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A country-wide examination of effects of urbanization on common birds

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Abstract

Urbanization forms one of the most drastic alterations of the environment and poses a major threat to wildlife. The human–induced modifications of the landscape may affect individual's fitness resulting in population declines. Research on how urbanization affects fitness traits has shown mixed results. However, studies typically contrasted data from a single species from few urban and non-urban sites collected over short timeframes. Examining multiple species across a broad urbanization gradient enables a more robust comparison and understanding of how different species are impacted by urbanization-knowledge crucial for generating population predictions, which are essential for conservation management. Here, we use data from a nation-wide citizen science project to examine variation in survival and relative body mass and size (wing length) of common passerine birds, collected along an urbanization gradient in the Netherlands over an 8-year period. Urbanization was measured as the distance from the city's border and the proportion of impervious surface area. Although the overall association between urbanization and survival was slightly negative, there was support for lower survival closer to the city in three species (chiffchaff *Phylloscopus collybita*, European robin *Erithacus rubecula*, European greenfinch *Chloris chloris*) and higher survival closer to the city in two (great tit *Parus major* and house sparrow *Passer domesticus*) of the 11 species examined. The contrasting survival successes among species suggest that ongoing urbanization may lead to shifts in community structure and loss of biodiversity. Impacts of urbanization on relative mass and size also exhibited varying effects, albeit less pronounced, and these effects were not correlated with the effects on survival. This implies that body mass and size cannot be used as indicators for urban-associated patterns of survival. Our results further imply that effective conservation management targeting bird communities should involve a range of diverse actions, as focusing on single measures is unlikely to simultaneously impact multiple species due to the variation in responses to urbanization.

Introduction

In Europe, the expansion of urban land use ('urban sprawl') has increased by 51% between 1990 and 2014 (Behnisch, Krüger, & Jaeger, 2022). Urbanization involves some of the most drastic alterations of the environment through loss of natural habitat (van Vliet, 2019), increased habitat fragmentation (Crooks, Suarez, & Bolger, 2004; Fischer & Lindenmayer, 2007), higher disturbance from humans (Fernandez, Lopez-Calleja, & Bozinovic, 2002), introduction of novel predator communities (Møller & Ibáñez-Álamo, 2012; Bonnington, Gaston, & Evans, 2013), increased light at night-time (Spoelstra & Visser, 2013; Aulsebrook *et al.*, 2020) and noise (Halfwerk *et al.*, 2011; Potvin, Mulder, & Parris, 2014). These anthropogenic disturbances can have large implications on biodiversity as they may change an organism's fitness, which in turn may lead to population declines. Despite these challenges, some species thrive in urbanized areas (McKinney, 2006; Isaksson, 2018), meaning that cities and towns have become important habitats by supporting a part of the world's biodiversity (Mcdonald, Kareiva, & Forman, 2008; Aronson *et al.*, 2014). Thus, the human-built environment offers a range of challenges and opportunities. With the predicted ongoing urbanization (Gao & O'Neill, 2020), it will become paramount for conservation management to comprehend the implications for wildlife populations. This understanding is crucial for identifying and implementing effective mitigation measures.

Survival is a major fitness component and understanding how survival of wildlife responds to urbanization will increase knowledge on the processes that regulate species abundance in such environments. For example, although some species may occur in cities, low survival could indicate that these populations are not self-sustained but driven by dispersal of juveniles into cities (Withey & Marzluff, 2005). Survival of birds in urban areas may be low because they suffer immediate lethal consequences from fatal collisions with buildings (Elmore *et al.*, 2021) or from feral predators, which occur at high density in urban areas (Loss, Will, & Marra, 2013; Legge *et al.*, 2017; but see Fischer *et al.*, 2012). On the other hand, 'natural' predators might avoid cities, resulting in lower predation rates (Eötvös, Magura, & Lövei, 2018). Also, higher year-round resource availability resulting from the extended plant growing seasons (Jochner *et al.*, 2013) and the availability of anthropogenic food sources may allow some species to increase their survival prospects.

A recent meta-analysis across ten studies on 15 bird species found higher survival in response to urbanization, which was suggested to be one of the most convincing intraspecific trends in life-history traits observed along the urbanization gradient (Sepp *et al.*, 2018). However, given that species do not uniformly suffer or benefit (McKinney, 2006; Isaksson, 2018), it is unclear whether such a generalization across species is meaningful. Furthermore, variation in how urbanization affects survival (e.g. Marzluff & Neatherlin, 2006; Horak & Lebreton, 2008; Evans *et al.*, 2015), may also reflect geographic variation or be the result from specific study designs. Most studies compared survival among the extreme ends of the urbanization gradient (notably urban versus rural populations but see: Evans *et al.*, 2015). However, this ignores intermediate habitats such as suburban areas that might be particularly relevant, because they typically cover significant areas and hold high populations of bird species (Cannon, 1999). So far, large-scale multi-species investigations of survival along a broad urban gradient are limited to a study from north-eastern USA, which found mixed survival responses with particularly the more generalist species benefitting from urbanization (Evans *et al.*, 2015). Whether this is a general pattern remains to be investigated.

We have even less knowledge about how urbanization alters physiological and behavioural processes that may result in variation in body mass and size of individuals. Since adult body mass reflects the degree to which an individual has fat reserves (Labocha & Hayes, 2012), mass may directly impact reproduction and survival (Verhulst *et al.*, 2004; Cresswell, 2009) and could thus reveal more details on the underlying mechanisms that regulate populations. In addition, if urbanization affects mass and survival in a similar way (or in opposite directions), the former may serve as an indicator that does not require multiple years of data collection. However, creating predictions for the response of body mass to urbanization is not straightforward. Positive associations can be expected because the high predicted food availability in urban areas will enable individuals to carry sufficient fat reserves that can serve as a buffer against potential food shortage in the future (Cresswell, 2009). On the other hand, negative associations can be predicted because fat reserves also come with costs to locomotion and metabolism (Witter & Cuthill, 1993). Thus, the highly predictable continuous input of food in urban areas could result in wildlife being less dependent on fat reserves and live on the credit of tomorrow's food ('credit card hypothesis', Shochat, 2004a).

Anthropogenic food sources may be of insufficient quality and negatively affect nutritional physiology, oxidative stress and ultimately survival, although such effects are still poorly known (Burt *et al.*, 2021; Bernat-Ponce *et al.*, 2023). Low-quality urban food may also affect development and growth, particularly during the nestling or juvenile stage (Seress *et al.*, 2020). At the same time, our cities are urban heat islands which experience higher temperatures than the surrounding areas (Merckx *et al.*, 2018). For example, temperatures in the Amsterdam region of the Netherlands were shown to be over 3°C higher compared to the surrounding countryside on moderately warm days (Koomen & Diogo, 2017). Warming temperatures have been suggested to select for smaller body sizes (Sepp *et al.*, 2018), because higher ambient temperatures increase metabolic rates and the associated costs for a given body size (Brown *et al.*, 2004). Thus, both lower food quality and urban heat island effects mean that urbanization is expected to be associated with smaller body size.

The reported associations between urbanization and body mass and size show mixed results (for review see Sepp *et al.*, 2018 and references therein). However, it should be noted that most studies are based on a single snapshot in time and compare small numbers of 'urban' and 'rural' locations. This may be problematic since a study comparing body mass and size of blackbirds (*Turdus merula*) among 11 paired 'urban' and 'rural' sites showed that the magnitude and direction of responses varied among sites (Evans *et al.*, 2009). Large-scale studies examining survival and biometry of multiple species along an urbanization gradient are thus crucial to better understand the differences in urbanization effects across species.

Here, we investigate the effects of urbanization on survival and biometry in 14 common passerine bird species (see Table S1) to determine whether there are general patterns in how fitness traits of such species respond to urbanization. Data were collected through capture-mark-recapture in citizen science projects along an urban gradient (>200 locations) in the Netherlands. This densely populated Western European country has a long history of urbanization, and the urban area now covers 16% of the country's surface, which forms an important part of the breeding habitat for many bird species (Snep *et al.*, 2016). Urbanization was measured through two metrics. Distance from the city's border serves as an indicator of infrastructure development and the degree of human population density and associated activities characteristic of urban environments. In addition, to capture fine-scale variation in land-use within urban areas (e.g. parks, buildings), we used the proportion of area covered by impervious surface (IMP). This measure reflects natural resources, because increased IMP not only reduces insect availability, but also other natural food sources, such as seeds. Structural equation modelling was used to account for the fact that larger individuals are also heavier, but do not necessarily carry more body fat. This allows us to determine the relative importance of urbanization on mass and size, while accounting for the correlation between mass and size. According to the urban heat island effect, we predict smaller size with increased urbanization. In addition, the lower dependency on fat reserves in urban areas is expected to result in lower body mass, which is predicted to be particularly pronounced for generalist species that are expected to be able to benefit from human derived food most.

Materials and methods

Data collection

Data utilized here combines data from >84,000 individuals of 14 common bird species which were encountered along the urban gradient (Table S1). Data were obtained through capture-mark-recapture from three citizen science projects carried out from 2011 to 2019 at 216 locations throughout the Netherlands (Fig. 1a). Each of the projects followed specific standardized procedures. First, the Dutch constant effort site (CES) project follows European protocols and collects capture-mark-recapture data 12 times per breeding season (13 April-13 August) for long-term monitoring of bird populations in rural areas (Robinson, Julliard, & Saracco, 2009). Second, in the '*ring*-MUS' project, a citizen science project coordinated by the Dutch Centre for Avian Migration and Demography with support from BirdLife Netherlands, capture-mark-recapture data were collected at least twice a month at private residences within the urban and suburban matrix, providing the data in built-up areas which are not normally collected in the CES project. Third, for some species (common starling (*Sturnus vulgaris*), house sparrow, common blackbird (*Turdus merula*), European greenfinch, great tit and blue tit (*Cyanistes caeruleus*)), additional data were available through species specific projects (RAS projects: Re-trapping Adults for Survival). In such projects, the focus was on capturing all individuals of a single species in a given area, from varying habitat types along the urban gradient. In addition to mist netting, catching techniques involved walk-in traps, clap traps and catching birds in nest boxes. To reduce bias with respect to differences in timing of data collection among the projects, the same recapture period was selected from each of the three projects (i.e. the CES period: 13 April-13 August), thereby also specifically focussing on resident birds on their breeding grounds.

All birds were banded with uniquely numbered alloy split bands, allowing for individual identification when recaptured at a later occasion. In addition, in both *ring*-MUS and RAS projects some species (house sparrow, common blackbird, common starling, European greenfinch and great tit) were colour banded, allowing for identification of individual birds through resightings. Data were collected by licensed volunteers, who received training in handling, banding and processing birds using standardized methods. Captured birds were aged and sexed based on plumage characteristics where possible, and when time allowed morphometric measurements were taken, including body mass to the nearest 0.1 g with

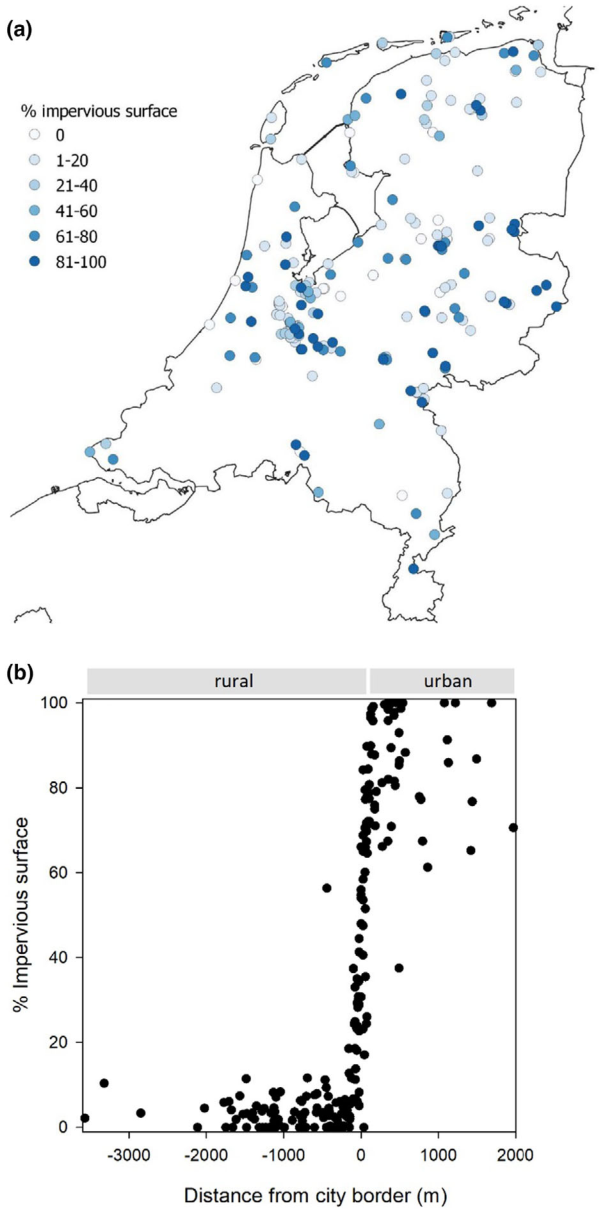

Figure 1 (a) Map showing capture locations with different colours indicating the degree of urbanization measured as the percentage impervious surface. (b) The association between percentage impervious surface and distance from the city border (with negative values indicating rural and positive urban areas) for each of the 216 capture locations.

an electronic balance and wing length (maximum flattened chord length) to the nearest 0.5 mm using a butt-ended ruler.

Degree of urbanization

For each of the 216 capture/resighting locations the percentage impervious surface (IMP) within a 200 m radius (size area = 12.6 ha) and the distance from the city border (with negative values indicating rural and positive urban areas) were calculated using software ArcGIS (Environmental Systems Research Institute, 2011). Land use maps obtained from Statistics Netherlands (https://www.pdok.nl/introductie/-/article/cbs-bestand-bodemgebruik, version 2015) were used to select infrastructure, residential areas (including gardens, of which most of their surface is paved (Stobbelaar, van der Knaap, & Spijker, 2021)), retail areas and industrial areas to calculate IMP and delineate city borders. Calculating IMP for a 100 m and 300 m radius shows effectively the same estimates compared to the 200 m radius ($r = 0.97$ and $r = 0.98$ respectively). Distance from the city border was highly correlated with IMP ($r = 0.69$), nevertheless there was still considerable variation in IMP within urban areas (Fig. 1b). Non-urban areas with less than 30% IMP consisted on average for 59% of agricultural land, 11% woodland and 14% of nature reserves (Fig. S1). The majority of the captures from CES projects had low levels of urbanization (Fig. S2, range IMP: 0–40%), whereas captures from RAS and *ring*-MUS projects were from more urbanized areas (Fig. S2, range IMP: 0–100%).

Survival analyses

To estimate whether apparent annual adult survival between breeding seasons is associated with urbanization, we adopted a live-recapture model approach in RMark (Laake, 2013). Encounter histories were created for each banded individual, with a ‘1’ if the bird was captured or resighted any time within a breeding season and a ‘0’ otherwise. We constructed *a priori* live-recapture models for each species separately to account for variation in survival and recapture/resighting rates among projects and groups of individuals (e.g. ring type). This was done as follows: recapture rates were allowed to vary among projects (CES, *ring*-MUS, RAS), ring type (colour or metal only), age class (first year versus older individuals), age at first capture (ring-age) and their interactions; survival was allowed to vary among age classes (first year versus older individuals), although we only examined effects of urbanization on adult survival, since the dispersive nature of juveniles means that their survival is a lot harder to estimate accurately. To avoid over-parametrization, we did not fit full time-dependent models. Models were further simplified where possible (i.e. not all species were colour banded or part of the RAS project) to derive a baseline (null) model which could be used as a starting point for our analyses (see Table S1 for details). We then tested whether adult survival was associated with urbanization by including the distance from the city border and IMP as covariates for the adult survival parameter. In addition, to investigate any non-linear association between adult survival and urbanization, models including the quadratic term of these covariates were also run (after a positive transformation on distance). The urbanization covariates were scaled to z-scores to facilitate model convergence.

Previous work has indicated the presence of resident and non-resident (i.e. transient) individuals in the dataset (Johnston *et al*., 2016). Such transients have a low probability of being reencountered, violating the capture-recapture assumption that all individuals have equal recapture probabilities (Lebreton *et al*., 1992). To account for transients, an extra time step after the first occasion was added to the capture history (Johnston *et al*., 2016). Individuals that have been captured more than once during the first capture season are assumed to be residents. For these individuals, a ‘1’ is inserted into the capture history after the first occasion. Birds that have been captured only once can either be a resident or a transient individual. For these individuals, a ‘0’ is inserted into the capture history after the first occasion. Using this approach allows for the separate estimation of a ‘transience probability’ with the estimated ‘Phi’ being the probability of a bird being a resident, while the estimated recapture gives the probability that a resident bird is identified as such (Johnston *et al*., 2016). Effectively, this means individuals that have only been caught once do not contribute to the estimation of the survival probability (Pradel *et al*., 1997). Unfortunately, using this method does not allow for goodness-of-fit testing.

Low recapture rates and/or ringing effort resulted in non-identifiable parameters in survival models for song thrush (*Turdus philomelos*), common chaffinch (*Fringilla coelebs*) and great spotted woodpecker (*Dendrocopos major*) and therefore only effects on biometry were considered for these species. For the remaining 11 species ringing effort varied between 2300 and 14,582 individuals per species (Table S1). The recapture/resighting rate was on average 0.45 ± 0.04 SE (range 0.05–0.74).

Model selection was based on Akaike’s Information Criterion corrected for sample size (AICc; Akaike, 1973), with lower AICc values being considered as better supported by the data. In addition, we report normalized Akaike weights to assess the relative support for competing models (Burnham & Anderson, 2002).

Biometry analyses

Since we aimed to investigate how both adult body mass and size vary with urbanization, but mass is also affected by size, we constructed structural equation models using R package piecewiseSEM (Lefcheck, 2016). These models allow for the evaluation of causal linkages among variables in a single multivariate framework. Wing length was used as an indication of size, whereby both body mass and wing length were fitted using a Gaussian distribution, with either distance from the city border or IMP as predictors (either linearly or quadratic). To account for the fact that larger individuals are also heavier, wing length was included as a linear predictor for body mass too (see Fig. S3 for path diagram), thereby effectively analysing relative body mass. We also accounted for potential confounding variables by including project (CES or *ring*-MUS/RAS) and sex as fixed factors, and Julian day as a covariate in the body mass and wing length equations. In addition, to account for variation in mass during the day, time of weighing since sunrise was calculated using package StreamMetabolism (Sefick Jr., 2016). All variables were scaled to z-scores before including them in the model. Individual identity, year and identity of the capture location were included as random intercepts to account for non-independence of the data. For great spotted woodpecker, common blackbird, common starling and Eurasian wren (*Troglodytes troglodytes*), the random intercept for year led to convergence issues and was therefore omitted from the model. Limited data on biometry measurements meant that effects on mass and size could not be examined for European robins. We evaluated the models based on the global goodness of fit of the null model (without urbanization predictors), which showed that the models fitted the data well (Fisher's C test, all $P > 0.07$). The importance of the urbanization predictors for explaining variation in relative mass and size was based on their estimated effect sizes and 95% CI's combined with the marginal (proportion of total variance explained by the fixed effects) and conditional (proportion of total variance explained by both fixed and random effects) R^2 (Nakagawa, Johnson, & Schielzeth, 2017).

Results

Survival

The survival models showed that after accounting for variation in recapture rates (e.g. among the different projects), there is a lot of variation in both magnitude and direction of the effects of urbanization on apparent adult survival between breeding seasons (Fig. 2a). There was little evidence for a general pattern with respect to effects of urbanization on survival across species: despite the overall weighed mean effect size between survival and urbanization being negative, the 95% CI's overlapped zero (Fig. 2a). Model selection results showed that at least one of the two urbanization parameters used as a predictor for variation in survival was strongly supported by the data in five of the 11 examined species (Table S2). Three species (chiffchaff, European robin, European greenfinch) showed reduced survival closer to the city centre (Fig. 2a) and this reduction was substantial, with respectively ~50%, ~25% and ~ 13% lower survival for greenfinches, robins and chiffchaffs living in city centres compared to those living 3.5 km from cities (Fig. S4). Although the estimated effect sizes for common starlings suggested a strong reduction in survival with increased urbanization, the CI's were large (Fig. 2a) and models including quadratic effects did not converge (Table S2), indicating the data were too limited to draw any conclusions. In two species (great tits and house sparrows) there was evidence that survival was higher closer to the city centre (Fig. 2a; Table S2, ΔAICc >6.3). Here too, the change in survival associated with urbanization was substantial, with an increase of 19% in great tits and 12% in house sparrows living in city centres compared to those living 3.5 km away from cities (Fig. S4). In general, both the distance from the city and IMP showed similar patterns, except for house sparrows and greenfinches (Fig. 2a and Fig. S4). House sparrows had higher survival closer to the city centre, yet higher IMP was associated with lower survival (Fig. 2a and Fig. S4). Survival of greenfinches showed the opposite pattern with survival decreasing closer to the city centre, but increasing with higher IMP (Fig. 2a and Fig. S4), although the latter association was much weaker and did not receive model support (Table S2, ΔAICc = +1.7). Finally, modelling the urbanization predictors as quadratic effects on survival improved the model fit for several species, although this did not provide evidence for peak survival at intermediate levels of urbanization (Table S2; Fig. S4). Rather, the positive association between survival and distance to the city did not improve further once reaching the city border in great tits (ΔAICc = 18.2; Fig. S4) and to some extent also in blue tits (ΔAICc = 0.9; Fig. S4), whereas the negative association between IMP and survival was particularly apparent at high IMP for house sparrows (ΔAICc = 2.7; Fig. S4) and to some extent in blackcaps (*Sylvia atricapilla*, ΔAICc = 1.7; Fig. S4).

Relative body mass

Results on the structural equation models showed that in contrast to our prediction that urbanization has a negative effect on relative body mass, there was little evidence for such a general pattern: the average effect sizes of both urbanization predictors were only slightly negative with 95% CI's that overlap zero (Fig. 2b). Interestingly, house sparrows were the only species where increased urbanization (both distance and IMP) was significantly associated with lower relative body mass (Fig. 2b; Table S3). In contrast, greenfinches and great spotted woodpeckers had significantly higher relative body mass with higher levels of IMP (Fig. 2b; Table S3). Although a large proportion of the conditional (through random and fixed effects) variance in relative body mass was accounted for in the models (26–89%, Table S3), the amount of marginal variance in relative body mass that could be attributed to effects of urbanization was low at 3% in great spotted woodpeckers, 2% in house sparrows and only <1% in greenfinches.

Body size

The results on the structural equation models for body size (wing length) showed that in contrast to our prediction there was little support for an overall negative effect of urbanization on body size (Fig. 2c). Most effects were weak, and the majority of CI's overlapped zero with only the effects of IMP for house sparrows and common chaffinch being significantly different from zero (Fig. 2c; Table S3). Similarly to the effects on mass, a large proportion of the conditional variance in body size was accounted for in the models

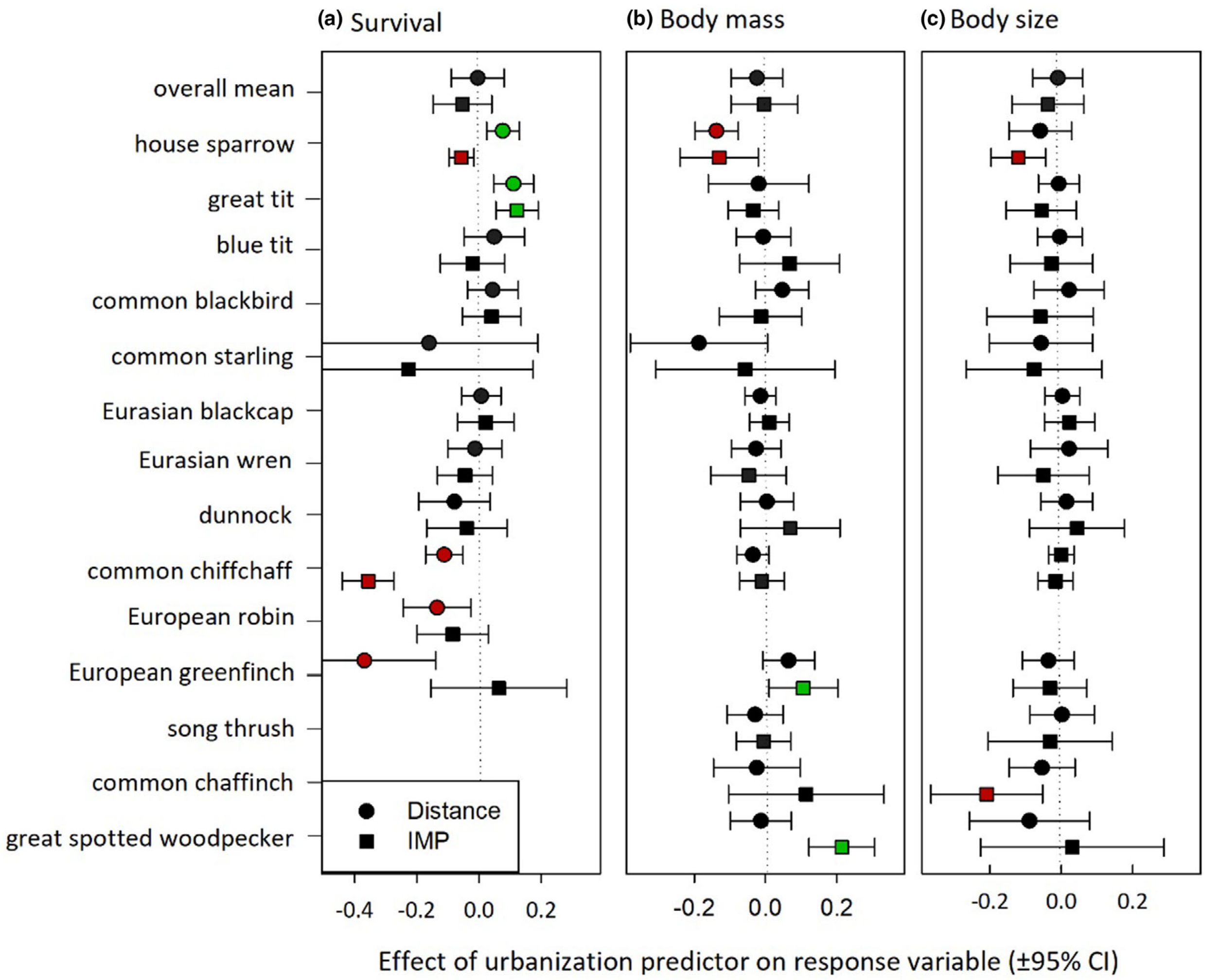

Figure 2 Standardized effects sizes (±95% CI) of the distance from the city border (distance) and the percentage of impervious surface (IMP) on (a) apparent annual adult survival, (b) body mass and (c) body size (wing length). Positive effects are shown in green whereas negative effects are shown in red. Effect sizes for survival are on logit scale. Note that urbanization effects on survival could not be estimated for song thrush, common chaffinch and great spotted woodpecker and urbanization effects on body mass and size could not be estimated for European robins.

(74–93%, Table S3), but the amount of marginal variance in body size explained through urbanization was very low at 1% in house sparrows and <1% in common chaffinches. Finally, there was no evidence that effects of urbanization on mass and size were mediated or traded-off against survival, as there was no significant correlation between effect sizes of survival and mass or size ($r < 0.25$, $P > 0.48$, df = 8; Fig. 2).

Discussion

Urbanization currently forms the most drastic change to the environment and since the expansion of urban land use is predicted to accelerate even further it will be crucial for conservation management to understand the consequences this has on wildlife populations. However, it is unclear how general such effects are given the largely mixed evidence from studies mostly focussing on single species, from few sites, over short timeframes. We addressed these issues by investigating effects of urbanization on survival and biometry in common bird species collected over an 8-year period in a nationwide capture-mark-recapture study. We found evidence for lower survival with increased urbanization in three species, higher survival in one species and contrasting effects depending on the urbanization metric in another one of the 11 species examined. Across all 11 species the association between urbanization and survival was slightly negative, although the 95% CI overlapped zero. These results contrast with a recent meta-analysis, which found a positive association between survival and urbanization across avian species (Sepp *et al.*, 2018). Effects of urbanization on relative mass or size were detected in four of 13 species examined, but these also varied among species and their effects were very weak. Our results show that studying effect of urbanization in multiple species simultaneously shows large heterogeneity in responses, which may not be surprising given the immense variation in ability to cope with urbanization (Isaksson, 2018). However, this suggests that large-scale generalizations may not actually be meaningful.

Effects of urbanization on survival

It has been argued (Shochat et al., 2004; Evans *et al.*, 2015) that lower survival due to urbanization mainly results from top-down processes like higher rates of predation (Bonnington, Gaston, & Evans, 2013; but see Fischer *et al.*, 2012) or collisions with manmade objects (Loss *et al.*, 2019), whereas higher survival results from bottom-up processes like higher resource availability (Shochat et al., 2004). This suggests that for the chiffchaff, European robin and European greenfinch – each experiencing survival costs in urban areas – top-down processes play a relatively more important role. One such process, predation by cats, has been identified as a leading cause of mortality in recovered specimens from ringing programs in France and Belgium, especially among species with ground-dwelling habits (Pavisse, Vangeluwe, & Clergeau, 2019). Whilst this can account for our findings of high mortality of robins and greenfinches in urban areas, other typical ground-dwellers in our dataset like common blackbirds, dunnocks and house sparrows did not conform this pattern. Another major source of avian mortality in urban areas is bird-building collision (Loss *et al.*, 2014; Pavisse, Vangeluwe, & Clergeau, 2019). Although building-collision has been shown to affect species during migration most (Loss *et al.*, 2014; Wittig *et al.*, 2017), local foliage gleaning species are also susceptible (Wittig *et al.*, 2017). While such species are represented in our dataset too (great tit, blue tit, Eurasian blackcap, common chiffchaff), and building-collisions likely contribute to mortality, we cannot directly link it to patterns in our results.

Higher survival in urban areas was detected in house sparrows and great tits, suggesting that bottom-up processes are relatively more important for these species compared to top-down processes. Both these species are considered generalists, whereas two of the three species showing reduced survival, the chiffchaff and European robin, are insectivorous. Urban environments are characterized by reduced abundance and diversity of invertebrates (Turrini & Knop, 2015), suggesting that food specialization could play an important role in the success of urban species. However, generalists also show flexibility in other aspects of their biology, like nesting behaviour, allowing them to take advantage of urban structures. Our findings thus seem to corroborate the results from a multi-species study from the north-eastern USA, where particularly generalist species had higher survival with increased urbanization (Evans *et al.*, 2015). Yet, given the heterogeneity in survival responses, care should be taken with predictions based on species' degree of specialism only. For example, the common starling is also typically considered a generalist species, but we found that its survival decreased with increased urbanization (although non-significantly so). Furthermore, even closely related species can vary in their response to urbanization: whereas great tits had higher survival in areas with higher IMP, such a pattern was not detected for blue tits.

Although the results between the different urbanization metrics largely corresponded, there are two notable exceptions. These could further shed light on the underlying mechanisms playing a role in differences in responses to urbanization. First, house sparrows benefitted from living closer to and within cities, but surprisingly had lower survival in areas with more impervious surface, particularly at very high levels of IMP. House sparrows are opportunistic eaters that may benefit from human derived food in cities. Yet, they may suffer survival costs due to reduced invertebrate prey in areas with high impervious surface, because insects still form an important part of their diet, both in urban and rural environments (Gavett & Wakeley, 1986). Also, nestling house sparrows are dependent on insects, and in areas with low insect availability, adults might have to work harder to provision the young, resulting in higher mortality. Furthermore, reduced vegetated areas not only reduce insect availability but also other natural food sources, such as seeds. Birds in such areas may thus be more reliant on human derived food which may not cover the nutritional requirements (Shochat et al., 2004, Burt *et al.*, 2021) and may negatively affect their physiology (Bernat-Ponce *et al.*, 2023).

The second contrasting result between the urbanization metrics was detected in the European greenfinch, which exhibited notably low survival rates in urban areas, but not in areas with high IMP. The extremely low survival of greenfinches in urban areas could likely largely be attributed to the prevalence of the highly infectious and fatal finch Trichomonosis disease caused by the parasite *Trichomonas gallinae*. This disease has already had a significant impact on the British greenfinch population (Lawson *et al.*, 2012; Rijks *et al.*, 2019). The spread of Trichomonosis is probably facilitated by increased intra-specific interactions at feeding stations in gardens (Lawson *et al.*, 2018). High resource availability through bird feeding may thus also negatively affect survival, although the precise role of urban bird feeding in disease systems is not yet well understood (Adelman *et al.*, 2015; Galbraith *et al.*, 2017; Reynolds *et al.*, 2017). The absence of reduced survival in areas with high IMP seems surprising, but could potentially be explained because such areas are less likely to have domestic housing and hence fewer feeders. It is also possible that birds in such areas have reduced movement and interaction with each other. Indeed, a tracking study of feeder-using great and blue tits in urban areas found that decreased vegetation cover reduced connectivity between feeders (Cox *et al.*, 2016). Paradoxically, high IMP might therefore limit the spread of this disease and thereby potentially reduce its negative impact on the survival of greenfinches.

The absence of a survival response to urbanization in many species could potentially be due to non-urban habitats for a large part consisting of intensively managed agricultural land (Fig. S1), which might even be of less value for birds compared to urban areas. For example, a study from

Switzerland showed that intensively managed agricultural ecosystems had even lower abundance of several indicator invertebrates compared to urban ecosystems (Turrini & Knop, 2015). This also emphasizes the importance of urban areas for biodiversity conservation, a topic that remains debated (Shwartz *et al*., 2014; Ives *et al*., 2016). Our results support this idea to some extent, in that significant negative associations with urbanization were absent for the majority of species.

Effects of urbanization on mass and size

Effects of urbanization on relative mass was generally weak, but nonetheless showed a few statistically significant patterns. For example, despite their higher survival, house sparrows had lower relative body mass closer to the city. This may suggest that they can afford to carry less reserves (Shochat, 2004a), an idea that is supported by recent experimental work which showed that supplementary fed urban birds had lower body condition than non-supplementary fed individuals (Demeyrier *et al*., 2017).

Another prediction from this 'credit-card hypothesis' is that the high food availability leads to a high proportion of weak competitors in urban environments. Although evidence for this is ambiguous (Shochat, 2004a; Bókony, Kulcsár, & Liker, 2010), our findings that house sparrow survival is actually higher in urban areas does support this idea. In contrast to house sparrows, woodpeckers' and greenfinches' relative body mass increased closer to city centres. This may suggest that these species benefit from the food available in urban areas and do accumulate body reserves. Alternatively, the high mortality of greenfinches in urban areas may result in selective disappearance of individuals with lower relative body mass (Nussey *et al*., 2011).

Our study provided little evidence for consistent reductions in body size with increased urbanization, which was only found in house sparrows and chaffinches. Size reductions could be expected based on the lower food quality or from increased temperatures favouring smaller body size (Gardner *et al*., 2018, 2019). In nearby Belgium, urban-heat-island effects have been shown to drive invertebrate diversity towards smaller species (Merckx *et al*., 2018). However, that study also showed that filtering for smaller species can be over-ruled by filtering for larger species when there is positive covariation between size and dispersal. A similar process could occur within species. Individuals with longer wing length are capable of longer flights (Pennycuick, 2008), facilitating movement through fragmented urban areas (Neate-Clegg *et al*., 2023). This process may counteract selection for smaller individuals arising from urban heat-islands, potentially explaining the lack of an urbanization-size association in many of the species we studied.

Conservation measures

To some extent our results align with the consensus that generalists, as opposed to specialists, can thrive in the city (Møller, 2009; Marzluff, 2017; Isaksson, 2018). These findings suggest that conservation actions should prioritize survival of insectivorous species in urban areas. Since both invertebrate abundance and diversity decrease with diminishing vegetated areas in cities (Turrini & Knop, 2015), increasing green space like parks and the conversion of paved gardens to more natural habitat could be fruitful conservation strategies. More natural resources associated with increasing green spaces could also benefit generalists like the house sparrow, one of the best-known urban dwellers, which has gone through a 50% population reduction in western Europe since the 1980s (Burns *et al*., 2021).

Some top-down processes that likely affect bird survival in cities could be relatively straightforward to remediate. Pet cats for example are estimated to kill millions of birds a year (Woods, McDonald, & Harris, 2003; Legge *et al*., 2020), but collar-worn predation deterrents or cat-containment measures are a relatively easy and cost-effective to implement (for review see: Legge *et al*., 2020). Reducing glass areas, treating existing glass and reducing light emission at night can help to reduce avian building-collisions (Loss *et al*., 2019). Considering the diverse range of responses to urbanization, employing a mix of management strategies is probably the most efficient approach.

Limitations of study

A limitation of our study is that data from different projects had to be combined to be able to determine the effects of urbanization across the complete urbanization gradient. However, we aimed to minimize any bias by including project specific recapture probabilities and accounting for confounding effects like time of capture (for analyses on biometry). We also ensured data were collected during the same season and years. By using this approach, we were able to examine changes in survival and biometry across the urbanization gradient, rather than the typical approach of comparing 'urban' with 'rural' sites (e.g. see references within Sepp *et al*., 2018).

Capture-mark-recapture studies in open populations typically suffer from the problem that patterns in survival may be confounded with patterns in dispersal, because individuals permanently emigrating from the capture sites will be assumed dead. Movement of breeding adults (i.e. breeding dispersal) remains one of the least understood processes driving population dynamics (Greenwood & Harvey, 1982), not least because of the difficulties in studying such behaviour. In our study we attempted to reduce bias in survival estimates due to dispersal by focussing on adult survival only (i.e. avoiding the natal dispersal phase); only using recaptures from the breeding season (i.e. from residents on their breeding grounds) and by accounting for transients (i.e. excluding individuals that were caught only once from contributing to the survival estimate) (Pradel *et al*., 1997; Johnston *et al*., 2016). Despite these measures, we cannot exclude the possibility that the observed survival patterns are driven by differences in breeding dispersal. As far as we are aware, only a single study examined such patterns, which found no evidence for differences in breeding dispersal of six songbird species among urban and natural landscapes in Washington, USA (Marzluff *et al*., 2016). The further development of tracking techniques will enable large-scale studies on how patterns of dispersal vary along the urban gradient.

Conclusion

Using data of 14 species collected over 8 years in >200 locations along a gradient of urbanization throughout the Netherlands showed a lot of variation in species' responses. Effects of urbanization on body mass and size were very weak and showed that mass and size cannot be used as reliable quick indicators of species' survival response to urbanization. Our findings tend to support the idea that generalists manage to benefit from urbanization, whereas more specialist species suffered from reduced survival. Given that avian reproductive success is generally lower in urban areas (even for generalists; Chamberlain *et al*., 2009; Sepp *et al*., 2018; Seress *et al*., 2020), the increased survival likely plays an important role in the success of these species in cities. Eventually, this is expected to lead to shifts in community composition through time and space and cause loss of biodiversity with ongoing urbanization. Still, the heterogeneity in responses means that care should be taken when predicting the effects of ongoing urbanization on communities, because even closely related species can show different responses. This means that conservation management actions targeting bird communities might be effective for some, but not all species, and a combination of management actions is likely most effective.

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Author contributions

LB conceived the idea for the study, designed the methodology, analysed the biometry data and wrote the paper, EHJdV performed the mark-recapture analyses, HS calculated the urbanization indices, HPvdJ designed the *ring*-MUS project and managed all data collection. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data and Rcode available at Zenodo: DOI 10.5281/zenodo11100738.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Boxplots showing the percentage land use that is (a) farmland, (b) woodland and (c) nature reserve shown for varying percentages of impervious surface of the 216 capture locations.

Fig. S2. The number of birds ringed in each of the projects with the percentage of impervious surface of their capture location for the dataset used for (a) survival and (b) analyses on mass and size. Note differences in the datasets due to data availability (e.g. missing data or too low recapture rates to include in CMR analyses).

Fig. S3. Path diagram showing the pathways in the structural equation model examining the effects of urbanization on body mass and size, while accounting for the effect of size on mass.

Fig. S4. Predicted survival probabilities (±95% CI) in relation to distance to the city border and percentage impervious surface for 11 bird species from the Netherlands. Estimates were derived from the models in Table S1 and include the linear effect of the urbanization predictors, except for great tit and blue tit (distance) and house sparrow and blackcap (IMP), where the results of the quadratic effects are shown (which received the strongest support: Table S2).

Table S1. Summary of number of individuals ringed in each of the projects, and description of the null models used for parametrization of the survival and recapture parameters for each of the species used in the analyses.

Table S2. Summary of model selection statistics examining the effects of distance from the city border and percentage impervious surface (IMP) on apparent annual adult survival of 11 avian species. Models are ranked according to their ΔAICc.

Table S3. Results from structural equation modelling showing effects sizes (±SE) for the effects of distance to the city edge and percentage impervious surface on body weight and wing length of 13 bird species. R^2 is the conditional value obtained from the null model (without the urbanization predictors).