2.58	0.93	4.56	0.81	4.17
Fen, marsh, swamp	0.05	0.36	0.13	0.99	0.16	1.55
Arable cereals	4.41	8.51	14.89	17.03	18.79	19.52
Arable horticulture	7.43	9.82	22.22	20.16	25.92	21.79
Arable non-rotational	0.28	1.89	0.49	2.05	0.63	2.45
Suburban / rural development	41.28	19.69	6.66	6.25	3.14	4.65
Continuous urban	12.80	12.84	2.42	3.85	1.18	2.71
Inland bare ground	0.92	2.88	0.47	1.30	0.74	3.06
Unclassified*	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2(a) The relationship between species diversity, species richness and the cover of suburban land per 1-km square. Statistics were derived from linear regression.

	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
All Species								
Species diversity	Suburban + Suburban^2	76.39	<0.0001	0.0639	1.43559 -1.90056	0.11778 0.15722	12.19 -12.09	<0.0001 <0.0001
Species richness (log)	Suburban + Suburban^2	86.54	<0.0001	0.0719	1.32727 -1.64338	0.10089 0.13468	13.16 -12.20	<0.0001 <0.0001
Indicator Species (61)								
Species diversity	Suburban + Suburban^2	101.09	<0.0001	0.0836	1.84249 -2.16097	0.13077 0.17431	14.09 -12.40	<0.0001 <0.0001
Species richness (log)	Suburban + Suburban^2	118.13	<0.0001	0.0965	1.89428 -2.07736	0.12836 0.17110	14.76 -12.14	<0.0001 <0.0001
Urban Species (27)								
Species diversity	Suburban + Suburban^2	168.65	<0.0001	0.1331	2.11949 -2.14393	0.12718 0.16933	16.67 -12.66	<0.0001 <0.0001
Species richness (log)	Suburban + Suburban^2	200.56	<0.0001	0.1546	2.16413 -2.02979	0.12677 0.16878	17.07 -12.03	<0.0001 <0.0001

Appendix 2b The relationship between the density of 27 urban indicator species and the cover of suburban land per 1-km square.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Blackbird	Suburban + Suburban^2	518.11	<0.0001	0.3252	152.05316 -21.56165	11.57920 15.41814	13.13 -1.40	<0.00010. 1621
Blackcap	Suburban + Suburban^2	15.81	<0.0001	0.0136	17.98432 -21.86669	3.20120 4.26252	5.62 -5.13	<0.0001 <0.0001
Blue Tit	Suburban + Suburban^2	137.55	<0.0001	0.1129	131.37119 -70.77143	13.80717 18.38475	9.51 -3.85	<0.00010. 0001
Carrion Crow	Suburban + Suburban^2	19.53	<0.0001	0.0170	23.20826 -18.48390	5.00053 6.65840	4.64 -2.78	<0.00010. 0056
Collared Dove	Suburban + Suburban^2	451.76	<0.0001	0.2958	21.77939 52.34396	5.43487 7.23674	4.01 7.23	0.0001 <0.0001
Chaffinch	Suburban + Suburban^2	36.64	<0.0001	0.0321	16.36669 -73.20410	12.76827 17.00142	1.28 -4.31	0.2000 <0.0001
Dunnock	Suburban + Suburban^2	91.29	<0.0001	0.0776	38.14528 -26.86541	4.17547 5.55980	9.14 -4.83	<0.0001<0 .0001
Green Woodpecker	Suburban + Suburban^2	6.81	0.0011	0.0054	1.85093 -2.19142	0.50454 0.67182	3.67 -3.26	0.0002 0.0011
Goldfinch	Suburban + Suburban^2	6.75	0.0012	0.0053	16.81212 -23.64497	4.83932 6.44373	3.47 -3.67	0.0005 0.0002
Greenfinch	Suburban + Suburban^2	138.52	<0.0001	0.1136	78.76034 -43.91507	8.10011 10.78560	9.72 -4.07	<0.0001 <0.0001
Great Tit	Suburban + Suburban^2	98.52	<0.0001	0.0833	82.41217 -78.21338	6.81735 9.07756	12.09 -8.62	<0.0001 <0.0001
House Martin	Suburban + Suburban^2	12.91	<0.0001	0.0110	22.61902 -25.23389	4.58799 6.10908	4.93 -4.13	<0.0001 <0.0001
House Sparrow	Suburban + Suburban^2	377.62	<0.0001	0.2598	133.11783 191.05162	26.87573 35.78602	4.95 5.34	<0.0001 <0.0001
Jay	Suburban + Suburban^2	10.33	<0.0001	0.0086	4.71245 -5.00060	1.10240 1.46789	4.27 -3.41	<0.00010. 0007
Jackdaw	Suburban + Suburban^2	12.11	<0.0001	0.0102	31.48152 -35.72672	6.53766 8.70514	4.82 -4.10	<0.0001 <0.0001
Long-tailed Tit	Suburban + Suburban^2	6.50	0.0015	0.0051	14.15139 -16.58578	3.96156 5.27496	3.57 -3.14	0.0004 0.0017
Mistle Thrush	Suburban + Suburban^2	20.31	<0.0001	0.0177	6.76343 -5.65997	1.37174 1.82653	4.93 -3.10	<0.00010. 0020
Mallard	Suburban + Suburban^2	13.25	<0.0001	0.0113	25.04089 -22.55807	5.90559 7.86352	4.24 -2.87	<0.00010. 0042
Magpie	Suburban + Suburban^2	274.99	<0.0001	0.2034	24.77852 5.17840	3.29540 4.38795	7.52 1.18	<0.00010. 2381
Pied Wagtail	Suburban + Suburban^2	7.95	0.0004	0.0064	6.50765 -10.38072	2.01939 2.68889	3.22 -3.86	0.0013 0.0001
Robin	Suburban + Suburban^2	44.48	<0.0001	0.0389	81.30228 -79.55537	9.75650 12.99114	8.33 -6.12	<0.0001 <0.0001
Starling	Suburban + Suburban^2	365.02	<0.0001	0.2533	118.89503 90.64483	18.50213 24.63626	6.43 3.68	<0.00010. 0002
Sparrowhawk	Suburban + Suburban^2	0.15	0.8625	-0.0008	-0.02191 -0.05469	0.30977 0.41247	-0.07 -0.13	0.9436 0.8945
Swift	Suburban + Suburban^2	11.84	<0.0001	0.0100	4.17885 3.58719	3.77455 5.02596	1.11 0.71	0.2684 0.4755
Song Thrush	Suburban + Suburban^2	19.90	<0.0001	0.0173	12.14732 -9.86341	2.55252 3.39877	4.76 -2.90	<0.00010. 0037
Woodpigeon	Suburban + Suburban^2	18.53	<0.0001	0.0161	100.12935 -84.19780	21.17887 28.20045	4.73 -2.99	<0.00010. 0029
Wren	Suburban + Suburban^2	18.45	<0.0001	0.0160	53.94425 -51.91772	10.19118 13.56993	5.29 -3.83	<0.00010. 0001

Appendix 2c The relationship between the density of woodland indicator species and the cover of suburban land per 1-km square.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Bullfinch	Suburban + Suburban^2	3.06	0.0469	0.0019	3.94163 -4.99404	1.59526 2.12414	2.47 -2.35	0.0136 0.0188
Chiffchaff	Suburban + Suburban^2	5.54	0.0040	0.0042	5.49543 -8.02480	1.81229 2.41313	3.03 -3.33	0.0025 0.0009
Coal Tit	Suburban + Suburban^2	7.14	0.0008	0.0057	-6.87466 4.90119	2.66680 3.55095	-2.58 1.38	0.0100 0.1677
Goldcrest	Suburban + Suburban^2	0.62	0.5402	-0.0004	-0.15873 -0.18067	0.70830 0.94312	-0.22 -0.19	0.8227 0.8481
Great Spotted Woodpecker	Suburban + Suburban^2	3.86	0.0212	0.0027	1.79394 -2.76559	0.75937 1.01113	2.36 -2.74	0.0182 0.0063
Garden Warbler	Suburban + Suburban^2	5.63	0.0037	0.0043	-0.04891 -1.70692	1.07560 1.43220	-0.05 -1.19	0.9637 0.2335
Hawfinch	Suburban + Suburban^2			.	0.00000 0.00000	0.00000 0.00000		
Lesser Redpoll	Suburban + Suburban^2	1.03	0.3585	0.0000	-0.87263 0.39351	1.15286 1.53507	-0.76 0.26	0.4492 0.7977
Lesser Spotted Woodpecker	Suburban + Suburban^2	1.01	0.3660	0.0000	0.12480 -0.15612	0.08803 0.11721	1.42 -1.33	0.1564 0.1830
Lesser Whitethroat	Suburban + Suburban^2	2.18	0.1129	0.0011	0.29756 -1.02773	0.65958 0.87825	0.45 -1.17	0.6519 0.2421
Marsh Tit	Suburban + Suburban^2	6.07	0.0024	0.0047	-0.98234 0.04451	0.74229 0.98839	-1.32 0.05	0.1858 0.9641
Nightingale	Suburban + Suburban^2	0.65	0.5225	-0.0003	0.15311 -0.14987	0.15201 0.20241	1.01 -0.74	0.3139 0.4591
Nuthatch	Suburban + Suburban^2	3.50	0.0304	0.0023	2.02543 -3.17334	0.92185 1.22747	2.20 -2.59	0.0281 0.0098
Redstart	Suburban + Suburban^2	23.26	0.0000	0.0203	-6.39713 5.72554	1.14515 1.52480	-5.59 3.75	<0.0001 0.0002
Spotted Flycatcher	Suburban + Suburban^2	7.59	0.0005	0.0061	0.68712 -3.00338	1.14136 1.51976	0.60 -1.98	0.5472 0.0483
Treecreeper	Suburban + Suburban^2	5.16	0.0058	0.0039	0.99828 -2.86622	1.08140 1.43992	0.92 -1.99	0.3560 0.0467
Tawny Owl	Suburban + Suburban^2	0.60	0.5469	-0.0004	0.40509 -0.52014	0.37028 0.49304	1.09 -1.05	0.2741 0.2916
Tree Pipit	Suburban + Suburban^2	12.07	0.0000	0.0102	-3.26287 2.69105	0.86912 1.15727	-3.75 2.33	0.0002 0.0201
Willow Tit	Suburban + Suburban^2	0.17	0.8408	-0.0008	0.28694 -0.44136	0.57135 0.76077	0.50 -0.58	0.6156 0.5619
Willow Warbler	Suburban + Suburban^2	22.78	0.0000	0.0199	-14.60139 6.57532	4.09710 5.45545	-3.56 1.21	0.0004 0.2282

Appendix 2d The relationship between the density of farmland indicator species and the cover of suburban land per 1-km square.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Corn Bunting	Suburban +	3.45	0.0318	0.0023	-2.04010	1.25776	-1.62	0.1049
	Suburban^2				1.25221	1.67476	0.75	0.4547
Kestrel	Suburban +	1.17	0.3115	0.0002	0.86825	0.57230	1.52	0.1294
	Suburban^2				-1.12570	0.76204	-1.48	0.1398
Lapwing	Suburban +	5.36	0.0048	0.0040	-1.65953	1.64803	-1.01	0.3141
	Suburban^2				-0.45992	2.19441	-0.21	0.8340
Linnet	Suburban +	5.05	0.0065	0.0038	4.75103	6.76511	0.70	0.4826
	Suburban^2				-16.15025	9.00799	-1.79	0.0731
Grey Partridge	Suburban +	3.61	0.0271	0.0024	-0.73150	1.04789	-0.70	0.4852
	Suburban^2				-0.42687	1.39531	-0.31	0.7597
Reed Bunting	Suburban +	4.98	0.0069	0.0037	-1.74585	1.46426	-1.19	0.2333
	Suburban^2				0.06534	1.94972	0.03	0.9733
Rook	Suburban +	1.42	0.2424	0.0004	0.56459	7.02923	0.08	0.9360
	Suburban^2				-6.49105	9.35968	-0.69	0.4881
Skylark	Suburban +	48.78	<0.0001	0.0426	-21.58494	4.17559	-5.17	<0.0001
	Suburban^2				9.51052	5.55995	1.71	0.0873
Stock Dove	Suburban +	1.56	0.2112	0.0005	0.54955	1.67434	0.33	0.7428
	Suburban^2				-2.10200	2.22945	-0.94	0.3459
Turtle Dove	Suburban +	5.13	0.0060	0.0038	0.95774	0.59460	1.61	0.1074
	Suburban^2				-1.99237	0.79173	-2.52	0.0119
Tree Sparrow	Suburban +	0.51	0.6004	-	0.38965	2.53125	0.15	0.8777
	Suburban^2			0.0005	-1.72042	3.37046	-0.51	0.6098
Whitethroat	Suburban +	11.62	<0.0001	0.0098	12.77044	4.70484	2.71	0.0067
	Suburban^2				-24.99487	6.26467	-3.99	0.0001
Yellowhammer	Suburban +	32.72	<0.0001	0.0287	-6.10754	5.53579	-1.10	0.2700
	Suburban^2				-14.17092	7.37110	-1.92	0.0547
Yellow Wagtail	Suburban +	1.98	0.1390	0.0009	0.71068	1.19093	0.60	0.5507
	Suburban^2				-1.98589	1.58577	-1.25	0.2106

Appendix 3 A series of tables and results from the modelling exercise to identify the strongest model combinations that determine species diversity and species richness respectively, for various bird groups (all indicator species - tables (a) and (b); all species - tables (c) and (d); urban species only – tables e and (f).

(a) Species diversity – all Farmland, Woodland and Urban indicator species (61)

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	1.44	0.2299	0.0002	0.07637	0.06359	1.20	0.2299
Suburban	45.34	<0.0001	0.0198	0.33496	0.04975	6.73	<0.0001
Woodland	160.82	<0.0001	0.0679	0.61075	0.04816	12.68	<0.0001
Farmland	185.45	<0.0001	0.0776	0.52276	0.03839	13.62	<0.0001
Farmland + Woodland	310.08	<0.0001	0.2198	0.77575 0.93702	0.03750 0.04680	20.69 20.02	<0.0001 <0.0001
Farmland + Woodland + Suburban	441.55	<0.0001	0.3759	1.19661 1.20034 1.05890	0.03804 0.04334 0.04518	31.46 27.70 23.44	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	381.68	<0.0001	0.4097	1.36735 1.31603 0.88812 0.68619	0.03999 0.04339 0.04649 0.06105	34.19 30.33 19.10 11.24	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	6.53	0.0107	0.0025	-0.22342	0.08744	-2.55	0.0107
Suburban^2	3.37	0.0667	0.0011	0.12281	0.06694	1.83	0.0667
Woodland^2	42.03	<0.0001	0.0184	0.37983	0.05859	6.48	<0.0001
Farmland^2	96.79	<0.0001	0.0418	0.26808	0.02725	9.84	<0.0001
Farmland^2 + Woodland^2	129.85	<0.0001	0.1051	0.42784 0.77684	0.02928 0.06218	14.61 12.49	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2	169.50	<0.0001	0.1873	0.73411 1.18263 1.12682	0.03464 0.06521 0.07553	21.19 18.14 14.92	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Urban^2	101.33	<0.0001	0.1206	0.53386 0.92217 0.60205	0.03354 0.06582 0.9554	15.92 14.01 6.30	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	144.24	<0.0001	0.2071	0.86182 1.35732 1.15713 0.67848	0.03825 0.06852 0.07472 0.09086	22.53 19.81 15.49 7.47	<0.0001 <0.0001 <0.0001 <0.0001

(b) Log Species Richness – all Farmland, Woodland and Urban indicator species (61)

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	7.45	0.0064	0.0029	0.17140	0.06278	2.73	0.0064
Suburban	83.30	<0.0001	0.0362	0.44507	0.04877	9.13	<0.0001
Woodland	108.70	<0.0001	0.0468	0.50196	0.04815	10.43	<0.0001
Farmland	281.33	<0.0001	0.1133	0.62405	0.03721	16.77	<0.0001
Farmland + Woodland	314.50	<0.0001	0.2212	0.65860 0.55271	0.02801 0.03544	23.52 15.60	<0.0001 <0.0001
Farmland + Woodland + Suburban	377.69	<0.0001	0.3385	0.90939 0.70262 0.69379	0.02875 0.03353 0.03502	31.63 20.96 19.81	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	567.70	<0.0001	0.5082	1.55685 1.31089 1.04454 0.81909	0.03609 0.03915 0.04195 0.05509	43.14 33.48 24.90 14.87	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	2.00	0.1578	0.0005	-0.12228	0.08653	-1.41	0.1578
Suburban^2	16.82	<0.0001	0.0072	0.27060	0.06597	4.10	<0.0001
Woodland^2	18.45	<0.0001	0.0079	0.25008	0.05822	4.30	<0.0001
Farmland^2	156.11	<0.0001	0.0660	0.33229	0.02659	12.49	<0.0001
Farmland^2 + Woodland^2	142.53	<0.0001	0.1136	0.36873 0.43214	0.02204 0.04720	16.73 9.15	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2	154.51	<0.0001	0.1726	0.55626 0.67886 0.72388	0.02600 0.04965 0.05756	21.40 13.67 12.58	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	221.57	<0.0001	0.2868	1.02911 1.43255 1.46231 0.89407	0.03586 0.06424 0.07005 0.08518	28.70 22.30 20.88 10.50	<0.0001 <0.0001 <0.0001 <0.0001

(c) Species Diversity – all species

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	4.66	0.0311	0.0017	-0.12245	0.05675	-2.16	0.0311
Suburban	6.24	0.0126	0.0024	0.11182	0.04476	2.50	0.0126
Woodland	123.56	<0.0001	0.0526	0.48003	0.04318	11.12	<0.0001
Farmland	272.79	<0.0001	0.1096	0.54639	0.03308	16.52	<0.0001
Farmland + Woodland	335.14	<0.0001	0.2323	0.73540 0.76937	0.03232 0.04090	22.75 18.81	<0.0001 <0.0001
Farmland + Woodland + Suburban	338.28	<0.0001	0.3142	0.97908 0.91503 0.67409	0.03402 0.03968 0.04145	28.78 23.06 16.26	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Urban	285.76	<0.0001	0.2790	0.94993 0.90723 0.66924	0.03608 0.04127 0.05584	26.33 21.98 11.99	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	271.76	<0.0001	0.3291	1.06972 0.97505 0.56445 0.40641	0.03602 0.04016 0.04384 0.05760	29.70 24.28 12.87 7.06	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	38.93	<0.0001	0.0169	-0.48408	0.07758	-6.24	<0.0001
Suburban^2	3.95	0.0471	0.0013	-0.11877	0.05978	-1.99	0.0471
Woodland^2	30.86	<0.0001	0.0133	0.29123	0.05242	5.56	<0.0001
Farmland^2	152.59	<0.0001	0.0642	0.29444	0.02384	12.35	<0.0001
Farmland^2 + Urban^2	77.83	<0.0001	0.0651	0.27716 -0.14069	0.02588 0.08217	10.71 -1.71	<0.0001 0.0870
Farmland^2 + Woodland^2	159.86	<0.0001	0.1258	0.42943 0.68144	0.02544 0.05449	16.88 12.51	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2	169.50	<0.0001	0.1873	0.73411 1.18263 1.12682	0.03464 0.06521 0.07553	21.19 18.14 14.92	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Urban^2	101.33	<0.0001	0.1206	0.53386 0.92217 0.60205	0.03664 0.06582 0.09554	15.92 14.01 6.30	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	112.83	<0.0001	0.1685	0.65056 0.97434 0.69814 0.23918	0.03350 0.06105 0.06710 0.08227	19.42 15.96 10.40 2.91	<0.0001 <0.0001 <0.0001 0.0037

(d) Log Species Richness – all species

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	0.00	0.9628	-0.0005	0.002288	0.04887	0.05	0.9628
Suburban	22.66	<0.0001	0.0097	0.18263	0.03836	4.76	<0.0001
Woodland	60.77	<0.0001	0.0264	0.29359	0.03766	7.80	<0.0001
Farmland	347.64	<0.0001	0.1357	0.52281	0.02804	18.65	<0.0001
Farmland + Woodland	314.50	<0.0001	0.2212	0.65860 0.55271	0.02801 0.03544	23.52 15.60	<0.0001 <0.0001
Farmland + Woodland + Suburban	377.69	<0.0001	0.3385	0.90939 0.70262 0.69379	0.02875 0.03353 0.03502	31.63 20.96 19.81	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	317.60	<0.0001	0.3645	1.01204 0.77059 0.56962 0.46025	0.3016 0.03363 0.03671 0.04823	33.56 22.92 15.52 9.54	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	16.15	<0.0001	0.0068	-0.26957	0.06708	-4.02	<0.0001
Suburban^2	0.01	0.9386	-0.0005	0.00397	0.05148	0.08	0.9386
Woodland^2	4.58	0.0.325	0.0016	0.09708	0.04537	2.14	0.0325
Farmland^2	193.98	<0.0001	0.0804	0.28313	0.02033	13.93	<0.0001
Farmland^2 + Woodland^2	142.53	<0.0001	0.1136	0.36873 0.43214	0.02204 0.04720	16.73 9.15	<0.0001 <0.0001
Farmland^2 + Urban^2	97.96	<0.0001	0.0807	0.29490 0.09580	0.02207 0.07009	13.36 1.37	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Urban^2	103.49	<0.0001	0.1222	0.42694 0.51157 0.34569	0.02512 0.04985 0.07269	17.00 10.26 4.76	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	124.21	<0.0001	0.1825	0.62055 0.76648 0.73187 0.36950	0.02858 0.05208 0.05724 0.07018	21.71 14.72 12.79 5.26	<0.0001 <0.0001 <0.0001 <0.0001

(e) Species Diversity – Urban indicator species (27)

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	28.28	<0.0001	0.0123	0.33551	0.06309	5.32	<0.0001
Suburban	164.94	<0.0001	0.0699	0.62194	0.04843	12.84	<0.0001
Woodland	95.25	<0.0001	0.0414	0.47709	0.04888	9.76	<0.0001
Farmland	89.43	<0.0001	0.0389	0.37562	0.03972	9.46	<0.0001
Woodland + Suburban	152.28	<0.0001	0.1217	0.53529 0.66903	0.04697 0.04724	11.40 14.16	<0.0001 <0.0001
Farmland + Woodland + Suburban	427.65	<0.0001	0.3696	1.16332 1.10457 1.34251	0.03970 0.04428 0.04615	29.30 24.94 29.09	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	388.40	<0.0001	0.4152	1.38151 1.25423 1.15895 0.79960	0.04173 0.04417 0.04662 0.06119	33.11 28.40 24.86 13.07	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	1.73	0.1891	0.0003	0.11472	0.08734	1.31	0.1891
Suburban^2	52.86	<0.0001	0.0232	0.48039	0.06607	7.27	<0.0001
Woodland^2	11.57	0.0007	0.0048	0.20034	0.05891	3.40	0.0007
Farmland^2	39.49	<0.0001	0.0173	0.17428	0.02773	6.28	<0.0001
Farmland^2 + Suburban^2	94.81	<0.0001	0.0791	0.35449 0.89015	0.03067 0.07330	11.56 12.14	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2	139.02	<0.0001	0.1594	0.65847 0.97129 1.37821	0.03606 0.06713 0.07773	18.26 17.73 14.47	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	130.45	<0.0001	0.1917	0.83177 1.20884 1.43337 0.86670	0.03989 0.07053 0.07645 0.09235	20.85 17.14 18.75 9.39	<0.0001 <0.0001 <0.0001 <0.0001

(f) Log Species Richness – Urban indicator species (27)

Model	F value	p	Adjusted r^2	Parameter estimate	Standard Error	t value	p
Urban	59.83	<0.0001	0.0262	0.48905	0.06323	7.73	<0.0001
Suburban	240.66	<0.0001	0.0989	0.74631	0.04811	15.51	<0.0001
Woodland	60.06	<0.0001	0.0263	0.38536	0.04973	7.75	<0.0001
Farmland	117.84	<0.0001	0.0508	0.43249	0.03984	10.86	<0.0001
Farmland + Suburban	385.31	<0.0001	0.2604	0.85220 1.20298	0.03900 0.04834	21.85 24.89	<0.0001 <0.0001
Farmland + Woodland + Suburban	546.32	<0.0001	0.4284	1.27632 1.07834 1.52513	0.03816 0.04256 0.04436	33.45 25.34 34.38	<0.0001 <0.0001 <0.0001
Farmland + Suburban + Urban	286.14	<0.0001	0.2815	0.95853 1.05065 0.53360	0.04064 0.05124 0.06612	23.59 20.50 8.07	<0.0001 <0.0001 <0.0001
Farmland + Woodland + Suburban + Urban	539.64	<0.0001	0.4967	1.54578 1.26316 1.29844 0.98748	0.03907 0.04135 0.04365 0.05730	39.57 30.55 29.75 17.23	<0.0001 <0.0001 <0.0001 <0.0001
Urban^2	10.78	0.0010	0.0045	0.28879	0.08797	3.28	0.0010
Suburban^2	96.81	<0.0001	0.0420	0.64981	0.06604	9.84	<0.0001
Woodland^2	2.71	0.0996	0.0008	0.09815	0.05958	1.65	0.0996
Farmland^2	57.47	<0.0001	0.0252	0.21136	0.02788	7.58	<0.0001
Farmland^2 + Suburban^2	163.92	<0.0001	0.1299	0.44766 1.16727	0.03010 0.07192	14.87 16.23	<0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2	197.67	<0.0001	0.2127	0.75930 0.99575 1.66762	0.03522 0.06557 0.07593	21.56 15.19 21.96	<0.0001 <0.0001 <0.0001
Farmland^2 + Suburban^2 + Urban^2	122.77	<0.0001	0.1434	0.50843 1.12784 0.53226	0.03156 0.07166 0.08956	16.11 15.74 5.94	<0.0001 <0.0001 <0.0001
Farmland^2 + Woodland^2 + Suburban^2 + Urban^2	201.48	<0.0001	0.2687	0.98885 1.31040 1.74068 1.14800	0.03830 0.06771 0.07340 0.08866	25.82 19.35 23.72 12.95	<0.0001 <0.0001 <0.0001 <0.0001

Appendix 4a Effects of model predictor variables (%farmland, %woodland, %suburban and %urban habitat cover) on species densities for 27 urban indicator bird species.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Blackbird		282.39	<0.0001	0.3440				
	Farmland +				32.45162	4.14805	7.82	<0.0001
	Woodland +				23.77570	4.63032	5.13	<0.0001
	Suburban + Urban				147.75342	5.01866	29.44	<0.0001
					19.32519	6.56982	2.94	0.0033
Blackcap		65.35	<0.0001	0.1071				
	Farmland +				6.71610	1.10664	6.07	<0.0001
	Woodland +				19.65413	1.23530	15.91	<0.0001
	Suburban + Urban				6.38183	1.33890	4.77	<0.0001
					3.33909	1.75273	1.91	0.0569
Blue Tit		131.68	<0.0001	0.1959				
	Farmland +				36.59824	4.77633	7.66	<0.0001
	Woodland +				81.50613	5.33164	15.29	<0.0001
	Suburban + Urban				90.63772	5.77881	15.68	<0.0001
					41.68722	7.56491	5.51	<0.0001
Carrion Crow		14.95	<0.0001	0.0253				
	Farmland +				7.86409	1.80915	4.35	<0.0001
	Woodland +				5.88661	2.01949	2.91	0.0036
	Suburban + Urban				9.96781	2.18887	4.55	<0.0001
					12.17652	2.86540	4.25	<0.0001
Collared Dove		215.83	<0.0001	0.2859				
	Farmland +				0.03497	1.98853	0.02	0.9860
	Woodland +				-9.67623	2.21972	-4.36	<0.0001
	Suburban + Urban				59.10886	2.40589	24.57	<0.0001
					-3.89664	3.14950	-1.24	0.2161
Chaffinch		110.23	<0.0001	0.1692				
	Farmland +				55.94058	4.29836	13.01	<0.0001
	Woodland +				83.61662	4.79810	17.43	<0.0001
	Suburban + Urban				-0.64545	5.20052	-0.12	0.9012
					2.45310	6.80788	0.36	0.7186
Dunnock		69.37	<0.0001	0.1130				
	Farmland +				15.13356	1.48771	10.17	<0.0001
	Woodland +				4.92679	1.66068	2.97	0.0030
	Suburban + Urban				26.34623	1.79996	14.64	<0.0001
					2.81372	2.35629	1.19	0.2326
Green Woodpecker		22.59	<0.0001	0.0387				
	Farmland +				0.59126	0.18023	3.28	0.0011
	Woodland +				1.83539	0.20118	9.12	<0.0001
	Suburban + Urban				0.76750	0.21805	3.52	0.0004
					0.00029	0.28545	0.00	0.9992
Goldfinch		13.21	<0.0001	0.0223				
	Farmland +				11.69876	1.74330	6.71	<0.0001
	Woodland +				1.51223	1.94598	0.78	0.4372
	Suburban + Urban				5.63985	2.10919	2.67	0.0076
					1.81390	2.76109	0.66	0.5113
Greenfinch		92.25	<0.0001	0.1454				
	Farmland +				21.22188	2.88990	7.34	<0.0001
	Woodland +				0.26093	3.22589	0.08	0.9355
	Suburban + Urban				64.34454	3.49645	18.40	<0.0001
					-13.89546	4.57712	-3.04	0.0024
Great Tit		120.07	<0.0001	0.1816				
	Farmland +				22.30569	2.34043	9.53	<0.0001
	Woodland +				48.03224	2.61254	18.39	<0.0001
	Suburban + Urban				36.73880	2.83165	12.97	<0.0001
					15.79713	3.70685	4.26	<0.0001

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
House Martin		7.19	<0.0001	0.0114				
	Farmland +				6.41009	1.66664	3.85	0.0001
	Woodland +				2.87571	1.86041	1.55	0.1223
	Suburban + Urban				9.24126	2.01645	4.58	<0.0001
					-1.93821	2.63968	-0.73	0.4629
House Sparrow		201.46	<0.0001	0.2720				
	Farmland +				3.01791	9.68419	0.31	0.7554
	Woodland +				-65.87407	10.81012	-6.09	<0.0001
	Suburban + Urban				239.87278	11.71676	20.47	<0.0001
					58.21376	15.33815	3.80	0.0002
Jay		25.79	<0.0001	0.0442				
	Farmland +				0.40430	0.39330	1.03	0.3041
	Woodland +				4.03474	0.43903	9.19	<0.0001
	Suburban + Urban				1.40737	0.47585	2.96	0.0031
					0.86784	0.62292	1.39	0.1637
Jackdaw		15.78	<0.0001	0.0268				
	Farmland +				14.07218	2.35544	5.97	<0.0001
	Woodland +				11.60264	2.62929	4.41	<0.0001
	Suburban + Urban				16.54824	2.84981	5.81	<0.0001
					-4.95294	3.73062	-1.33	0.1844
Long-tailed Tit		17.39	<0.0001	0.0297				
	Farmland +				6.18204	1.42152	4.35	<0.0001
	Woodland +				12.80604	1.58679	8.07	<0.0001
	Suburban + Urban				4.82431	1.71988	2.81	0.0051
					4.84424	2.25145	2.15	0.0315
Mistle Thrush		21.57	<0.0001	0.0369				
	Farmland +				1.20774	0.49350	2.45	0.0145
	Woodland +				4.03456	0.55088	7.32	<0.0001
	Suburban + Urban				3.09861	0.59708	5.19	<0.0001
					1.64709	0.78163	2.11	0.0352
Mallard		12.51	<0.0001	0.0210				
	Farmland +				3.87928	2.13518	1.82	0.0694
	Woodland +				2.04530	2.38343	0.86	0.3909
	Suburban + Urban				3.95653	2.58333	1.53	0.1258
					18.95994	3.38178	5.61	<0.0001
Magpie		149.48	<0.0001	0.2168				
	Farmland +				2.88414	1.18727	2.43	0.0152
	Woodland +				5.16236	1.32531	3.90	0.0001
	Suburban + Urban				26.08069	1.43646	18.16	<0.0001
					10.64772	1.88044	5.66	<0.0001
Pied Wagtail		10.60	<0.0001	0.0176				
	Farmland +				4.25216	0.72960	5.83	<0.0001
	Woodland +				-0.03174	0.81442	-0.04	0.9689
	Suburban + Urban				0.33308	0.88273	0.38	0.7060
					2.74164	1.15556	2.37	0.0178
Robin		161.66	<0.0001	0.2304				
	Farmland +				26.43080	3.17214	8.33	<0.0001
	Woodland +				84.82413	3.54094	23.96	<0.0001
	Suburban + Urban				41.14443	3.83792	10.72	<0.0001
					12.21496	5.02414	2.43	0.0151
Starling		196.84	<0.0001	0.2674				
	Farmland +				-3.31830	6.65878	-0.50	0.6183
	Woodland +				-38.37144	7.43296	-5.16	<0.0001
	Suburban + Urban				159.68249	8.05636	19.82	<0.0001
					45.10735	10.54640	4.28	<0.0001
Sparrowhawk		0.63	0.6392	-0.0007				
	Farmland +				0.10943	0.11255	0.97	0.3310
	Woodland +				0.17891	0.12563	1.42	0.1546
	Suburban + Urban				-0.00665	0.13617	-0.05	0.9611
					0.04164	0.17825	0.23	0.8153

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Swift		7.24	<0.0001	0.0115				
	Farmland +				-0.01262	1.37041	-0.01	0.9927
	Woodland +				-2.36539	1.52974	-1.55	0.1222
	Suburban + Urban				5.24428	1.65804	3.16	0.0016
					3.15956	2.17050	1.46	0.1456
Song Thrush		71.07	<0.0001	0.1155				
	Farmland +				4.18669	0.87987	4.76	<0.0001
	Woodland +				14.91856	0.98217	15.19	<0.0001
	Suburban + Urban				9.09702	1.06454	8.55	<0.0001
					-1.31630	1.39357	-0.94	0.3450
Woodpigeon		20.17	<0.0001	0.0345				
	Farmland +				52.35928	7.62279	6.87	<0.0001
	Woodland +				40.51616	8.50904	4.76	<0.0001
	Suburban + Urban				56.09983	9.22269	6.08	<0.0001
					38.19379	12.07322	3.16	0.0016
Wren		96.23	<0.0001	0.1507				
	Farmland +				17.82490	3.44002	5.18	<0.0001
	Woodland +				71.46491	3.83997	18.61	<0.0001
	Suburban + Urban				30.21535	4.16203	7.26	<0.0001
					5.70036	5.44842	1.05	0.2956

Appendix 4b Effects of model predictor variables (%farmland, %woodland, %suburban and %urban habitat cover) on species densities for 33 woodland indicator bird species.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Bullfinch	Farmland + Woodland + Suburban + Urban	9.83	<0.0001	0.0162	1.36156 3.97430 1.21444 0.63230	0.57546 0.64237 0.69625 0.91144	2.37 6.19 1.74 0.69	0.0181 <0.0001 0.0813 0.4879
Chiffchaff	Farmland + Woodland + Suburban + Urban	54.89	<0.0001	0.0913	2.61522 10.16452 1.94230 0.22997	0.62903 0.70217 0.76106 0.99628	4.16 14.48 2.55 0.23	<0.0001 <0.0001 0.0108 0.8175
Coal Tit	Farmland + Woodland + Suburban + Urban	144.37	<0.0001	0.2109	-5.70266 17.33533 -4.01241 -2.39113	0.86321 0.96357 1.04439 1.36718	-6.61 17.99 -3.84 -1.75	<0.0001 <0.0001 0.0001 0.0804
Goldcrest	Farmland + Woodland + Suburban + Urban	0.97	0.4244	-0.0001	-0.19652 -0.44782 -0.43089 0.02646	0.25731 0.28723 0.31132 0.40754	-0.76 -1.56 -1.38 0.06	0.4451 0.1191 0.1665 0.9482
Great Spotted Woodpecker	Farmland + Woodland + Suburban + Urban	36.33	<0.0001	0.0618	0.69645 3.51764 0.28079 0.55169	0.26761 0.29872 0.32377 0.42384	2.60 11.78 0.87 1.30	0.0093 <0.0001 0.3859 0.1932
Garden Warbler	Farmland + Woodland + Suburban + Urban	23.72	<0.0001	0.0406	0.87375 3.85154 -0.58415 0.24195	0.38361 0.42821 0.46412 0.60758	2.28 8.99 -1.26 0.40	0.0228 <0.0001 0.2083 0.6905
Hawfinch	Farmland + Woodland + Suburban + Urban	.	.	.	0.0000 0.0000 0.0000 0.0000	0.0000 0.0000 0.0000 0.0000		
Lesser Redpoll	Farmland + Woodland + Suburban + Urban	3.92	0.0036	0.0054	-1.02471 0.64561 -0.67741 -0.98653	0.41775 0.46632 0.50543 0.66165	-2.45 1.38 -1.34 -1.49	0.0142 0.1664 0.1803 0.1361
Lesser Spotted Woodpecker	Farmland + Woodland + Suburban + Urban	1.54	0.1887	0.0010	0.00606 0.06218 0.04935 -0.06483	0.03197 0.03569 0.03868 0.05063	0.19 1.74 1.28 -1.28	0.8497 0.0816 0.2022 0.2005
Lesser Whitethroat	Farmland + Woodland + Suburban + Urban	5.89	0.0001	0.0090	0.89930 -0.13101 0.00516 0.05143	0.23870 0.26645 0.28880 0.37806	3.77 -0.49 0.02 0.14	0.0002 0.6230 0.9857 0.8918
Marsh Tit	Farmland + Woodland + Suburban + Urban	16.57	<0.0001	0.0282	0.45817 2.14384 -0.70302 0.39649	0.26650 0.29748 0.32243 0.42209	1.72 7.21 -2.18 0.94	0.0857 <0.0001 0.0293 0.3477

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Nightingale	Farmland + Woodland + Suburban + Urban	2.03	0.0878	0.0019	0.00748 0.15248 0.07339 -0.02265	0.05517 0.06158 0.06675 0.08738	0.14 2.48 1.10 -0.26	0.8921 0.0134 0.2717 0.7955
Nuthatch	Farmland + Woodland + Suburban + Urban	28.24	<0.0001	0.0483	0.65597 3.64237 0.66742 -0.59272	0.32713 0.36517 0.39579 0.51812	2.01 9.97 1.69 -1.14	0.0451 <0.0001 0.0919 0.2528
Redstart	Farmland + Woodland + Suburban + Urban	8.79	<0.0001	0.0143	-0.15096 0.46288 -2.16037 -0.70578	0.41735 0.46588 0.50495 0.66102	-0.36 0.99 -4.28 -1.07	0.7176 0.3206 <0.0001 0.2858
Spotted Flycatcher	Farmland + Woodland + Suburban + Urban	11.59	<0.0001	0.0194	1.06630 2.30258 -0.26879 -1.05710	0.41193 0.45982 0.49838 0.65242	2.59 5.01 -0.54 -1.62	0.0097 <0.0001 0.5897 0.1053
Treecreeper	Farmland + Woodland + Suburban + Urban	26.05	<0.0001	0.0446	0.49608 4.03062 -0.43818 0.02464	0.38480 0.42954 0.46556 0.60945	1.29 9.38 -0.94 0.04	0.1975 <0.0001 0.3467 0.9678
Tawny Owl	Farmland + Woodland + Suburban + Urban	2.11	0.0774	0.0021	0.12845 0.39674 0.18436 -0.11572	0.13437 0.15000 0.16258 0.21283	0.96 2.64 1.13 -0.54	0.3392 0.0082 0.2569 0.5867
Tree Pipit	Farmland + Woodland + Suburban + Urban	24.95	<0.0001	0.0427	-1.88369 1.19640 -1.73598 -1.28793	0.31056 0.34666 0.37574 0.49187	-6.07 3.45 -4.62 -2.62	<0.0001 0.0006 <0.0001 0.0089
Willow Tit	Farmland + Woodland + Suburban + Urban	1.34	0.2515	0.0006	0.07964 0.50912 0.07473 -0.03756	0.20745 0.23157 0.25099 0.32856	0.38 2.20 0.30 -0.11	0.7011 0.0280 0.7659 0.9090
Willow Warbler	Farmland + Woodland + Suburban + Urban	64.22	<0.0001	0.1054	-6.43832 16.67640 -9.78512 -5.46754	1.42222 1.58757 1.72072 2.25256	-4.53 10.50 -5.69 -2.43	<0.0001 <0.0001 <0.0001 0.0153

Appendix 4c Effects of model predictor variables (%farmland, %woodland, %suburban and %urban habitat cover) on species densities for 19 farmland indicator bird species.

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Corn Bunting	Farmland + Woodland + Suburban + Urban	10.52	<0.0001	0.0174	0.93019 -2.15724 -0.95331 0.21950	0.45351 0.50624 0.54870 0.71829	2.05 -4.26 -1.74 0.31	0.0404 <0.0001 0.0825 0.7600
Kestrel	Farmland + Woodland + Suburban + Urban	1.85	0.1168	0.0016	0.53388 0.12038 0.18283 0.45656	0.20779 0.23195 0.25141 0.32911	2.57 0.52 0.73 1.39	0.0103 0.6038 0.4672 0.1655
Lapwing	Farmland + Woodland + Suburban + Urban	8.37	<0.0001	0.0135	0.57833 -2.55832 -1.83687 -0.14162	0.59593 0.66522 0.72101 0.94386	0.97 -3.85 -2.55 -0.15	0.3319 0.0001 0.0109 0.8807
Linnet	Farmland + Woodland + Suburban + Urban	17.11	<0.0001	0.0292	12.46791 -8.83886 -2.67647 4.47907	2.42650 2.70862 2.93579 3.84318	5.14 -3.26 -0.91 1.17	<0.0001 0.0011 0.3620 0.2440
Grey Partridge	Farmland + Woodland + Suburban + Urban	10.91	<0.0001	0.0181	1.70771 -0.72050 -0.70400 1.22625	0.37773 0.42165 0.45701 0.59827	4.52 -1.71 -1.54 2.05	<0.0001 0.0876 0.1236 0.0405
Reed Bunting	Farmland + Woodland + Suburban + Urban	7.10	<0.0001	0.0112	0.51706 -1.99758 -1.75532 0.39916	0.53001 0.59163 0.64125 0.83944	0.98 -3.38 -2.74 0.48	0.3294 0.0007 0.0062 0.6345
Rook	Farmland + Woodland + Suburban + Urban	6.23	0.0001	0.0096	10.38244 -0.16324 1.34158 -0.14711	2.54215 2.83772 3.07571 4.02635	4.08 -0.06 0.44 -0.04	<0.0001 0.9541 0.6627 0.9709
Skylark	Farmland + Woodland + Suburban + Urban	59.95	<0.0001	0.0990	5.87704 -13.70617 -12.16424 -2.28155	1.47182 1.64293 1.78073 2.33111	3.99 -8.34 -6.83 -0.98	0.0001 <0.0001 <0.0001 0.3278
Stock Dove	Farmland + Woodland + Suburban + Urban	5.44	0.0002	0.0082	2.55814 1.07090 -0.55978 2.60320	0.60601 0.67647 0.73321 0.95982	4.22 1.58 -0.76 2.71	<0.0001 0.1136 0.4453 0.0067
Turtle Dove	Farmland + Woodland + Suburban + Urban	5.09	0.0004	0.0076	0.81046 0.16570 -0.03598 0.06773	0.21564 0.24071 0.26090 0.34153	3.76 0.69 -0.14 0.20	0.0002 0.4913 0.8903 0.8428
Tree Sparrow	Farmland + Woodland + Suburban + Urban	4.28	0.0019	0.0061	2.12362 -2.11295 -0.19098 0.72831	0.91670 1.02328 1.10910 1.45190	2.32 -2.06 -0.17 0.50	0.0206 0.0391 0.8633 0.6160

Species	Model	F value	p	Adj. r^2	Parameter estimate	Standard Error	T value	p
Whitethroat	Farmland + Woodland + Suburban + Urban	31.44	<0.0001	0.0537	15.12848 -3.25063 -0.17944 7.38369	1.67115 1.86544 2.02190 2.64682	9.05 -1.74 -0.09 2.79	<0.0001 0.0816 0.9293 0.0053
Yellowhammer	Farmland + Woodland + Suburban + Urban	64.01	<0.0001	0.1051	22.99140 -1.46064 -5.64943 3.01842	1.93066 2.15513 2.33588 3.05785	11.91 -0.68 -2.42 0.99	<0.0001 0.4980 0.0157 0.3237
Yellow Wagtail	Farmland + Woodland + Suburban + Urban	7.58	<0.0001	0.0121	1.33916 -1.24989 -0.34362 0.62589	0.43028 0.48031 0.52059 0.68149	3.11 -2.60 -0.66 0.92	0.0019 0.0093 0.5093 0.3585