Review

# Avian productivity in urban landscapes: a review and meta-analysis

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There is an urgent need to thoroughly review and comprehend the effects of urbanization on wildlife in order to understand both the ecological implications of increasing urbanization and how to mitigate its threat to biodiversity globally. We examined patterns in comparative productivity of urban and non-urban passerine birds, using published estimates from paired comparisons, and by reviewing and developing explanations in terms of resources, competitors, predators and other specifically urban environmental factors. The most consistent patterns were for earlier lay dates, lower clutch size, lower nestling weight and lower productivity per nesting attempt in urban landscapes; these were supported by a formal meta-analysis. Nest failure rates did not show consistent patterns across the species considered. We suggest that food availability is a key driver of differences in passerine demography between landscapes. In urban habitats, human-provided food may improve adult condition over winter, leading to earlier lay dates and, in some species, to higher survival and higher breeding densities, but paucity of natural food may lead to lower productivity per nesting attempt. We demonstrate that additional comparative research is needed on a wider range of species, on the effects of natural and human-provided food availability, and on the differences in survival and dispersal between urban and non-urban populations. Importantly, better-targeted research and monitoring is needed in areas that are at greatest threat from urbanization, especially in the developing world.

**Keywords:** bird food, clutch size, predation, survival, urbanization.

Urbanization is increasing; its extensive modification of the landscape (McDonnell & Pickett 1990) leads to a profound restructuring of habitats and avifaunas (Shochat *et al.* 2006). The majority of humans now live in urban areas (United Nations 2004), and household density is growing even faster than human population density and is strongly correlated with negative impacts on wildlife (Peterson *et al.* 2007). Urban landscapes encompass significant variation in bird habitat, from city centres dominated by the

built environment to suburban areas of low-density housing, often with a relatively high proportion of green space in the form of parks or private gardens. Nonetheless, urban landscapes as a whole differ broadly and markedly from natural/semi-natural habitats (Marzluff *et al.* 2001a, Chace & Walsh 2006), for example in food resources, weather conditions (Haggard 1990), predator communities (Haskell *et al.* 2001, Sorace 2002), pollution (Eeva *et al.* 2000) and disturbance, including increased noise levels (Fuller *et al.* 2007). There have been numerous studies on bird community composition in urbanized landscapes and across urban–rural gradients (e.g. Chace & Walsh 2006). Although responses to urban gradients differ between individual studies, in part due to variations

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in gradient composition, some general patterns emerge. Several studies found a non-linear response, where species richness or diversity was higher at intermediate levels of urbanization (Blair 1996, Marzluff 2001, Tratalos *et al.* 2007). A number of studies have indicated biotic homogenization of urban communities (McKinney 2006), city faunas tending to similarity across large geographic scales (Dinetti *et al.* 1996, Jokimäki *et al.* 2002). Such urban avifaunas are typically dominated by granivores, medium-sized omnivores and sedentary or partially migratory species (Bezzel 1985), with ground-nesters, migrants and forest species, especially foliage gleaning invertebrate feeders (e.g. White *et al.* 2005), less common.

As urbanization continues, urban avifaunas are becoming increasingly appropriate targets for research and conservation efforts (Fornaroff 1974, Mörtberg & Wallentius 2000), particularly as human population, social and demographic trends predict further urbanization. Many bird species nest in urbanized areas, with private gardens sometimes holding nationally significant populations (e.g. Mason 2000, Bland *et al.* 2004). Habitats associated with human habitation already support significant proportions of the British populations of Common Blackbird *Turdus merula* and the red-listed Song Thrush *Turdus philomelos*, Common Starling *Sturnus vulgaris* (Gregory & Baillie 1998, Eaton *et al.* 2004) and House Sparrow *Passer domesticus* (Siriwardena *et al.* 2002).

Bird abundances and community compositions in urban areas have been well described (Chace & Walsh 2006) and a number of studies have compared demographic parameters (such as timing of nesting, clutch size, fledging rate, annual survival) between urban and semi-natural populations. However, the few attempts to assess general effects of urbanization on avian demography (e.g. Jerzak 1995, Marzluff 2001) have not been comprehensive, as their authors point out. Chace and Walsh (2006) state: 'Studies of passerine responses to urbanization are often devoid of important reproductive information …'. We attempt to redress this by assessing the demographic characteristics of urban passerine populations in order to understand more fully the processes that affect biodiversity in urban landscapes. We achieve this by (1) quantifying, where possible, differences in demographic parameters between populations of passerine birds in urban and other habitats; (2) explaining the observed quantified differences in terms of resources, competitors, predators and other factors characteristic of the urban environment, and (3) discussing the general implications of the review and highlighting future research priorities. Although non-passerine birds occur in urban areas and some have been studied there, including gulls (Rock 2005) and raptors (Chace & Walsh 2006), this review focuses exclusively on passerines, which typically dominate avifaunas across the wider urban environment.

## METHODS

### Literature search

Key references were identified from review sources on the topic of urban bird populations (e.g. Marzluff *et al.* 2001a, Cannon 2005, Chace & Walsh 2006). A search for references was also carried out on *Web of Science* using the terms '(bird* OR avian) AND (urban* OR garden* OR yard*)' for a subject search and '(breeding OR survival OR reproduct*) AND (urban* OR garden* OR yard*)' for a title search. The former yielded a list of 754 references, the latter 178 references (not mutually exclusive). Further references were identified from *BWP Interactive* (Anon. 2006) using the same search terms.

### Quantifying differences

Both variation in demographic estimates caused by factors other than landscape (e.g. clutch size increasing with latitude; Lack 1947) and temporal trends in population size, survival rates and measures of reproductive output (e.g. Baillie *et al.* 2007) may bias comparisons between urban and non-urban populations. To reduce bias, only studies including paired comparisons of urban and non-urban parameters were considered, i.e. they used the same methods over a similar time period at similar scales (including both single and multiple study sites) in both urban and non-urban landscapes. Gradient studies were included by taking estimates from sites at either end of the urban–rural gradient (although, in practice, very few such studies presented data in a form that was usable in our analyses). A number of published comparisons were either fully or partly based on earlier published work (e.g. Snow 1958b and Lack 1968; McGowan 2001 and Marzluff *et al.* 2001b) and we took particular care to avoid such duplicated estimates.

Our comparisons were based on broadly defined urban and non-urban landscape classes. Ideally, these

would have been between urban and natural (or at least semi-natural) habitats. This was broadly achievable for primarily woodland species, but many other studies were carried out in highly modified landscapes. Comparisons for species of open country were usually from rural habitats dominated by agriculture; in Europe and parts of North America such landscapes are probably the closest available to many species' natural habitat. The urban classification included all landscapes in which buildings dominated, including commercial and industrial (e.g. city centre) and residential (e.g. suburbs) habitats, and green spaces embedded within an urban matrix (e.g. parks, gardens, small urban woods).

Quantitative definitions of 'urban' land use are rarely provided in the literature (Marzluff 2001), a deficiency common with the majority of studies considered here. Any definitions provided varied between studies, presumably reflecting national, regional or cultural differences in what is considered 'urban'. For example, some study sites defined as 'urban' were apparently in residential locations (e.g. Beck & Heinsohn 2006, Mennechez & Clergeau 2006) typically considered 'suburban' by other authors. This lack of habitat descriptions and inconsistent terminology forced us to restrict quantified comparisons to simple broad landscape classifications. Where sample size was available, we used a mean (or, for lay date, median) value across any sub-habitats within an urbanized landscape (e.g. where 'urban' and

'suburban' estimates had been derived separately). Nevertheless, we consider finer-scale habitat differences as part of our wider literature review, we highlight cases where there is significant variation within urbanized landscapes (e.g. 'urban' vs. 'suburban' habitats) and we meta-analyse a subset of studies with more specifically defined suburban habitat.

Differences in most parameters are presented as the total number of studies in which a given estimate was higher in urban or non-urban landscape, and the number of cases where this difference was significant, non-significant, or not reported, for each species (Figs 1–6). A summary of quantified differences, source references and a full list of scientific names are given in the Appendices S1–S3, available as on-line supplementary material. Simple 'vote-counting' summaries of data are problematic (Gurevitch & Hedges 2001), so formal meta-analysis was undertaken to determine general patterns in demographic parameters across species. Standardized mean differences and confidence intervals were calculated using the method of Gurevitch and Hedges (2001), which requires the means, variances and sample sizes of all urban and non-urban parameter estimates. Wherever sources quoted estimates from several years or study sites, those derived from the largest sample were used. In a few cases, sample sizes not explicitly associated with parameter estimates were deduced from supporting material or variances estimated from error bars.
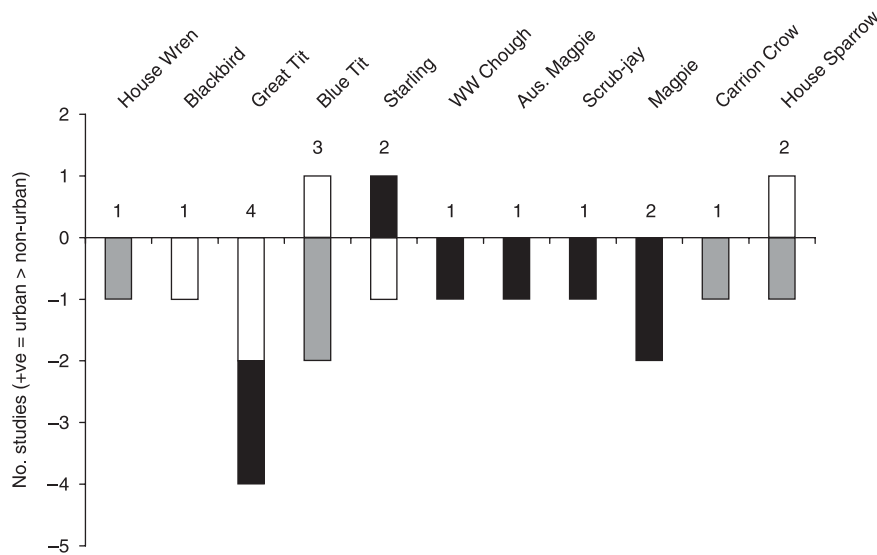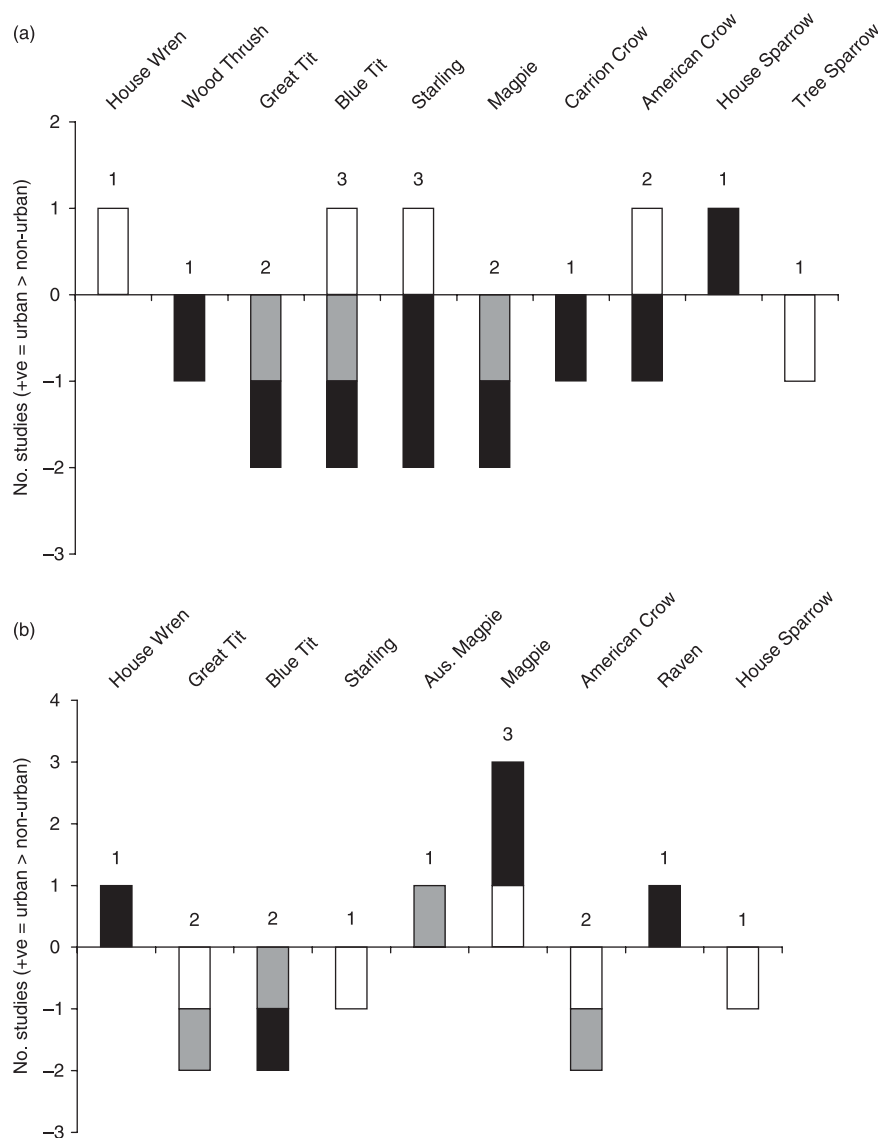


**Figure 1.** A summary of the number of studies comparing lay date of bird populations in urban and non-urban landscapes. Positive values indicate urban lay date later than non-urban. Black bars are studies reporting significant differences, grey bars are those reporting no significant difference and white bars are studies where significance tests were not given. The number of studies is given above the bars. Aus. Magpie = Australian Magpie, WW Chough = White-winged Chough.
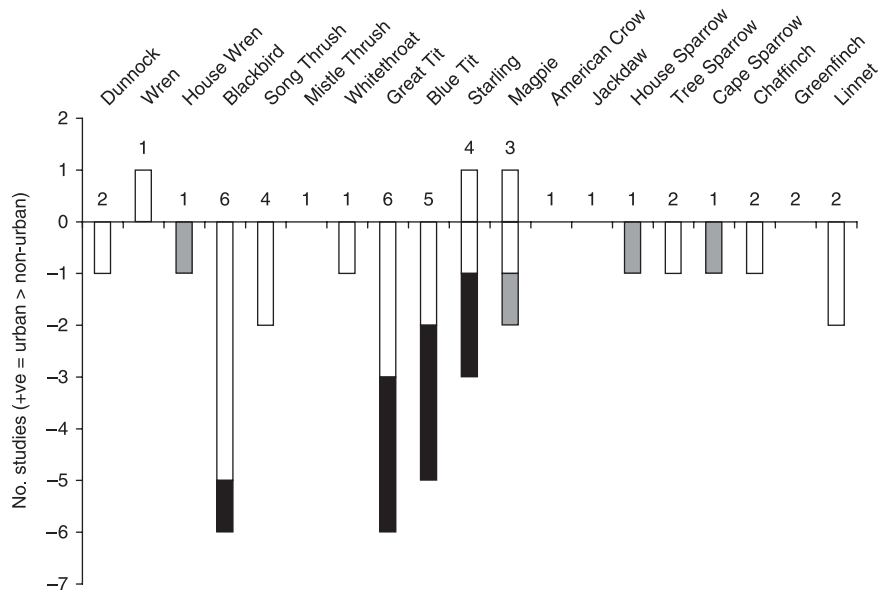
**Figure 2.** A summary of the number of studies comparing clutch size of bird populations in urban and non-urban landscapes. Positive values indicate urban clutch size larger than non-urban. Black bars are studies reporting significant differences, grey bars are those reporting no significant difference and white bars are studies where significance tests were not given. A difference in means of 0 is shown as sample size without bar. The number of studies is given above the bars.
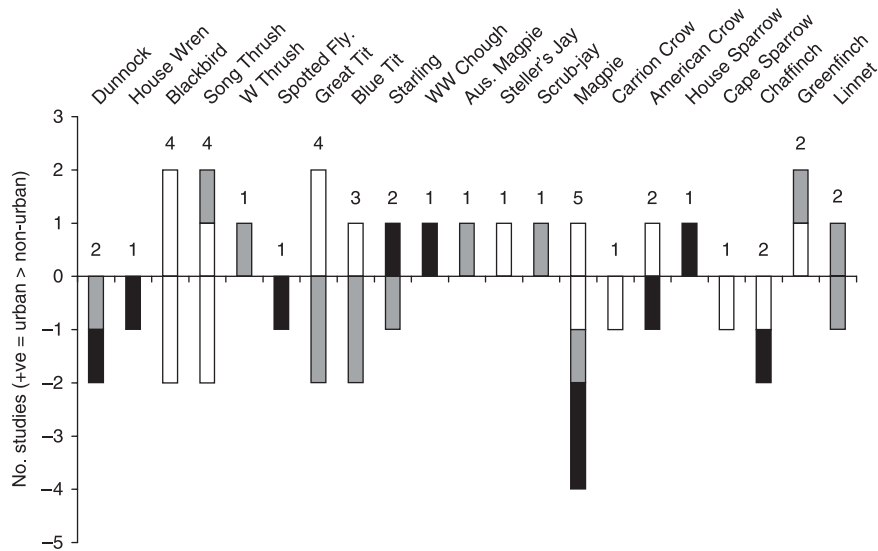


**Figure 3.** A summary of the number of studies comparing nest failure of bird populations in urban and non-urban landscapes. Positive values indicate urban failure rates higher than non-urban. Different measures of failure rates are included in the Figure: whole nest failures ($n = 25$), the proportion of eggs laid that fail to result in fledged young ($n = 12$), the proportion of young hatching that fail to fledge ($n = 4$) and daily nestling mortality rate ($n = 1$). Black bars are studies reporting significant differences, grey bars are those reporting no significant difference and white bars are studies where significance tests were not given. The number of studies is given above the bars. Aus. Magpie = Australian Magpie, Scrub-jay = Florida Scrub Jay, Spotted Fly. = Spotted Flycatcher. WW Chough = White-winged Chough, W Thrush = Wood Thrush.
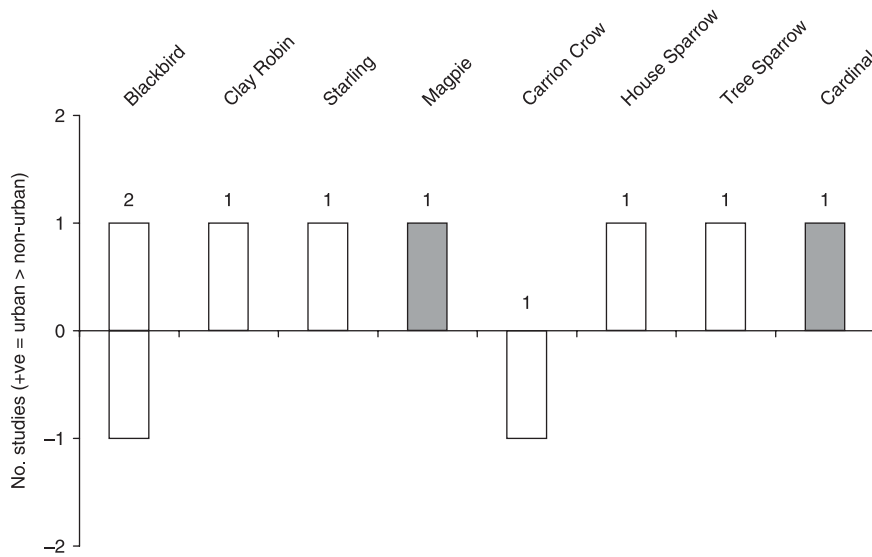
**Figure 4.** A summary of the number of studies comparing the number of fledglings produced in urban and non-urban landscapes. (a) Fledglings per successful attempt, (b) fledglings per all attempts. Positive values indicate more fledglings in urban than non-urban. Black bars are studies reporting significant differences, grey bars are those reporting no significant difference and white bars are studies where significance tests were not given. The number of studies is given above the bars. Three studies in Figure 4a, on Blue Tit, Great Tit and House Sparrow, gave brood size close to fledging rather than the number of fledglings leaving the nest. Aus. Magpie = Australian Magpie.

## URBAN AND NON-URBAN DEMOGRAPHIC PARAMETERS

### Lay date

Figure 1 summarizes 19 lay date comparisons in 10 species. Urban laying was earlier in 16 of 19 comparisons and in seven of the 13 studies using a significance test. This difference was consistent across studies in Great

Tit *Parus major* and Eurasian Magpie *Pica pica*. Blue Tit *Cyanistes caeruleus* had generally earlier urban lay dates, although in one study the date was earliest in oak woodland. For Common Starling and House Sparrow, differences were small and the directions conflicting. The only study in which urban lay date was significantly later was for Common Starling, although significance was detected only in certain years (Mennechez & Clergeau 2006). For both Common Starling and House Sparrow,

**Figure 5.** A summary of the number of studies comparing annual productivity (fledglings/pair/year) of bird populations in urban and non-urban landscapes. Positive values indicate urban productivity greater than non-urban. Grey bars are those reporting no significant difference and white bars are studies where significance tests were not given. The number of studies is given above the bars.
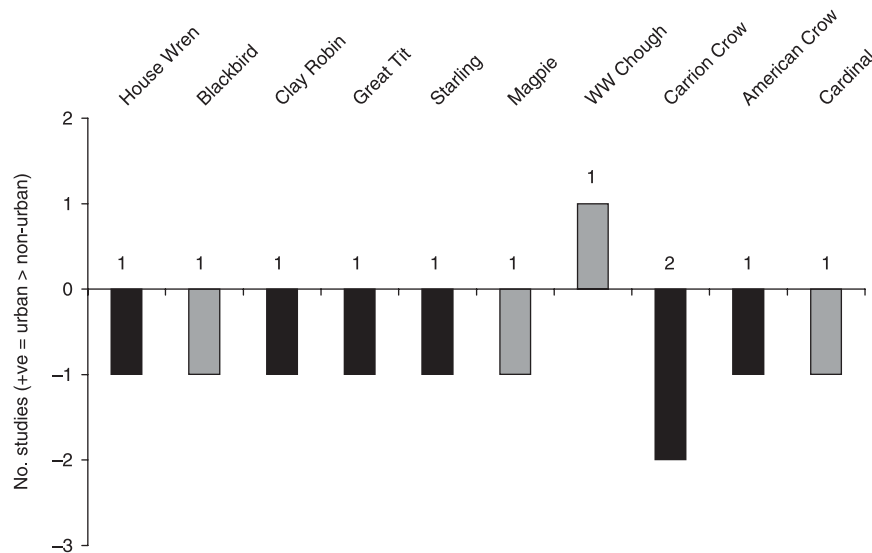


**Figure 6.** A summary of the number of studies comparing nestling weight of bird populations in urban and non-urban landscapes. Positive values indicate nestling weight greater in urban than non-urban. Black bars are studies reporting significant differences and grey bars are those reporting no significant difference. The number of studies is given above the bars. WW Chough = White-winged Chough.

analysis of UK nest record data (Crick & Siriwardena 2002, Siriwardena & Crick 2002) suggested marked differences within the urban landscape; estimates of lay date in 'urban' habitat were earliest and 'suburban' latest, 'rural' lay dates being intermediate. However, urban sample sizes were relatively small. Other species reported laying earlier in urban landscapes include European Robin *Erithacus rubecula*, Song

Thrush (Snow 1958a) and Northern Cardinal *Cardinalis cardinalis* (Burhans & Thompson 2006), although differences were not quantified.

## Clutch size

Figure 2 summarizes 46 clutch size comparisons in 19 species. In general, clutch size was larger in

non-urban landscapes (*n* = 33). For Common Blackbird, Great Tit and Blue Tit, clutch sizes in woodland were consistently larger than in urban landscapes (*n* = 6, 5, and 6 respectively) and, where tested, differences were significant (*n* = 1, 3 and 3). Two studies of Common Starling (Siriwardena & Crick 2002, Mennechez & Clergeau 2006) also found significantly lower clutch size in urban landscapes, but for American Crow *Corvus brachyrhynchos* (McGowan 2001), Eurasian Magpie (Eden 1985, Antonov & Atanasova 2003), Song Thrush (Kelleher & O'Halloran 2007) and House Sparrow (Crick & Siriwardena 2002), no significant differences were found. Cape Sparrow *Passer melanurus* clutch sizes were similar in urban and rural landscapes (Earlé 1988; Fig. 2) but varied within the urban landscape; rural clutch size was intermediate between urban (low) and suburban (high).

## Productivity per nesting attempt

The studies reviewed used several different measures of nest failure, including whole nest failure rates, Mayfield-derived daily failure rates (Mayfield 1975) and simple proportions of eggs laid or nests producing fledglings. Where possible, published daily nest failure estimates were converted to overall failure rates, assuming uniform nest exposure days (from Robinson 2006) across habitats. Figure 3 summarizes 42 comparisons in 21 species. There was no consistent pattern across species and there were conflicting patterns within species with respect to landscape.

Considering brood size and the number of fledglings produced per successful attempt, there was no particular pattern across species (Fig. 4a) and in a number of cases (American Crow, Common Blackbird, Blue Tit, Common Starling) there were conflicting results between studies. However, there was some trend towards higher productivity in non-urban landscapes when considering only significant effects: only House Sparrow showed a significantly greater number of fledglings produced per successful attempt in urban habitats, while seven species showed a significantly greater number in non-urban habitats in at least one study (Fig. 4a). More fledglings were produced on average by American Crows in urban landscapes compared to nearby 'wildland', but there was large variation within the urban landscape, Crows in the urban centre showing lower productivity than those in suburban areas (Marzluff *et al.* 2001b). Conversely, McGowan (2001) found that rural Crows produced on average about 0.5 more fledglings

per successful attempt than suburban Crows, a significant difference. The average number of fledglings per attempt including whole nest failures (Fig. 4b) showed results similar to those in Figure 4a for most species, but the general pattern for urban productivity to be relatively low was less apparent. Interestingly, in urban landscapes the Eurasian Magpie had a lower productivity per successful attempt, but a higher productivity of all attempts, possibly due to generally lower nest failure rates (Fig. 3). House Wren *Troglodytes aedon* and Northern Raven *Corvus corax* also produced significantly more fledglings per attempt in urban landscapes.

## Annual productivity

Paired studies multiplying the number of fledglings per successful attempt by the number of attempts per season are rare but, where reported, differences were small. The largest was in Great Tit: forest birds averaged 0.5 more attempts because a greater proportion laid second clutches (Luniak *et al.* 1992). Cowie and Hinsley (1987) found the opposite pattern: 8% of their suburban Great Tit pairs laid second clutches, but none did so in a mixed deciduous wood in the same year. In the majority of comparisons (seven of nine) annual productivity was greater in urban landscapes, although differences were often small (e.g. < 0.25 for Eurasian Magpie, Common Blackbird and Northern Cardinal; Fig. 5) and significance was not generally tested. In some cases, greater annual productivity occurred in urban landscapes despite a greater number of fledglings produced per successful attempt in non-urban landscapes (Fig. 4).

## Nestling weight

Of 11 comparisons (involving 10 species), only one species (White-winged Chough *Corcorax melanorhamphos*) showed higher (though non-significant) mean nestling weight in urban habitats (Fig. 6). Significantly higher nestling weight in non-urban habitat was reported for House Wren, American Crow, Carrion Crow *Corvus corone*, Clay-coloured Robin *Turdus grayi*, Great Tit and Common Starling.

## Meta-analysis

The mean standardized differences and confidence limits for those parameters for which data from at least five studies could be used in the meta-analysis
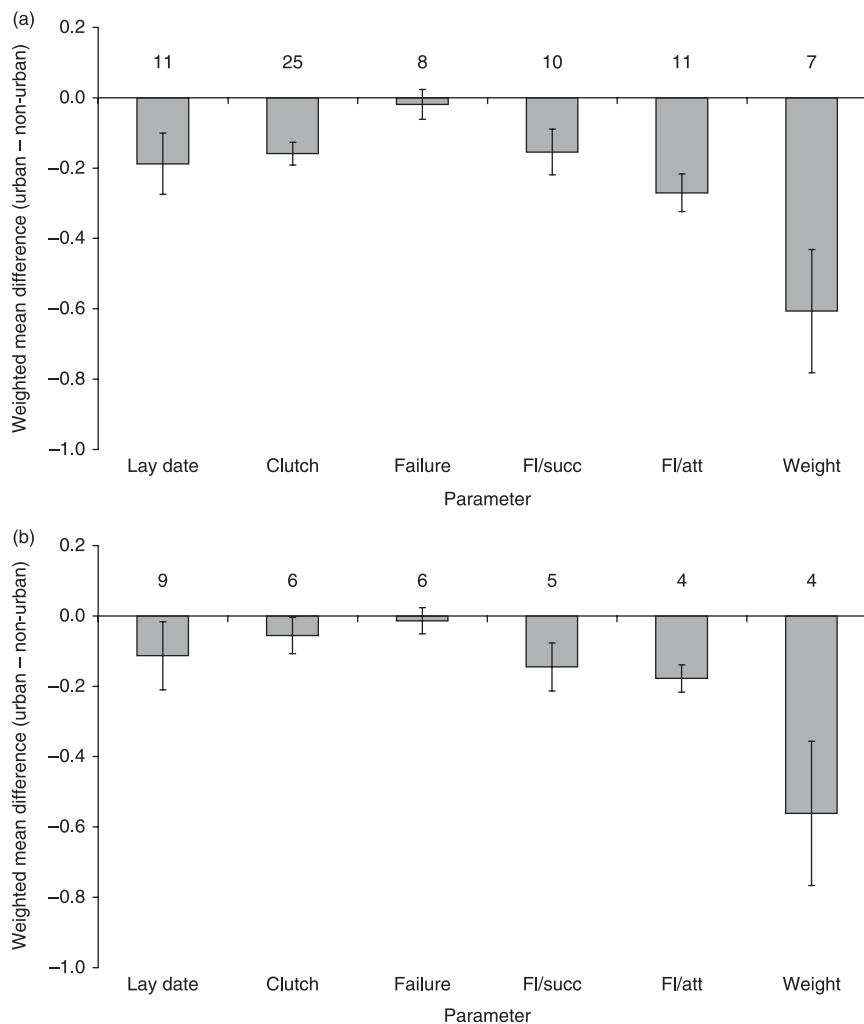
**Figure 7.** Mean standardized differences in selected parameter estimates between passerine populations in urban and non-urban landscapes determined from meta-analysis. (a) All urban /suburban landscapes. (b) Suburban landscapes only. Error bars represent 95% confidence intervals. Sample sizes (number of separate studies) are given above columns. Positive values indicate urban > non-urban. Failure = whole nest failure rates only; Fl/succ = fledgling per successful attempt; Fl/att = fledglings per attempt; weight = nestling weight.

are given in Figure 7a. Sample sizes were small, due to non-availability of means, sample sizes and variances in many studies; nonetheless, overall patterns were usefully summarized. Urban lay dates were consistently earlier but measures of productivity (clutch size, fledglings per attempt and per successful attempt) were higher in non-urban landscapes, where nestling weight was also higher. Only for nest failure rate was there no marked difference (i.e. confidence limits overlapped zero) between landscape types.

Our over-riding aim was to elucidate general patterns across broadly classified landscape pairs. However, recognizing that some studies show con-

siderable variation within urban landscapes, typically between urban and suburban areas (e.g. Earlé 1988, Marzluff *et al.* 2001b), we repeated the meta-analysis focusing on studies comparing suburban and non-urban habitats. Authors' landscape classifications were highly variable, so we imposed consistency by re-classifying study sites dominated by residential housing (not high-rise apartments) and adjacent to rural or semi-natural habitat as 'suburban'. There were insufficient habitat data to achieve this in many cases and sample sizes were reduced (< five studies in some cases). Nonetheless, the patterns observed (Fig. 7b) were very similar to those from the full analysis (Fig. 7a).

## FACTORS CAUSING THE DIFFERENCES

### Food availability

The availability of anthropogenic food is likely to have substantial effects on avian demography in urban landscapes. In Northern Europe and North America, bird feeding in private gardens is common and provides easily available energy-rich resources (Cowie & Hinsley 1988a, Brittingham & Temple 1992, Clergeau *et al*. 1997, Gaston *et al*. 2005, 2007). Additional food sources such as refuse are also likely to provide important resources for some species (e.g. Jerzak 2001, Kristan & Boarman 2007). It is questionable whether such foods are of sufficient quality to enhance reproductive performance as they are relatively rare in nestling diets and natural foods are preferred when available (Cowie & Hinsley 1988b, Mennechez & Clergeau 2001, O'Leary & Jones 2006). There is much variation in the responses of arthropods to urbanization (McIntyre 2000). Several studies, however, have reported higher starvation rates (Perrins 1965, Berressem *et al*. 1983, Cowie & Hinsley 1987, Solonen 2001, Shawkey *et al*. 2004) or lower nestling weights (Fig. 4a) in urban populations, suggesting that for many species, chick food is in poor supply and that human-provided food does not constitute an adequate substitute.

One of the clearest patterns in the review was that lay dates were advanced in urban landscapes, perhaps due to better pre-laying feeding conditions. Food supplementation experiments often advance laying dates (Boutin 1990, Robb *et al*. 2008a, 2008b) and human-provided food at bird tables, refuse and water in arid regions probably have similar effects, improving the body condition of adults. Laying may also be advanced by generally higher urban temperatures (Haggard 1990) reducing pre-breeding energy requirements, just as raised nestbox temperatures advanced laying dates in Great Tits (Dhondt & Eyckerman 1979). Relatively early laying in natural or semi-natural habitats often results in higher productivity (e.g. Perrins 1979, Perrins & Birkhead 1983), but this may not be the case in the urban landscape when earlier laying is caused by human-provided food and is not linked to subsequent natural food availability, resulting in mistiming of reproduction (Schoech & Bowman 2001).

There was a tendency for clutch size to be lower in urban landscapes. This is unlikely to be related to condition of laying females as this should be improved, if anything, by supplementary food and, furthermore, significant effects of supplementary foods on clutch size are uncommon (Boutin 1990, Robb *et al*. 2008a, 2008b). One hypothesis is that smaller urban clutches are adaptive, given relatively poor food resources for nestlings. However, Hõrak (1993) suggested that smaller urban clutches were not adaptive in Great Tits because fledging rates were still lower than in forest populations, a pattern shown by the majority of species considered here (Fig. 4a). He suggested that urban clutch size reduction was due to a constant influx of genotypes from other habitats, which may cause clutches to be larger than optimum in poor habitats and smaller in good habitats (Dhondt *et al*. 1990). Other studies of tits have found population interchange between urban and rural landscapes (Perrins & Moss 1975, Berressem *et al*. 1983), although Schmidt (1988) found no such evidence for Great Tits.

Food supplementation experiments typically result in increased population density (Källander 1981, Boutin 1990, Morneau *et al*. 1999, Robb *et al*. 2008a), and urban environments may therefore buffer the effects of severe winters. There is some evidence that increases in human-provided food over time have enhanced Common Blackbird over-winter survival rates (Batten 1978), facilitated changes in overwintering strategies, especially of short-distance migrants (Luniak & Mulsow 1988, Berthold *et al*. 1992), and contributed to population increases in certain species, especially corvids (e.g. Kavanagh 1987, Gorski 1997, Marzluff *et al*. 2001b). Despite this, adult condition may not be better in urban populations. For example, Liker *et al*. (2008) found that body size and condition of House Sparrows was lower in urban habitat, and that this difference was maintained when captive adult Sparrows from both urban and rural populations were fed identical diets. This difference could be due to poorer nestling development (due to a poorer diet), an adaptive advantage to be being smaller in urban habitats, or human-provided food leading to enhanced survival of poorer quality birds.

### Predation

Whole nest failures were caused mostly by predation in the species considered. There was no general pattern of nest failure either across species or within species. Several studies have considered predation on artificial nests in areas of differing urbanization,

but results have been similarly conflicting, with some studies finding higher predation rates in urban landscapes (Jokimäki & Huhta 2000, Thorington & Bowman 2003) and some the opposite pattern (Gering & Blair 1999) or no difference (Haskell *et al.* 2001). Whilst there are a number of problems with drawing conclusions from artificial nest experiments (Burke *et al.* 2004), the above studies suggest that the relationship between urbanization and predation may depend on the landscape context (Thorington & Bowman 2003).

It is likely that predator communities will differ between urban and non-urban landscapes and there is evidence suggesting that urban densities are higher in corvids (Richner 1989, Jerzak 2001, Antonov & Atanasova 2003), cats (Lepczyk *et al.* 2003, Gaston *et al.* 2005, Sims *et al.* 2008), avian predators (Sorace 2002) and all predators (Jokimäki & Huhta 2000, Haskell *et al.* 2001). However, predation rates may not be closely linked to predator populations, especially in urban landscapes where greater food availability may lead to lower predation pressure, as many predators are effectively 'subsidized' in terms of food, either through refuse or food deliberately provided. Therefore, it may not be the numbers of predators in urban landscapes but the frequency with which they exhibit predatory behaviour mediated by food demands that drives differences between urban and non-urban nest predation rates. It should also be acknowledged that whether there is a difference between predation rates across landscapes, and the direction of that difference, may depend on the degree to which predators have adapted to urban living, which may vary between study areas and also over time.

### Habitat structure

Vegetation structure and composition is important for birds but is so variable in urban landscapes that its overall effects across studies could not be generalized. Differences in structure often were not reflected in overall differences between urban and non-urban nest failure (e.g. Burhans & Thompson 2006) in which, as discussed above, we found no general pattern. Nonetheless, urban plant communities are often very different in structure and composition from the natural vegetation of the surrounding area (Beissinger & Osborne 1982, Smith *et al.* 2006) and such differences may affect the quality of nesting habitat, nesting behaviour and success. For example, predation pressure may influence nest-site choice

(Eden 1985, Burhans & Thompson 2006) and in some cases predation is higher in exotic than in native vegetation (Remes 2003, Borgmann & Rodewald 2004). However, Leston and Rodewald (2006) found that higher densities of urban Northern Cardinals were best explained by denser understorey vegetation (in particular exotic shrubs) than in rural forest; there was no difference in survival or productivity.

Urban habitats are often even more highly fragmented than the natural landscapes in which numerous studies have demonstrated the negative effects of fragmentation on birds (e.g. Paton 1994, Maina & Jackson 2003). Breininger (1999) suggested that isolation of suitable habitat patches was a key factor in relatively low productivity and non-breeder survival of urban Florida Scrub Jays *Aphelocoma coerulescens*. Habitat fragmentation can increase brood parasitism in forest habitats (Gates & Geysel 1978), and brood parasitism by the Brown-headed Cowbird *Molothrus ater* can be higher in urban than rural landscapes for several hosts (Burhans & Thompson 2006), including Wood Thrush *Hylocichla mustelina* (Phillips *et al.* 2005), Acadian Flycatcher *Empidonax virescens* (Rodewald & Shustack 2008) and Chipping Sparrow *Spizella passerina*. However, for American Goldfinch *Carduelis tristis*, an opposite pattern was found (Middleton 1988), and Thorington and Bowman (2003) found no edge effects on artificial nest predation in natural scrub patches within a suburban landscape.

### Other factors affecting productivity and survival

Other urban environmental factors potentially affecting passerine productivity include increased levels of disease associated with bird feeders (Brittingham & Temple 1989, Friend *et al.* 2001, Pennycot *et al.* 2002), higher parasite infestation (Gregoire *et al.* 2002), increased pollution reducing breeding output (Dmowski 1999, Eeva *et al.* 2000) and increased light levels advancing breeding (Partecke *et al.* 2004). Although many such factors may primarily affect adult survival, they may indirectly reduce productivity when deaths occur during breeding. Collisions with buildings can cause significant adult mortality in some urban areas (Klem 1990, Ogden 2002), although the impact on wider urban bird populations is unknown. Road proximity can reduce habitat quality for birds (Reijnen & Foppen 1995) and road size and average speed can increase

mortality (Clevenger *et al.* 2003). However, these studies were not specific to urban landscapes and Batten (1978) estimated that traffic was a greater cause of Common Blackbird mortality in rural than in urban landscapes, based on ringing returns, suggesting that road mortality may be related to factors other than relative urbanization, such as traffic speed.

## GENERAL DISCUSSION

Although we considered several species from a wide geographic range, and have used broad definitions of urban and non-urban landscapes in our comparisons of demographic parameters, some consistent patterns nevertheless emerged. The majority of species showed earlier lay dates, lower clutch sizes, lower nestling weights and lower fledging success in urban landscapes. Although there are many factors that may influence overall differences in demographic parameters between landscape types, we suggest the effects of food availability are paramount. Human-provided food is likely to induce earlier laying, possibly through improving the body condition of females. In terms of breeding productivity, for the majority of species human-provided food provides a poor chick diet, but these foods are often taken, presumably due to a lower availability of natural (especially invertebrate) food, which leads to consistently lower nestling weights and, for some species, higher starvation rates in urban landscapes (e.g. Cowie & Hinsley 1987, Mennechez & Clergeau 2006). It is less clear why clutch sizes are generally lower. Lower food quality, a greater proportion of young or lower quality breeders in the urban population or even an adaptive response to poorer feeding conditions may all influence this result.

Artificial food resources in urban landscapes may enhance adult survival rates, but there are very few comparative survival studies. Across the 10 located, there was little consistency in survival rate patterns (Table 1) and much variation in how survival rates were measured. It has been suggested that higher winter survival rates lead to higher urban breeding densities (e.g. Snow 1958a, Källander 1981, Eeva *et al.* 1989) for some species, partly due to more young birds in the population (Snow 1958a, Schmidt 1988, Heij & Moeliker 1990). For urban species living at high density, some of the patterns in demographic parameters could be a result of density-dependent processes. For example, greater competition for food in the breeding season could lead to lower clutch sizes and lower productivity. The extent to which these processes influence demographic differences between habitats has not, to our knowledge, been addressed in an urban context.

**Table 1.** Annual survival rates ± se (*n*) in urban and non-urban landscapes from paired studies. Errors and sample sizes (number of birds ringed) are given if reported in the source reference. †Indicates author-derived mean calculated over multiple years or sites of a given study. Difference = urban − non-urban, where * = significant, (*) significant in at least one year/site (where author derived estimates presented), ns = not significant, ‡ = not reported. Method: M = model-derived parameters that attempt to control for effects such as detection probability; R = radio-telemetry; S = a simple comparison of ringing recoveries or re-sightings

| Species | Age group | Method | Urban survival | Non-urban survival | Difference (U − non-U) | Source |
|---|---|---|---|---|---|---|
| Common Blackbird | All | S | 0.58 ± 0.01 (1373) | 0.65 ± 0.05 (5177) | −0.08‡ | Batten (1978) |
| Common Blackbird | All | S | 0.72 | 0.51 | 0.21‡ | Erz (1966) |
| Great Tit | All female | M | 0.47 (257) | 0.38 (182) | 0.09* | Hõrak & Lebreton (1998) |
| Great Tit | All male | M | 0.34 (186) | 0.26 (102) | 0.08* | Hõrak & Lebreton (1998) |
| White-winged Chough | 1st year | S | 0.60 | 0.74 | −0.14 ns | Beck & Heinsohn (2006) |
| Australian Magpie | Post-fledging¶ | S¶ | 0.80† (40) | 1.00† (18) | −0.2 (*) | Rollinson & Jones (2002) |
| American Crow | Adult | M | 0.76 ± 0.02 (591§) | 0.72 ± 0.07 (162§) | 0.04 ns | McGowan (2001) |
| American Crow | 1st year | M | 0.52 ± 0.02 (591§) | 0.35 ± 0.05 (162§) | 0.17* | McGowan (2001) |
| American Crow | 2nd year | M | 0.81 ± 0.03 (591§) | 0.73 ± 0.14 (162§) | 0.08 ns | McGowan (2001) |
| American Crow | Adult | R | 0.92† | 0.86 (29) | 0.06‡ | Marzluff *et al.* (2001b) |
| House Sparrow | Adult | S | 0.66 | 0.43 | 0.23‡ | Heij & Moeliker (1990) |
| House Sparrow | Post-fledging | S | 0.63 (138) | 0.44 (48) | 0.19‡ | Heij & Moeliker (1990) |
| House Sparrow | 1st year | S | 0.41 | 0.32 | 0.09‡ | Heij & Moeliker (1990) |
| Northern Cardinal | Female adult | M | 0.38 ± 0.12 (76§) | 0.20 ± 0.08 (76§) | 0.18 ns | Leston & Rodewald (2006) |
| Northern Cardinal | Male adult | M | 0.49 ± 0.09 (104§) | 0.53 ± 0.09 (104§) | −0.04 ns | Leston & Rodewald (2006) |

§The total number of birds rather than by age group (American Crow) or landscape (Northern Cardinal) is given in the reference.
¶Nesting attempts that fledged where at least one young was alive at the end of the summer.

It has been suggested that urban landscapes are 'ecological traps' for birds which might, for example, select nesting habitats (particularly exotic vegetation) having high predation rates (Remes 2003) or with an abundance of adult food but poor resources for chick rearing (Robb *et al.* 2008a). The latter may apply to Blue Tits and Great Tits in the UK, where they are single brooded and where urban productivity is relatively low (Perrins 1965, Cowie & Hinsley 1987), but we found little general evidence to suggest urban 'ecological trap' effects. Urban annual productivity and survival were, if anything, higher (although measured in few species, see Fig. 5 and Table 1) and predation rates were generally lower. For multi-brooded species, this suggests that more successful nesting attempts can compensate for lower productivity per nest, to produce at least equivalent annual productivity to that in non-urban landscapes. This may be due to longer urban breeding seasons; an earlier start to breeding was a common pattern, but unfortunately no studies reported breeding cessation dates.

## Defining the urban landscape

The comparisons presented in this paper have used a very broad definition of urban landscapes to incorporate the wide range of habitats represented in the available literature. This was necessary as urban habitats were often not formally defined and underlying habitat data were rarely presented. Where there was some description, it was clear that 'urban' sites varied greatly in habitat composition (e.g. amount of green space, residential housing, industrial/commercial buildings) from study to study. For some species, there are marked differences in reproductive parameters between different habitats within cities (especially urban/suburban comparisons; Earlé 1988, Marzluff *et al.* 2001b, Crick *et al.* 2002). Similarly, there was a wide range of non-urban landscapes used in the comparisons across studies. For the most part, these were broadly consistent within species (e.g. usually woodland for thrushes and tits, and farmland for corvids and sparrows), but there still may have been significant variation in non-urban habitat within species between studies. Such variation meant that the urban/non-urban comparisons were very diverse and may have masked more subtle effects. This fact makes the results all the more striking and suggests that there are some general features common to all urban habitats that have similar effects in many passerine populations.

## Sources of bias

There is an inherent species bias in this review in that those covered are relatively common in urban landscapes and must therefore be reasonably well-adapted to this environment. In particular, there were several comparative studies each for Blackbird, Blue and Great Tit, Starling, House Sparrow and corvids, all common urban species. Whilst there were generally consistent (but by no means universal) patterns for certain demographic parameters evident within these species, it should not be concluded that such patterns exist for other species that are perhaps less well-adapted to the urban environment. Furthermore, almost all studies reviewed concerned residents or short-distance migrants. In one of the few studies on long-distance migrants, Rodewald and Shustack (2008) found that apparent survival rates and nest predation rates of Acadian Flycatchers did not vary in forest fragments along an urban–rural gradient. However, overall productivity was lower as urbanization increased in the landscape due to greater brood parasitism and, in contrast to many other species, a later start to nesting. This suggests that long-distance migrants may respond differently to urban landscapes.

We have attempted to locate as much information as possible at a global level. However, at least in terms of the quantified comparisons (Figs 1–7, Table 1), there is a preponderance of studies from Europe ($n = 34$ references) compared to North America ($n = 9$), Australia ($n = 2$) and elsewhere ($n = 2$). To what extent this represents a failure to locate key references, or a genuine lack of studies outside of Europe, is unclear. A few European references already known to us did not include our search terms, so Internet searches may have missed other studies (although further informal searches found none). However, there were many American references on avian ecology in urban landscapes, although few took a comparative approach, suggesting that such studies are relatively uncommon compared to Europe. There were also a number of non-European studies that were not included as they were of non-native species (e.g. Kentish *et al.* 1995, Anderson 2006). Nevertheless, the dearth of studies from outside the developed world is almost certainly real.

Publication bias, whereby significant results are more likely to be published (Rosenthal 1979, Gates 2002), is a potential problem in any review. However, of 158 comparisons in Figures 1–6, 65 were merely descriptive (and usually older references) and did

not conduct statistical tests. General patterns across these 65 estimates resembled those across significance-tested studies, so we believe publication bias was minimal. There were two notable exceptions, fledglings per successful attempt (Fig. 4a) and nestling weight (Fig. 6), where a relatively high proportion of studies conducted significance tests and, in the latter example, where a significant difference had been found. If there is a publication bias in the results presented here, it seems that it would most probably occur in these two parameters.

## Recommendations for future research

We have examined some common assumptions of urban ornithology systematically for the first time, finding, for example, consistent support in the species considered, for widely held beliefs that urban passerines lay earlier, yet produce smaller clutches and chicks and fewer fledglings per attempt. However, we also expose a shortage of simple data that would allow the response of birds to urbanization to be tested more thoroughly. This is an important deficiency, given the prominence of suggestions about the 'plight' of urban species in public discourse on bird conservation, and the relative importance of urban birds both numerically and as the only direct, personal experience of wildlife for increasing numbers of people.

We conclude by highlighting some of the key knowledge gaps in avian demographic research in urban landscapes, and making some recommendations for future research priorities. A key general point is that the findings of this review are based mostly on studies of urban-adapted species. However, it is important both to understand the demographic responses of species that do not thrive in urban environments (Crick *et al.* 2002, Vincent 2006), and to address under what ecological conditions and for what species the general patterns found in this review are not likely to be valid. This will assist in improving the quality of urban habitats, and in mitigating for effects of increasing urbanization of (semi-)natural habitats. To achieve this will entail research on species that are less common in, and less well-adapted to, urban landscapes in all areas discussed below.

### Impacts of food availability
Robb *et al.* (2008a) and Jones and Reynolds (2008) reviewed the effects of supplementary feeding on birds and highlighted future research priorities, with particular reference to the urban environment. Although there is much information on fed and unfed semi-natural habitats and on fed urban landscapes, to understand the effects of the food 'subsidy', autecological studies in urban habitats where no food is provided are required. This review indicates that such a habitat would be suboptimal for many of the species considered (although finding such a study site, given the increasing popularity of bird feeding, may be difficult). The evidence that the abundance of invertebrate food is lower in urbanized landscapes, with a few exceptions (e.g. Vincent 2006), is largely indirect and is based on the generally lower nestling weights, higher starvation rates and lower amounts of normally preferred invertebrate foods that occur in urban populations. However, the responses of invertebrates to urbanization are clearly complex and variable (McIntyre 2000). Further research into the availability of key food groups for birds along an urban–rural gradient is therefore needed to fully understand the effects of natural and human-provided food on avian productivity within urban landscapes.

### Survival and dispersal
One of the key differences between urban and non-urban populations could be enhanced survival in urban landscapes due to human-provided food. However, it is clear that survival rates are poorly known in an urban context. Nestling weight may function as a surrogate for survival estimates (Garnett 1981, Magrath 1991), but the comparison of nestling weights as a measure of nestling quality is only valid if the functions relating weight to survival are equivalent in different landscape types. We know of no study that has attempted to analyse this; intensive mark–recapture studies (as per Magrath 1991) on paired urban and non-urban sites would serve to fill this knowledge gap. In addition, such studies may provide vital information on the rates of dispersal between urban and non-urban landscapes, and on the structure and dynamics of urban bird populations, which are largely unknown, and the degree to which they are self-sustaining. This information would also improve understanding of the relationship between adjacent urban and rural populations and the degree of differentiation – behavioural, ecological or genetic – between them.

### Urban greenspace
Urbanization may not only impact on (semi-)natural habitats, but may also cause the degradation or loss

of existing urban greenspace, for example through 'infilling' of private gardens (Pauleit *et al.* 2005, Davies *et al.* 2008). Sympathetic management of green space may be an important strategy to ameliorate the effects of urbanization on biodiversity. Avian ecology in urban parks has been relatively well-studied (e.g. Luniak 1981, Jokimäki 1999, Morneau *et al.* 1999, Chamberlain *et al.* 2007), but there are few studies from private gardens, particularly of the demographic parameters considered here, in spite of the fact that this habitat covers significant areas in many countries and is likely to hold high populations of some species (Cannon 1999). Further research into avian demography in private gardens would enable a better assessment of their value to bird populations.

### Landscape and habitat issues

This review has shown that whilst much is known about the ecology of birds in urban landscapes, surprisingly few studies have attempted to quantify differences in key demographic parameters between urban and non-urban populations. With some exceptions (e.g. Common Blackbird, Blue Tit, Great Tit, Florida Scrub Jay, Eurasian Magpie, Common Starling) there was little replication within species. Further comparative research is to be welcomed, but future studies should be more focused in terms of the habitats that are being compared. To facilitate more comparisons of urban and non-urban data in the future, we propose that published data must record the exact position of the study sites on some universally understood scale of relative urbanization. Habitat descriptions of urban and non-urban habitats in paired comparisons should also be provided. In an increasingly urbanized world (Marzluff 2001) it seems logical to target those non-urban habitats that are most likely to be developed in order to understand the wider impacts of urbanization on avian demography. A clear priority is to adopt this approach in the developing world where habitats of global biodiversity importance may be under threat of urbanization.

### Monitoring

General evidence in field data for higher annual productivity casts doubt on the common belief that urban habitat is an 'ecological trap', but this may be strongly species-dependent and we found no consistent patterns among the limited data available for nest failure or predation rates. These parameters could be elucidated by the collection of systematic nest records,

from as wide a range of species as possible, and we encourage urban bird enthusiasts to do so. We ourselves assert that urban habitats support bird populations of conservation significance, but in fact data to support this are scarce and the definition of 'urban' is fluid. It is vital that national bird censuses cover unambiguously characterized urban habitat. We look forward to increasing availability of population, density and diversity data to allow assessment of the true contribution of urban populations to bird conservation and, perhaps more important in an increasingly urbanizing world, to forecast it. We call on the urban ornithology community to collaborate and agree urgently on how the relative urbanization of a bird community should be consistently measured and documented.

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## SUPPORTING INFORMATION

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

**Appendix S1.** Mean difference (± SE for estimate derived from multiple studies) in demographic parameters between urban and non-urban populations, derived from paired studies, for individual species. *n* = number of comparisons. *Includes author-derived estimate(s) where means have been calculated over separate years/study sites within a given reference. Note in some cases, more than one comparison was used from the same study (indicated in parentheses after the relevant reference). Non-urban habitats defined as rural were typically predominantly (and sometimes exclusively) agricultural land, but in some cases, this definition also included small human settlements and semi-natural habitats (e.g. small woods, scrub patches, ponds) within the agricultural matrix. 'Woodland' indicates any wooded or forested habitat.

**Appendix S2.** Scientific names of species considered in the analysis.

**Appendix S3.** References used in Appendix S1.

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