Diversity and Distributions, (Diversity Distrib.) (2009) **15**, 328–337

BIODIVERSITY RESEARCH

How many birds are there in a city of half a million people?

Richard A. Fuller[1,2]*, Jamie Tratalos[1]† and Kevin J. Gaston[1]

[1]*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK,* [2]*The Ecology Centre, The University of Queensland, Queensland 4072, Australia*

*Correspondence: Richard A. Fuller, Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.
E-mail: r.a.fuller@dunelm.org.uk
†Present address: British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

ABSTRACT

Aim Urban environments are often characterized as supporting a few abundant, generalist species best adapted to living alongside humans, and as such, cities are seen as agents of biotic homogenization. However, there are surprisingly few descriptions of biological populations found in cities. Here, we provide the first complete city-wide population estimates of birds for any UK city, and examine the conservation status of the assemblage in comparison with the country's avifauna at large.

Location Sheffield city, central UK

Methods We surveyed birds in every 500 m × 500 m square across the 160 km^2 of the city. Using a Distance sampling protocol, we estimated bird population sizes for the city and compared these with the size of the human population. We also compared the conservation status of the city's avian population with that of birds across the UK as a whole.

Results Aggregation of population estimates for the 77 species observed during the surveys produced a total estimate of 602,995 (95% confidence interval (CI): 404,565–942,573) breeding birds, equating to 1.18 birds per person. The size of the non-breeding population was similar at 578,603 (464,396–728,574) individuals, or 1.13 birds per person. Surveys revealed only three non-native species, but relatively few species of national conservation concern. However, some species of conservation concern achieved very high population densities within the city, and the overall density of birds was more than six times that of the nation at large.

Main conclusions If declines in some species are to be arrested or reversed, conservation effort will need to focus much more strongly on understanding and managing urban populations, because these might buffer some species against wholesale regional population depletion, particularly where intensive agriculture in the surrounding hinterland has led to declines in bird populations at large. Such a focus will require a significant increase in the priority and resources devoted to conservation activities in urban areas.

Keywords
Bird populations, conservation, urban ecology.

INTRODUCTION

The human enterprise has transformed global ecology, precipitating an extinction crisis (Lawton & May, 1995). Many anthropogenic impacts arise through changes in land cover (Meyer & Turner, 1992), and humans have now fundamentally altered between a third and a half of the Earth's terrestrial surface (Vitousek *et al*., 1997). Concomitantly, the human population has become increasingly concentrated into urban centres, such that about half of the world's people currently live in cities (United Nations, 2004). Although urbanization represents one of the most spectacular ways in which humans have altered landscapes, broad-scale quantitative studies on urban assemblages are scarce, and the conservation tools are often lacking to identify, understand and manage ecological change in such areas (Collins *et al*., 2000; Marzluff *et al*., 2001; Miller & Hobbs, 2002; Adams *et al*., 2006).

Ecological change wrought by urbanization is complex, and varies greatly both taxonomically and geographically (McKinney, 2008). For example, there is generally a positive

DOI: 10.1111/j.1472-4642.2008.00537.x

correlation between human population density and species richness at broad scales (Kerr & Currie, 1995; Gaston, 2005; Luck, 2007), but local gradients of species richness with urbanization range from negative (Zanette *et al.*, 2005; Donnelly & Marzluff, 2006; Sandström *et al.*, 2006), through peaks at intermediate levels of urbanization (Kowarik, 1990; Blair, 2001; Clergeau *et al.*, 2001; Germaine & Wakeling, 2001), to positive (Hardy & Dennis, 1999; Kühn *et al.*, 2004; Turner *et al.*, 2005; Wania *et al.*, 2006), depending on the system under study. Perhaps even more striking are the numerous documented cases of increases in species' population densities in response to urbanization, at all but the most extreme levels of urban development (Niemelä *et al.*, 2002; Green & Baker, 2003; Vähä-Piikkiö *et al.*, 2004; Zanette *et al.*, 2005; Tratalos *et al.*, 2007).

Despite these examples, studies that quantify entire urban assemblages are largely wanting, and little is known about how urban assemblages compare with the regional species pool from which they are drawn. This is important for at least three reasons.

First, many common and widespread species are in decline across much of Europe and North America, and such declines are perhaps underemphasized in modern conservation biology (Gaston & Fuller, 2007, 2008; Voříšek *et al.*, 2007). Urban habitats in Europe support significant populations of several native common and widespread bird species, some of which are declining rapidly and hence listed as nationally threatened (Gregory & Baillie, 1998; Mason, 2000; Bland *et al.*, 2004; Cannon *et al.*, 2005; Newson *et al.*, 2005; Robinson *et al.*, 2005; Brichetti *et al.*, 2008). Despite covering only about 7% of the land surface area of the UK, urban and suburban habitats support about 40% of the British population of common starlings *Sturnus vulgaris*, 12% of song thrushes *Turdus philomelos* (Gregory & Baillie, 1998) and 49% of house sparrows *Passer domesticus* (Robinson *et al.*, 2005). Because of national declines in these native species of over 50% in the last 25 years, all three were red-listed in the most recent review of the conservation status of UK birds (Gregory *et al.*, 2002). The Europe-wide conservation status of common starling and house sparrow has been listed as unfavourable (BirdLife International, 2004), and if such populations of declining species form a significant part of urban avifaunas, we may need to reappraise the fundamental conservation importance of such habitats.

Second, a relatively limited set of synanthropic species appears particularly well adapted to urban environments, and gross similarities in the design and function of cities across the world in combination with human-assisted dispersal might promote global and regional biotic homogenization (Johnston, 2001; Kühn & Klotz, 2006; McKinney, 2006). This has led to concerns that urban faunas may appear rich, but simply reflect local subsets of a homogeneous group of largely non-native species particularly well adapted to urban living at the expense of populations of native and/or rare species (McKinney & Lockwood, 1999). However, without comprehensive data on urban assemblages, it is difficult to assess the conservation significance of urban faunas.

Third, many of the interactions between people and nature occur in urban environments (Miller & Hobbs, 2002; Turner *et al.*, 2004; Miller, 2005), and the psychological benefits derived by visits to urban green spaces increase with their biodiversity (Fuller *et al.*, 2007). Moreover, the activities of people in urban environments directly influence urban assemblages for example through patterns of public and private green space management (Sandström *et al.*, 2006), disturbance (Matlack, 1993), cultivation of large numbers of non-native plants (Marco *et al.*, 2008) and the provision of feeding and nesting resources for wildlife (Daniels & Kirkpatrick, 2006; Gaston *et al.*, 2007; Fuller *et al.*, 2008). An understanding of the dimensions of urban assemblages gives an insight into the opportunities for such interactions to take place.

Here, we present population estimates for birds across a UK city of half a million people. We then examine the conservation significance of the assemblage by comparing the richness and abundance of species of national conservation concern with those of the national avifauna.

METHODS

With a human population of *c.* 513,000, Sheffield is the fifth largest municipality in the UK, and the ninth largest urban area (Office for National Statistics, 2001; Beer, 2005). For the purposes of this study, the urban area of Sheffield (53°22′N, 1°20′W) was defined as the set of 1 km squares within the administrative city boundary with more than 25% of their area comprising urban built form as assessed by eye using 1 : 25,000 Ordnance Survey maps (see Gaston *et al.*, 2005). This resulted in a set of squares totalling 160 km^2. Each square was split into four 500 m × 500 m cells, and a sampling point was randomly located within each cell, yielding a final set of 640 sampling locations distributed across the city. While this approach will inevitably include some cells in predominantly non-urban local environments, the aim of our study was to generate citywide bird population estimates rather than restrict our sample to cells with intense local urbanization.

Each sampling point was visited twice, once in winter (4 November 2004 to 28 February 2005) and once in summer (24 May to 1 July 2005). Sampling points were located in the field using a hand-held GPS receiver. A single observer (R. A. Fuller) conducted all survey work. Five-minute point transects (Buckland *et al.*, 2001) were conducted between 0535 h and 1313 h in summer and between 0830 h and 1300 h in winter. Observations were begun immediately on arrival at the point location, and any birds disturbed by the observer prior to arrival at the point were recorded, together with an estimate of their distance from the point location. As might be expected in an urban setting, many of the birds seemed well habituated to human presence, and movement in response to the observer was minimal. Solitary birds were recorded individually, but those clearly associated with other individuals were recorded as clusters. For each detected solitary individual or cluster of birds, species identity, group size, radial distance from the observer and activity (perched or in flight) were recorded. Distances were estimated in the field in 14 bands (0–4.9 m, 5–9.9 m, 10–14.9 m, 15–19.9 m, 20–24.9 m, 25–29.9 m, 30–39.9 m, 40–49.9 m, 50–59.9 m, 60–69.9 m, 70–79.9 m, 80–89.9 m, 90–99.9 m, 100 m +). Distances were estimated with reference to features of the surrounding urban environment and after intensive practice in estimating distances in an urban setting involving measuring exact distances to birds after their estimation. Distances close to the observer (and hence less prone to error) are disproportionately important in calculating the detection function.

Bird density estimates were calculated using Distance software (version 5; Thomas *et al*., 2005). Where sample sizes permitted, analyses were conducted separately by season (summer, winter) and by species. First, four plausible candidate key functions (uniform with cosine expansion, uniform with simple polynomial expansion, half-normal with hermite polynomial expansion, and hazard-rate with cosine expansion) were used to model how detection declined with distance, and the model with the lowest value for Akaike's Information Criterion (AIC) was chosen. The distance data were truncated beyond the point where the probability of detection in this initial model fell below 0.1 (usually 40–50 m). The analyses were then re-run using the same four candidate models, and options for grouping the distance bands were explored until a good fit between model and data was obtained, as judged by comparing the modelled detection function against the observed distance data, the goodness of fit statistics and AIC values for alternative grouping and detection function options.

Detectability of birds showed very little variation with the degree of urbanization, and resulting density estimates were not biased by urban form (there was no correlation between detection distance and urban form as measured by the proportion of impervious surface in the 100 m radius around a survey point; for details of these analyses see Fuller *et al*., 2008). Detection functions were therefore estimated globally for each species/season combination. In cases where there were too few (typically < 30) observations of a species to allow adequate independent modelling of the detection function, the probability of detection of a more frequently observed 'surrogate' species of similar size with apparently comparable detection characteristics was used to correct the distance data using a multiplier (Buckland *et al*., 2001; see Appendix S1 in Supporting Information for sample sizes and details of surrogate species assignment). The best fitting model for the detection function of each species/season combination was used to generate density and population estimates, together with their associated confidence intervals.

National population estimates for breeding birds across the UK were taken from Baker *et al.* (2006). A consortium of national conservation agencies recently reviewed the conservation status of all bird species regularly occurring in the UK (Gregory *et al*., 2002). This assessment used a three-level system to classify species as green, amber or red according to seven criteria including international threat status, and various aspects of historical and recent declines in population or geographical range size within the UK. Species that were red or amber listed were considered to be of national conservation concern for the purpose of our analyses.

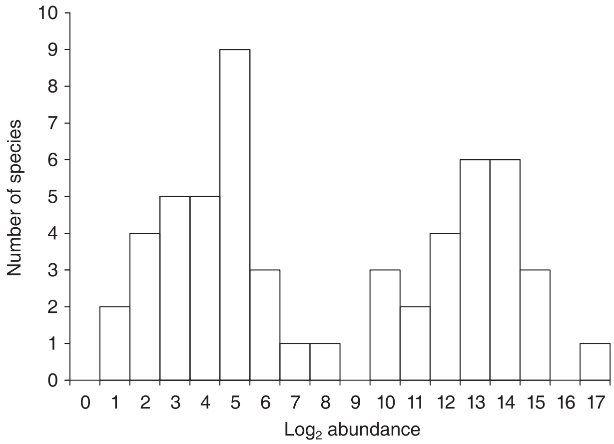

Figure 1 Species-abundance distribution for breeding birds in Sheffield. Following Williamson & Gaston (2005), each bin is centred over the powers of two, and the boundaries are at $2^{n-1/2}$ individuals.

RESULTS

A total of 77 species was observed during the survey work (61 in summer, 64 in winter). Only three non-native species were observed (ring-necked pheasant *Phasianus colchicus*, feral pigeon *Columba livia* and little owl *Athene noctua*; Table 1). Species detected only in flight or only beyond the truncation distance of the candidate surrogate species were excluded from analyses, leaving 55 species in summer and 53 in winter. Resulting Sheffield-wide population estimates for these species are presented in Table 1. The species-abundance distribution was strongly bimodal, characterized by many rare species, yet with an unusually large group of highly abundant species dominating the right-hand side of the plot (Fig. 1). The overall number of individuals estimated to be present in Sheffield was 602,995 (95% confidence interval (CI): 404,565–942,573) during the breeding season and 578,603 (464,396–728,574) during the winter. Using a human population estimate of 513,000 for the city (Office for National Statistics, 2001), these numbers equate to 1.18 birds per person in the breeding season and 1.13 in the winter. Populations of the three non-native species comprised only 2% of the total number of breeding birds in the city (Table 1). To assess the robustness of the values arising from the Distance sampling analysis, we constructed a 'retrospective' point-count data set with a fixed radius of 20 m, a distance at which we can be confident that a high proportion of birds was detected. This resulted in total population estimates for the city's birds of 517,453 birds in summer (compared with 602,995 derived from Distance sampling) and 423,750 birds in winter (compared with 578,603 derived from Distance sampling). The smaller population estimates are consistent with some individuals within 20 m eluding detection, but could also result from overestimation of the true values by the Distance sampling method. However, species population estimates derived in the two ways are extremely highly correlated (summer, $r_s = 0.955$; winter, $r_s = 0.910$), and thus our conclusions would be qualitatively identical whichever method is used.

Table 1 Population estimates for breeding and wintering birds in Sheffield, UK. Values in parentheses are 95% confidence intervals for the Sheffield data. Species codes are shown in parentheses after the English name, superscript symbols indicate current national conservation status (Gregory *et al.*, 2002): *Green listed, †Amber listed, ‡Red listed. Non-native species are indicated by an asterisk, although the historical distribution of feral pigeon is uncertain (Cramp, 1985). An additional nine species were observed for which density estimates could not be calculated because detections were beyond the truncation distance employed in the analysis, or were exclusively of flying birds (great cormorant *Phalacrocorax carbo*, greylag goose *Anser anser*, northern lapwing *Vanellus vanellus*, European golden plover *Pluvialis apricaria*, glaucous gull *Larus hyperboreus*, lesser black-backed gull *Larus fuscus*, great black-backed gull *Larus marinus*, brambling *Fringilla montifringilla* and lesser redpoll *Carduelis cabaret*).

Species	Sheffield population estimates	
	Summer	Winter
Grey heron (H)* *Ardea cinerea*	0	12 (3–58)
Mallard (MA)* *Anas platyrhynchos*	81 (16–416)	124 (38–402)
Eurasian sparrowhawk (SH)* *Accipiter nisus*	59 (24–140)	88 (44–176)
Common kestrel (K)† *Falco tinnunculus*	29 (13–63)	12 (4–34)
Grey partridge (P)‡ *Perdix perdix*	0	12 (3–58)
Common quail (Q)‡ *Coturnix coturnix*	4 (0–18)	0
Ring-necked pheasant (PH)* *Phasianus colchicus**	17 (5–58)	17 (6–49)
Common moorhen (MH)* *Gallinula chloropus*	5 (2–24)	17 (5–70)
Common coot (CO)* *Fulica atra*	5 (2–24)	6 (2–29)
Black-headed gull (BH)† *Larus ridibundus*	0	522 (252–1080)
Common gull (CM)† *L. canus*	0	65 (25–169)
Herring gull (HG)† *L. argentatus*	0	26 (5–133)
Feral pigeon (FP)* *Columba livia**	12,130 (7757–18,970)	17,847 (10,840–29,383)
Stock pigeon (SD)† *C. oenas*	8 (2–26)	6 (2–29)
Common wood pigeon (WP)* *C. palumbus*	13,643 (10,004–18,607)	12,218 (9124–16,359)
Eurasian collared dove (CD)* *Streptopelia decaocto*	1,3271 (11,312–15,568)	9044 (6391–12,797)
Common cuckoo (CK)† *Cuculus canorus*	8 (2–39)	0
Little owl (LO)* *Athene noctua**	0	4 (1–18)
Common swift (SI)* *Apus apus*	26,447 (21,004–33,301)	0
Common kingfisher (KF)† *Alcedo atthis*	2 (0–10)	0
Green woodpecker (G)† *Picus viridis*	10 (4–26)	8 (2–40)
Great spotted woodpecker (GS)* *Dendrocopos major*	31 (16–56)	43 (22–84)
Skylark (S)‡ *Alauda arvensis*	46 (23–95)	50 (17–154)
Barn swallow (SL)† *Hirundo rustica*	5161 (2999–8884)	0
House martin (HM)† *Delichon urbicum*	12,353 (8610–17,722)	0
Meadow pipit (MP)† *Anthus pratensis*	6 (2–16)	32 (12–86)
Grey wagtail (GL)† *Motacilla cinerea*	2 (0–10)	32 (14–74)
Pied wagtail (PW)* *M. alba*	41 (23–72)	112 (65–194)
Bohemian waxwing (WX)* *Bombycilla garrulus*	0	872 (308–2476)
Winter wren (WR)* *Troglodytes troglodytes*	15,997 (14,434–17,730)	18,162 (13,467–24,495)
Hedge accentor (D)† *Prunella modularis*	20,968 (16,845–26,101)	17,722 (13,306–23,604)
European robin (R)* *Erithacus rubecula*	23,999 (19,676–29,271)	27,068 (23,391–31,320)
Common blackbird (B)* *Turdus merula*	35,712 (31,597–40,365)	50,844 (41,951–61,624)
Fieldfare (FF)† *T. pilaris*	0	40 (11–140)
Song thrush (ST)‡ *T. philomelos*	1540 (1116–2127)	426 (297–613)
Redwing (RE)† *T. iliacus*	0	984 (523–1851)
Mistle thrush (M)† *T. viscivorus*	96 (56–165)	222 (112–443)
Lesser whitethroat (LW)* *Sylvia curruca*	19 (4–96)	0 (0–0)
Common whitethroat (WH)* *S. communis*	2199 (1452–3330)	0
Garden warbler (GW)* *S. borin*	23 (12–47)	0
Blackcap (BC)* *S. atricapilla*	4782 (3360–6805)	12 (3–62)
Common chiffchaff (CC)* *Phylloscopus collybita*	1653 (933–2928)	0
Willow warbler (WW)† *P. trochilus*	1707 (976–2981)	0
Goldcrest (GC)† *Regulus regulus*	70 (32–152)	211 (110–405)
Spotted flycatcher (SF)‡ *Muscicapa striata*	10 (2–50)	0
Long-tailed tit (LT)* *Aegithalos caudatus*	508 (268–962)	950 (606–1490)
Willow tit (WT)‡ *Poecile montanus*	0	10 (2–50)

Table 1 *Continued*

Species	Sheffield population estimates: Summer	Winter
Coal tit (CT)* *Periparus ater*	49 (20–124)	177 (108–292)
Blue tit (BT)* *Cyanistes caeruleus*	59,653 (47,112–75,532)	102,440 (85,941–1221,09)
Great tit (GT)* *Parus major*	17,164 (10,204–28,869)	29,818 (22,480–39,552)
European nuthatch (NH)* *Sitta europaea*	48 (26–92)	174 (91–334)
Eurasian treecreeper (TC)* *Certhia familiaris*	0	9 (2–44)
Eurasian jay (J)* *Garrulus glandarius*	51 (26–101)	141 (81–247)
Black-billed magpie (MG)* *Pica pica*	24,938 (20,260–30,698)	19,522 (16,728–22,783)
Eurasian jackdaw (JD)* *Corvus monedula*	4584 (2986–7037)	2498 (1444–4321)
Rook (RO)* *C. frugilegus*	264 (164–428)	493 (267–911)
Carrion crow (C)* *C. corone*	2353 (1877–2948)	5214 (3911–6951)
Common starling (SG)‡ *Sturnus vulgaris*	54,788 (39,984–75,071)	61,818 (44,868–85,173)
House sparrow (HS)‡ *Passer domesticus*	207,792 (109,268–395,120)	177,456 (151,940–207,264)
Eurasian tree sparrow (TS)‡ *P. montanus*	0	33 (7–167)
Chaffinch (CH)* *Fringilla coelebs*	6283 (4908–8045)	8389 (6252–11,255)
European greenfinch (GR)* *Carduelis chloris*	22,834 (9440–55,229)	12,274 (9140–16,484)
European goldfinch (GO)* *C. carduelis*	9427 (5644–15,749)	290 (152–552)
Eurasian siskin (SK)* *C. spinus*	0	7 (2–33)
Common linnet (LI)‡ *C. cannabina*	40 (23–66)	0
Common bullfinch (BF)‡ *Pyrrhula pyrrhula*	38 (23–66)	30 (18–53)
Yellowhammer (Y)‡ *Emberiza citrinella*	33 (13–90)	0
Reed bunting (RB)‡ *E. schoeniclus*	14 (4–53)	0
Total	602,995 (404,565–942,573)	578,603 (464,396–728,574)

The 61 species observed during the summer surveys comprise about 76% of the total of 84 species known to breed regularly within the boundaries of urban Sheffield (Hornbuckle & Herringshaw, 1985). The five commonest breeding species in Sheffield were house sparrow, blue tit, common starling, common blackbird and common swift, which between them comprised 64% of all individual birds (see Table 1 for scientific names). Twenty-seven species occurred at higher breeding densities in Sheffield than in the country as a whole, 10 by more than an order of magnitude (feral pigeon, Eurasian collared dove, common swift, house martin, blue tit, black-billed magpie, common starling, house sparrow, European greenfinch, European goldfinch; Fig. 2). The mean density of bird species breeding in Sheffield was much higher than the mean density across the country as a whole ($t = 6.47$, d.f. = 272, $P < 0.001$). The total bird density in Sheffield was 3769 individuals per km^2, more than six times the national average of 551 individuals per km^2 (obtained by dividing total area of the UK by summed population estimates for all breeding species). If calculated based on birds detected within a fixed radius of 20 m, estimated total bird density drops to 3234 individuals per km^2, still 5.9 times the national average. Very few species with a national density of < 1 individual per km^2 occurred above that density in Sheffield (Fig. 2), indicating that the majority of the city's avifauna comprised nationally common species, something reflected in the bimodal species abundance distribution (Fig. 1).

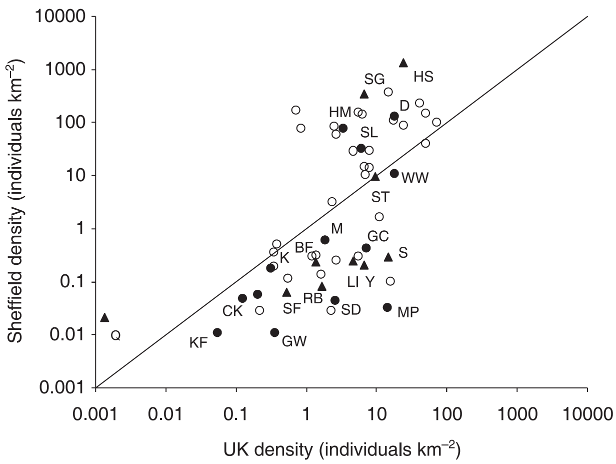

Figure 2 Density of breeding birds in Sheffield in comparison with average density across the UK. Red listed species are represented by filled triangles, amber listed species by filled circles, and green listed species by open circles. Species of conservation concern are labelled with species codes (see Table 1). Line represents 1 : 1 density comparison.

Nationally, of 223 breeding species assessed by Gregory *et al.* (2002), 76 (34%) were green listed, and the remaining 147 (66%) amber or red listed. Proportionately fewer species of national conservation concern bred in Sheffield compared with these

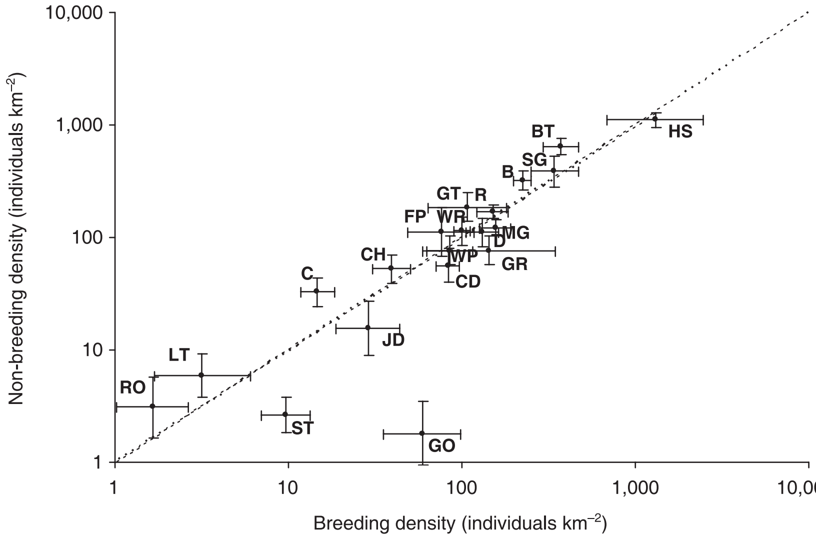

Figure 3 Comparison of breeding and non-breeding densities of the 20 commonest resident breeding species in Sheffield (all those species with a breeding density > 1 bird per km^2). Error bars are 95% confidence intervals, dotted line represents a 1 : 1 relationship. Only species resident in the UK are plotted, hence differences from parity indicate changes in density relating to partial migration in or out of the city (see Table 1 for species codes).

national figures. This held using our survey data (32 (58%) green listed, 23 (42%) amber or red listed; $G_{adj} = 10.43$, $P = 0.001$) and using data from the intensive atlas-based work reported by Hornbuckle & Herringshaw (1985) (43 (50%) green listed, 43 (50%) amber or red listed; $G_{adj} = 6.5$, $P = 0.011$). Summing the relevant population estimates for Sheffield from Table 1 gives a total of 298,270 (224,568–413,622) individuals of green listed species and 304,725 (179,997–528,951) individuals of amber or red listed species (i.e. 50.5% of individuals are of national conservation concern). The equivalent national figures are 90,719,062 (89,315,916–92,122,208) individuals from green listed species and 43,833,640 (41,535,272–46,232,008) individuals from amber or red listed species (i.e. 32.6% of individuals are of national conservation concern). Nationally threatened breeding bird species occurred at a significantly greater frequency in Sheffield than across the country as a whole ($G_{adj} = 82{,}426$, $P < 0.0001$).

As might be expected for birds resident in the UK as a whole, there was a strong positive relationship between the density of Sheffield birds in summer and winter (Fig. 3). However, of these resident species, significantly more common blackbirds, blue tits and carrion crows but fewer European goldfinches and song thrushes were present in the city in winter than in summer (Fig. 3). This increase in numbers of green-listed species resulted in a significantly lower frequency of individuals of threatened species in Sheffield in winter than in summer ($G_{adj} = 3893$, $P < 0.0001$).

DISCUSSION

Birds occur at very high densities within Sheffield city, much higher than across the UK at large. Moreover, some of the commonest species within the city's avifauna are nationally (Table 1) and continentally threatened, having experienced large population declines across much of their native ranges. At least some cities, therefore, as well as supporting very high densities of birds *per se* could play a significant part in overall conservation effort in urbanized nations.

In terms of simple species richness, the surveyed Sheffield avifauna (61 species) is comparable with data from France, Finland and Italy summarized in Clergeau *et al.* (2006), where an average of 43 species was observed in surveys restricted to suburban areas. Atlas-derived data, while more comprehensive will include species only occasionally breeding within city limits. Such data indicate an average of 115 species in the breeding avifauna of 16 large cities (mean population of 1.9 million people) across Europe (Kelcey & Rheinwald, 2005). A citywide survey of Washington, D.C. detected 91 bird species, with the total avifauna estimated at 115 (Hadidian *et al.*, 1997). Sheffield, therefore, does not appear to be particularly unusual in terms of overall bird species richness.

There are some 134.6 million breeding birds in the UK (from data in Baker *et al.*, 2006), equivalent to *c.* 2.24 birds per person, while within the city of Sheffield, this ratio falls to 1.18. That it does not fall further is remarkable given the extremely densely aggregated human population. The species-abundance distribution was an unusual shape, with distinct peaks of rare and common species, and rather few species of intermediate abundance in the assemblage (Fig. 1). This strongly bimodal pattern differs markedly from the more obviously unimodal and closer to (albeit not actually) log-normal species-abundance distribution of UK farmland birds and British birds as a whole (Preston, 1948; Gregory, 1994; Williamson & Gaston, 2005). Heavily urbanized sites have been associated with low levels of evenness in abundances for several taxonomic groups including lizards (Germaine & Wakeling, 2001), birds (Clergeau *et al.*, 1998; Marzluff, 2001) and bats (Kurta & Teramino, 1992), and this is usually attributed to local extinctions of rare native species (Donnelly & Marzluff, 2004). However, the peaks in rare and common species shown by Sheffield's birds suggest that a significant proportion of species are well adapted to urban environments, while many others achieve only very low densities. This is consistent with predictions that high food density and low predation risk in urban environments will result in a few species becoming superabundant (Shochat *et al.*, 2004; Shochat, 2004).

However, the magnitude of the peak on the right-hand side of the species-abundance distribution (Fig. 1) suggests that the proportion of such 'winners' in an urban assemblage might be unexpectedly high.

The rural/urban contrast in population densities reported here is probably quite common in areas with intensive agriculture, and likely to spread as regions become more developed, and with recent trends toward increasing production as grain prices have soared. Historical declines in house sparrows and common starlings, two of the commonest species in Sheffield's avifauna, have been most dramatic outside urban habitats and particularly in farmland, where both were formerly abundant. The breeding population of common starlings has declined by at least 92% since 1965 in woodland habitats, and by 66% since 1962 in farmland (Crick *et al*., 2002). Declines in urban habitats have been less severe, although comparable long-term data are lacking because urban habitats were poorly covered before the advent of a national UK Breeding Bird Survey in 1994 (Newson *et al*., 2005). In the 4 years between 1979 and 1983, rural populations of house sparrows declined by 38%, although more recently regional differences in decline rates have become apparent. The decline of urban house sparrow populations commenced later, around 1983, and appears to be continuing such that by the late 1990s populations in suburban gardens had declined by *c.* 60% (Cannon *et al*., 2005; Robinson *et al*., 2005). Recent declines in these species exemplify the wider point that cities can function as refugia for some species in the face of widespread intensive agriculture, and we believe that significant conservation effort should now be directed towards urban bird populations. This is true not only for birds. Many rare plants in the USA and Europe are concentrated in and near urban centres (Schwartz *et al*., 2002; Kühn *et al*., 2004), highlighting the importance of urban green spaces for plant conservation (Stalter *et al*., 1996).

Most species nationally resident in the UK showed consistent breeding and non-breeding densities in Sheffield (Fig. 3), suggesting that our results are valid year-round for resident species. Exceptions were carrion crow, common blackbird, blue tit (disproportionately abundant in the non-breeding season), song thrush and European goldfinch (disproportionately abundant in the breeding season). No trait obviously unites the species in these two groups and the results highlight the need to understand in more detail how individual species utilize urban habitats over the course of the annual cycle. Many resident species are more mobile outside the breeding season, perhaps as a result of resource fluxes, and there may be significant movements into (and out of) cities during the winter (Wernham *et al*., 2002). For example, urban robins are sedentary in urban habitats yet only breeding visitors to nearby woodlands (Adriaensen & Dhondt, 1990), and movement into gardens of passerine birds occurs in years where levels of beech *Fagus sylvatica* fruiting are low (Chamberlain *et al*., 2007).

Given that urban areas can support high densities of nationally threatened bird species, our results suggest that greater priority needs to be given to conservation of urban populations. This is particularly crucial given the trend toward building new urban developments at high density in the UK (Department of Communities and Local Government, 2006), which could adversely affect urban bird richness and abundance (Tratalos *et al*., 2007). Urban bird declines show strong regional variation (Sanderson, 1996; Dott & Brown, 2000; Prowse, 2002; Robinson *et al*., 2005), and an investigation of within- and between-city factors leading to such changes will help predict the trajectory of such changes in the future.

ACKNOWLEDGEMENTS

This work was supported by the Engineering and Physical Sciences Research Council (through the CityForm research consortium). R.A. Fuller is additionally supported by the Applied Environmental Decision Analysis research hub, funded through the Commonwealth Environment Research Facilities programme, Australia, and K.J. Gaston holds a Royal Society-Wolfson Research Merit Award. Ordnance Survey supplied MasterMap data under license to the CityForm consortium. We are grateful to J. Booth, R.G. Davies, K.L. Evans, B. Goettsch, S.E. Newson and P.H. Warren for comments and discussion. Two anonymous referees provided useful comments on an earlier draft of this manuscript.

REFERENCES

Adams, C.E., Lindsey, K.J. & Ash, S.J. (2006) *Urban wildlife management*. Taylor & Francis, Boca Raton, FL.

Adriaensen, F. & Dhondt, A.A. (1990) Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology*, **59**, 1077–1090.

Baker, H., Stroud, D.A., Aebischer, N.J., Cranswick, P.A., Gregory, R.D., McSorley, C.A., Noble, D.G. & Rehfisch, M.M. (2006) Population estimates of birds in Great Britain and the United Kingdom. *British Birds*, **99**, 25–44.

Beer, A. (2005) The green structure of Sheffield. *Green structure and urban planning* (ed. by A.C. Werquin, B. Duhem, G. Lindholm, B. Oppermann, S. Pauleit and S. Tjallingii), pp. 40–51. Brussels, Belgium.

BirdLife International (2004) *Birds in the European Union: a status assessment*. BirdLife International, Wageningen, The Netherlands.

Blair, R.B. (2001) Creating a homogenous avifauna. *Avian ecology and conservation in an urbanizing world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 459–486. Kluwer Academic Publishers, London.

Bland, R.L., Tully, J. & Greenwood, J.J.D. (2004) Birds breeding in British gardens: an underestimated population? *Bird Study*, **51**, 96–106.

Brichetti, P., Rubolini, D., Galeotti, P. & Fasola, M. (2008) Recent declines in urban Italian sparrow *Passer* (*domesticus*) *italiae* populations in northern Italy. *Ibis*, **150**, 177–181.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.

Cannon, A.R., Chamberlain, D.E., Toms, M.P., Hatchwell, B.J. & Gaston, K.J. (2005) Trends in the use of private gardens by wild birds in Great Britain 1995–2002. *Journal of Applied Ecology*, **42**, 659–671.

Chamberlain, D.E., Gosler, A.G. & Glue, D.E. (2007) Effects of the winter beechmast crop on bird occurrence in British gardens. *Bird Study*, **54**, 120–126.

Clergeau, P., Savard, J.-P.L., Mennechez, G. & Falardeau, G. (1998) Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. *Condor*, **100**, 413–425.

Clergeau, P., Jokimäki, J. & Savard, J.-P.L. (2001) Are urban bird communities influenced by the bird diversity of adjacent landscapes? *Journal of Applied Ecology*, **38**, 1122–1134.

Clergeau, P., Croci, S., Kokimaki, J., Kaisanlahti-Jokimaki, M.-L. & Dinetti, M. (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation*, **127**, 336–344.

Collins, J.P., Kinzig, A., Grimm, N.B., Fagan, W.F., Hope, D., Wu, J. & Borer, E.T. (2000) A new urban ecology. *American Scientist*, **88**, 416–425.

Cramp, S., ed. (1985) *The birds of the Western Palaearctic*, Vol. 4. Oxford University Press, Oxford.

Crick, H.Q.P., Robinson, R.A., Appleton, G.F., Clark, N.A. & Rickard, A.D. (2002) *Investigation into the causes of the decline of starlings and house sparrows in Great Britain*. BTO Research report No. 290. British Trust for Ornithology, Thetford, UK.

Daniels, G.D. & Kirkpatrick, J.B. (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation*, **133**, 326–335.

Department of Communities and Local Government. (2006) *Planning policy statement 3 (PPS3): housing*. HMSO, London.

Donnelly, R. & Marzluff, J.M. (2004) Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology*, **18**, 733–745.

Donnelly, R. & Marzluff, J.M. (2006) Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystems*, **9**, 99–117.

Dott, H.E.M. & Brown, A.W. (2000) A major decline in house sparrows in central Edinburgh. *Scottish Birds*, **21**, 61–68.

Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H. & Gaston, K.J. (2007) Psychological benefits of greenspace increase with biodiversity. *Biology Letters*, **3**, 390–394.

Fuller, R.A., Warren, P.H., Armsworth, P.R., Barbosa, O. & Gaston, K.J. (2008) Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and Distributions*, **14**, 131–137.

Gaston, K.J. (2005) Biodiversity and extinction: species and people. *Progress in Physical Geography*, **29**, 239–247.

Gaston, K.J. & Fuller, R.A. (2007) Biodiversity and extinction: losing the common and the widespread. *Progress in Physical Geography*, **31**, 213–225.

Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, **23**, 14–19.

Gaston, K.J., Warren, P.H., Thompson, K. & Smith, R.D. (2005) Urban domestic gardens (IV): the extent of the resource and its associated features. *Biodiversity and Conservation*, **14**, 3327–3349.

Gaston, K.J., Fuller, R.A., Loram, A., MacDonald, C., Power, S. & Dempsey, N. (2007) Urban domestic gardens (XI): variation in urban wildlife gardening in the UK. *Biodiversity and Conservation*, **16**, 3227–3238.

Germaine, S.S. & Wakeling, B.F. (2001) Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation*, **97**, 229–237.

Green, D.M. & Baker, M.G. (2003) Urbanization impacts on habitat and bird communities in a Sonoran desert ecosystem. *Landscape and Urban Planning*, **63**, 225–239.

Gregory, R.D. (1994) Species abundance patterns of British birds. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **257**, 299–301.

Gregory, R.D. & Baillie, S.R. (1998) Large-scale habitat use of some declining British birds. *Journal of Applied Ecology*, **35**, 785–799.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, R.A., Brown, A.F., Hughes, J., Procter, D.A., Gibbons, D.W. & Galbraith, C.A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–07. *British Birds*, **95**, 410–450.

Hadidian, J., Sauer, J., Swarth, C., Handly, P., Droege, S., Williams, C., Huff, J. & Didden, G. (1997) A citywide breeding bird survey for Washington, D.C. *Urban Ecosystems*, **1**, 87–102.

Hardy, P.B. & Dennis, R.L.H. (1999) The impact of urban development on butterflies within a city region. *Biodiversity and Conservation*, **8**, 1261–1279.

Hornbuckle, J. & Herringshaw, D. (1985) *Birds of the Sheffield area including the north-east Peak District*. Sheffield Bird Study Group, Sheffield, UK.

Johnston, R.F. (2001) Synanthropic birds of North America. *Avian ecology and conservation in an urbanizing world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 49–67. Kluwer Academic Publishers, London.

Kelcey, J.G. & Rheinwald, G. (2005) *Birds in European cities*. GINSTER-Verlag, St. Katharinen, Germany.

Kerr, J.T. & Currie, D.J. (1995) Effects of human activity on global extinction risk. *Conservation Biology*, **9**, 1528–1538.

Kowarik, I. (1990) Some responses of flora and vegetation to urbanization in central Europe. Urban ecology. *Plants and plant communities in urban environments* (ed. by H. Sukopp and S. Hejny), pp. 45–74. SPB Academic Publishing, The Hague.

Kühn, I. & Klotz, S. (2006) Urbanization and homogenization – comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.

Kühn, I., Brandl, R. & Klotz, S. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.

Kurta, A. & Teramino, J.A. (1992) Bat community structure in an urban park. *Ecography*, **15**, 257–261.

Lawton, J.H. & May, R.M., eds. (1995) *Extinction rates*. Oxford University Press, Oxford.

Luck, G.W. (2007) A review of the relationships between human population density and biodiversity. *Biological Reviews*, **82**, 607–645.

Marco, A., Dutoit, T., Deschamps-Cottin, M., Mauffrey, J.-F., Vennetier, M. & Bertaudière-Montes, V. (2008) Gardens in urbanizing rural areas reveal an unexpected floral diversity related to housing density. *Comptes Rendus Biologies*, **331**, 452–465.

Marzluff, J.M. (2001) Worldwide urbanization and its effects on birds. *Avian ecology and conservation in an urbanizing world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 19–48. Kluwer Academic Publishers, London.

Marzluff, J.M., Bowman, R. & Donnelly, R., eds. (2001) *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, London.

Mason, C.F. (2000) Thrushes now largely restricted to the built environment in eastern England. *Diversity and Distributions*, **6**, 189–194.

Matlack, G.R. (1993) Sociological edge effects: spatial distribution of human impact in suburban forest fragments. *Environmental Management*, **17**, 829–835.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

McKinney, M.L. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**, 161–176.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.

Meyer, W.B. & Turner, B.L.I.I. (1992) Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics*, **23**, 39–61.

Miller, J.R. (2005) Biodiversity conservation and the extinction of experience. *Trends in Ecology and Evolution*, **20**, 430–434.

Miller, J.R. & Hobbs, R.J. (2002) Conservation where people live and work. *Conservation Biology*, **16**, 330–337.

Newson, S.E., Woodburn, R.J.W., Noble, D.G., Baillie, S.R. & Gregory, R.D. (2005) Evaluating the Breeding Bird Survey for producing national population size and density estimates. *Bird Study*, **52**, 42–54.

Niemelä, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D. & de Oca, E.M. (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, **17**, 387–401.

Office for National Statistics (2001) *Census: standard area statistics (England and Wales)*. ESRC/JISC Census Programme, London.

Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254–283.

Prowse, A. (2002) The urban decline of the house sparrow. *British Birds*, **95**, 143–146.

Robinson, R.A., Siriwardena, G.M. & Crick, H.Q.P. (2005) Size and trends of the house sparrow *Passer domesticus* population in Great Britain. *Ibis*, **147**, 552–562.

Sanderson, R.F. (1996) Autumn bird counts in Kensington Gardens. *London Bird Report*, **60**, 170–176.

Sandström, U.G., Angelstam, P. & Mikusiñski, G. (2006) Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning*, **77**, 39–53.

Schwartz, M.W., Jurjavcic, N.L. & Brien, J.M. (2002) Conservation's disenfranchised urban poor. *BioScience*, **52**, 601–606.

Shochat, E. (2004) Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos*, **106**, 622–626.

Shochat, E., Lerman, S.B., Katti, M. & Lewis, D.B. (2004) Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *The American Naturalist*, **164**, 232–243.

Stalter, R., Byer, M.D. & Tanacredi, J.T. (1996) Rare and endangered plants at Gateway National Recreation Area: a case for protection of urban natural areas. *Landscape and Urban Planning*, **35**, 41–51.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. & Marques, T.A. (2005) *Distance 5.0. Release beta 5*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D. & Gaston, K.J. (2007) Bird densities are associated with household densities. *Global Change Biology*, **13**, 1685–1695.

Turner, K., Lefler, L. & Freedman, B. (2005) Plant communities of selected urbanized areas of Halifax, Nova Scotia, Canada. *Landscape and Urban Planning*, **71**, 191–206.

Turner, W.R., Nakamura, T. & Dinetti, M. (2004) Global urbanization and the separation of humans from nature. *BioScience*, **54**, 585–590.

United Nations (2004) *World urbanization prospects: the 2003 revision*. United Nations, New York.

Vähä-Piikkiö, I., Kurtto, A. & Hahkala, V. (2004) Species number, historical elements and protection of threatened species in the flora of Helsinki, Finland. *Landscape and Urban Planning*, **68**, 357–370.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of earth's ecosystems. *Science*, **277**, 494–499.

Voříšek, P., Klvaòová, A., Gregory, R., Auninš, A., Chylarecki, P., Crowe, O., de Carli, E., del Moral, J.C., Escandell, V., Foppen, R.P.B., Fornasari, L., Heldbjerg, H., Hilton, G., Husby, M., Jawinska, D., Jiguet, F., Joys, A., Kuresoo, A., Lindström, Å., Martins, R., Noble, D.G., Reif, J., Schmid, H., Schwarz, J., Szép, T., Teufelbauer, N., Väisänen, R.A., Vansteenwegen, C.H. & Weiserbs, A. (2007) *State of Europe's common birds, 2007*. CSO/RSPB, Prague, Czech Republic.

Wania, A., Kühn, I. & Klotz, S. (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, **75**, 97–110.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The migration atlas: movements of the birds of Britain and Ireland*. T & AD Poyser, London.

Williamson, M. & Gaston, K.J. (2005) The lognormal distribution is not an appropriate null hypothesis for the species–abundance distribution. *Journal of Animal Ecology*, **74**, 409–422.

Zanette, L.R.S., Martins, R.P. & Ribeiro, S.P. (2005) Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning*, **71**, 105–121.

Editor: Ralph MacNally

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of species entered into Distance analyses, together with the number of detections of each during the breeding and non-breeding seasons.

Appendix S2 Sample detection function plots for four breeding species (a) blue tit, $n = 244$ observations (b) dunnock, $n = 248$ (c) song thrush, $n = 94$, and (d) common swift, $n = 266$.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.