Biological Conservation 244 (2020) 108423

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Effects of urbanization on bird migration

Anne-Sophie Bonnet-Lebrun[a,b,*], Andrea Manica[a], Ana S.L. Rodrigues[b]

[a] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[b] CEFE, UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, 34293 Montpellier, France

ARTICLE INFO

Keywords:
Anthropogenic effects
Human population
Partial migration
North American passerines
Residency

ABSTRACT

Nearly one in five bird species is migratory, but not all individuals within a migratory species necessarily migrate: in partially migratory species, some do and some do not. Such within-species variability provides a natural experiment for investigating the mechanisms driving bird migration. Previous studies at the species level suggest that migrating provides a way to escape harsh winters, and to secure an increased access to resources, particularly important during the breeding season. Urbanization, by altering local temperatures ('heat island' effect) and resource availability (e.g. through garbage or garden feeders) can buffer the effects of winter harshness and modify breeding-season resource availability, potentially affecting individual migratory strategies. Here, we use ringing data from twelve North American partially migratory bird species to investigate the effects of natural environmental conditions (winter temperature, breeding season resource surplus) and urbanization on the propensity of individuals to migrate. We find strong support for the hypothesis that individuals migrate to avoid harsh winters, with, for eleven species, significantly higher probabilities of residency in areas with milder winters. We also found (significant for five species) that resource surplus in the breeding season reduces the propensity to migrate. Finally, urbanization increased the likelihood that individuals remain year-round in their ranges, avoiding to migrate away from their breeding range (four species) or their wintering areas (eight species), after controlling for climate and resources. Our results thus indicate that bird migratory strategies will respond to global change – in climate and land use – and indeed are already doing so.

1. Introduction

Nearly one in five of the world's 10,000 bird species migrate seasonally between breeding and non-breeding ranges (Kirby et al., 2008), a global-scale ecological readjustment (Moreau, 1952) that radically changes the composition and diversity of bird communities across wide areas of the planet (Somveille et al., 2013). In practice, though, the migratory movements are not of species but of individuals. Furthermore, it is not a fixed species trait: in many species, some individuals migrate while others remain in the same region as year-round residents. This includes variation among populations – whereby some populations are resident and some migratory – but also within populations – in which only a fraction of the individuals found in a given region migrate. The term 'partial migration' is often applied to the latter (Chapman et al., 2011), but here we use it more broadly to refer to within-species variation in migratory-versus-resident behaviour.

Partial migration is widespread among animal taxa (e.g. ungulates, Hebblewhite and Merrill, 2011; fish, Chapman et al., 2012; insects, Dällenbach et al., 2018) and very common in bird species. For example, in a review of Australian land birds, Chan (2001) found that among 155 non-passerine and 317 passerine species studied, respectively 44% of and 32% are partial migrants. Partially migratory species provide opportunities for testing hypotheses on the ecological and evolutionary processes underpinning migration itself, by allowing for multiple replicates (i.e., the individuals) while controlling for the wider variation in ecological traits (e.g. trophic level, body size, habitat preferences) observed across species (see Chapman et al., 2011 for a review). Furthermore, given that individuals and populations can react faster to environmental changes than entire species, monitoring the responses of partially migratory species to anthropogenic activities can provide early insights into how species respond to global change (Pulido and Berthold, 2010; Podhrázský et al., 2017).

Conceptually, an individual bird in any given (breeding or non-breeding) location, can either remain in that same location as a resident, or move elsewhere for the following season. Recent studies at the species' level suggest that migration is largely driven by energetic trade-offs, with species migrating when the benefits derived from spending parts of the year in different areas exceed the costs of migration between them (Hurlbert and Haskell, 2003; Dalby et al., 2014; Somveille et al., 2015, 2018a, 2018b). More specifically, these studies

---

[*] Corresponding author at: British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.
E-mail address: anne-sophie.bonnet-lebrun@normale.fr (A.-S. Bonnet-Lebrun).

https://doi.org/10.1016/j.biocon.2020.108423
Received 23 October 2019; Received in revised form 10 January 2020; Accepted 18 January 2020

suggest that the main driver of migration out of the breeding range is winter harshness, either because of the thermoregulation costs of low temperatures, or because of a reduction in resources during winter, or both (Herrera, 1978; Lemoine and Böhning-Gaese, 2003; Carnicer and Diaz-Delgado, 2008; Schaefer et al., 2008; Somveille et al., 2015). At the individual level, this should translate into a higher probability of individuals to migrate out of their breeding locations if these locations face harsh winters, and conversely into a higher probability of remaining as resident in locations with mild winters. Accordingly, progressively milder winters linked to climate change have been proposed as a reason for increased rates at which some migratory species are being observed year-round in their breeding areas (e.g. Great Crested Grebes *Podiceps cristatus* in the Netherlands, Adriaensen et al., 1993; Blackbirds *Turdus merula* in Europe, Berthold, 1993; Main, 2000), likely reflecting an increase in the fraction of sedentary individuals in partially migratory populations (e.g. as observed for blackbirds in the Netherlands, Vliet et al. (2009); and Denmark, Kristensen and Thorup (2011)). A relationship between winter harshness and migratory propensity can also explain observations that some previously non-migratory species whose ranges recently expanded into higher latitudes have become migratory there (e.g., European Serins *Serinus serinus* spreading into northern Europe, Berthold (1999); House Finch *Carpodacus mexicanus* in eastern North America, Able and Belthoff (1998)).

The main drive to leave the wintering grounds, on the other hand, seems to be to obtain better access to resources during the breeding season. Indeed, previous studies at the species' level found that the resources available during the breeding season – or, more precisely, the surplus in relation to the resources in the non-breeding season – was the main predictor of the number of breeding migratory birds found in any given region, a pattern explained in terms of reduced competition with resident birds (Dalby et al., 2014; Somveille et al., 2015). At the individual level, one thus expects that the individuals wintering in areas with high levels of resource surplus in the breeding season have a higher probability of remaining as residents.

Given that anthropogenic activities are affecting both the climate (IPCC, 2014) and the distribution of natural resources (Haberl et al., 2014), it is not surprising that there is mounting evidence of human effects on bird migration (Visser et al., 2009; Plummer et al., 2015; Greig et al., 2017). One such major effect is by altering land cover, with urbanization in particular creating habitats that are in many ways radically distinct from natural ones. The resulting changes to local environmental conditions may plausibly affect the migratory decisions of urban birds. First, urban areas are often 'heat islands', multiple degrees warmer than surrounding areas (Collier, 2006), which may buffer birds against harsh winter temperatures (Shochat et al., 2006) and thus increase their probability of remaining over winter. Second, urban areas can provide particular resources, for example through bird feeders, garbage, and garden flowers and fruits (e.g. Robb et al., 2008a; Greig et al., 2017). These may either buffer populations against the low resources of winter, and thus increase the probability of breeding birds remaining over winter, or provide resources in the breeding season that increase the odds that wintering birds remain to breed. Overall, urbanization is thus expected to increase the propensity to residency among migratory birds.

Previous studies have already found evidence for such an effect, across a range of species. For example, evidence from ring recoveries (Kristensen and Thorup, 2011), stable isotopes (Evans et al., 2012), and physiological and behavioural studies (Partecke and Gwinner, 2007) of European Blackbirds (*Turdus merula*) indicates that urban birds have a lower tendency to migrate in relation to their non-urban counterparts. This effect is stronger at the northern part of the range (Evans et al., 2012), and seems to have played an important role in the relatively recent northwards expansion of the area in which the species is found year-round (Møller et al., 2014). Similarly, analysis of European Robins (*Erithacus rubecula*) across different habitats near Antwerp, Belgium, found only 30% of colour-marked breeding birds in a woodland plot remained locally over winter, whereas most birds (including nearly all males) did so in urban garden and urban park plots (Dhondt and Adriaensen, 1990). At a multi-species level, a study of wintering bird communities in Poland found higher abundances in urban compared to rural areas (Tryjanowski et al., 2015).

Some studies investigated the mechanisms behind changes in migratory behaviour. Among these, some highlighted the role of increasing resources on bird migration. For example, bird feeders were found to increase the frequency of wintering Eurasian Blackcaps (*Sylvia atricapilla*) in urban areas in Britain (Plummer et al., 2015) and of Carolina Wrens (*Thryothorus ludovicianus*) staying after winter at the northern edge of their range in Michigan (Job and Bednekoff, 2011). Also, the use of nectar feeders seems to play a key role in the northwards expansion of wintering Anna's Hummingbirds (*Calypte anna*) in the United States (Greig et al., 2017), whereas overwintering birds in a population of mainly breeding migrant White Storks (*Ciconia ciconia*) rely strongly on landfills (Gilbert et al., 2016). Some studies' results support the hypothesis that urban areas buffer migratory birds from winter harshness. For example, a study of ringing records of European Blackbirds in the Netherlands found that the fraction of birds migrating away from their breeding areas in the winter was inversely correlated with temperature in rural areas, but found no noticeable effect in urban areas (Vliet et al., 2009). The urban 'heat island effect' was also considered a factor explaining the above-mentioned winter range expansion of Anna's Hummingbirds in the United States, with the interaction between January minimum temperatures and housing densities being a significant predictor of winter presence (Greig et al., 2017).

Most of previous studies have however analysed the effects of urbanization on bird migration by focusing on small parts of the range (e.g. Dhondt and Adriaensen, 1990; Gilbert et al., 2016; Greig et al., 2017), and typically only at a specific season (usually winter). Additionally, measures of migratory propensity are oftentimes crude (e.g. contrasts between local bird densities, Tryjanowski et al., 2015; fraction of colour-marked birds, Dhondt and Adriaensen, 1990; stable isotopes sensitive to only very large differences in migratory distance, Evans et al., 2012), and can thus mask important differences in migratory behaviour (e.g. local post-breeding dispersion versus long-term migration).

Here, we take advantage of a continental-scale bird ringing scheme to test the hypothesis that urbanization is affecting bird migrations. Ringing data allow us to identify the precise seasonal locations of individual birds, and therefore unambiguously distinguish residency or short-distance dispersal from long-distance movements. We focus on ten North American partially migratory species for which we were able to obtain ringing recoveries data that cover their entire range. Furthermore, we investigate drivers in the migratory propensity of individuals in both seasons, breeding and non-breeding, when accounting both for natural factors (winter harshness and resource availability) and for anthropogenic factors (urbanization). Specifically, we test four hypotheses: that propensity to remain year-round in the breeding grounds is higher if (1a) winters are milder and (1b) urbanization levels stronger; and that propensity to remain year-round in the wintering grounds is higher if (2a) resource surplus is higher and (2b) urbanization is higher.

2. Data and methods

2.1. Individual bird data

Species' data come from the North American Bird Banding Programme (NABBP), run by the Bird Banding Laboratory of the USGS Patuxent Wildlife Research Center and the Bird Banding Office of the Canadian Wildlife Service (USGS Bird Banding Laboratory, 2016). The programme compiles records of birds captured and marked with a uniquely numbered band or ring, as well as any subsequent recoveries. Ringing localities are recorded in 10-arc minute blocks, which, at 40°N for example, correspond to 14.2 km in longitude and 18.5 km in latitude.

We focused on migratory species whose entire life cycle is well covered by the NABBP, i.e., whose breeding and non-breeding ranges (in the Western Hemisphere) fall mainly within the United States and southern Canada. We then searched within each species for individuals seen alive at least twice and in opposite seasons, i.e., one record in the breeding season (May to July), another in the non-breeding season (December to February). Whenever an individual was recorded more than once in a season, we retained only the first record. Using the great circle distance between the breeding and non-breeding locations, we classified each individual into either 'resident' (< 20 km) or 'migrant' (> 100 km; following Fiedler and Pulido (2006); Brown and Miller (2016)). We focused on twelve species for which we were able to obtain a reasonable number of individuals (≥ 50) including a mix of resident and migrant individuals: American Goldfinch (*Spinus tristis*), American Robin (*Turdus migratorius*), Blue Jay (*Cyanocitta cristata*), Brown-headed Cowbird (*Molothrus ater*), Common Grackle (*Quiscalus quiscula*), European Starling (*Sturnus vulgaris*), Evening Grosbeak (*Coccothraustes vespertinus*), House Finch (*Haemorhous mexicanus*), Pine Siskin (*Carduelis pinus*), Purple Finch (*Haemorhous purpureus*), Red-winged Blackbird (*Agelaius phoeniceus*) and White-throated Sparrow (*Zonotrichia albicolis*). The eastern House Finch population has been recently introduced and is mostly resident (Able and Belthoff, 1998), so we exclude it from the analysis, by removing all House Finch records east of 95°W. Total number of birds and number of residents are presented in Fig. 1. Records span the 1920–2016 period (Appendix A). Ringing/recovery effort, and thus NABBP records, are spatially clustered in regions of higher human density and those with more nature-friendly habitants, but we have no reason to expect ringing/recovery effort to affect the propensity of individuals to migrate.

2.2. Environmental data

2.2.1. Winter harshness

Somveille et al. (2015) found that the diversity of bird species that overwinter in their breeding locations was inversely related to both the winter temperature and to winter resources (measured by mean winter NDVI), with both variables being highly correlated and the former being the best predictor. Accordingly, we focused on winter temperature as an indicator of harshness of conditions during the non-breeding season. For any given location, we measured winter harshness as the mean of the monthly average temperature values from December to February within a 10 km buffer around the location. To avoid focusing on an unrepresentative year, we used the Worldclim dataset (Worldclim database at resolution 30″; Hijmans et al., 2005), averaging values across all available years (1970–2000).

2.2.2. Breeding resource surplus

Following Hurlbert and Haskell (2003) and Somveille et al. (2015, 2018a, 2018b), we used values of mean monthly Normalized Difference Vegetation Index (NDVI) as a general indicator of resources (food, nesting sites and roosting sites). For any given location, we first calculated the mean monthly NDVI in the breeding season (May to July) and in the wintering season (December to February) within a buffer of 10 km around the location, and then measured the resource surplus in the breeding season (ΔNDVI) as the difference between the former and the latter. Assuming (in a simple way) that resident species use the same resources year-round, this surplus is a measure of the resources available to migratory species (Somveille et al., 2018a, 2018b). We obtained mean monthly NDVI values from NASA's Earth Observatory (2016; resolution 0.1°), again averaging across all available years (May 2000 – February 2016) to create seasonal means.

2.2.3. Urbanization levels

We considered local human population density as a proxy for the level of urbanization. The median ringing/re-sighting year for the pooled species data was 1956 (interquartile: 1946–1968; Appendix A), so we used the closest spatially explicit data on reconstructed population density across North America that we were able to obtain (1970; Center for International Earth Science Information Network – CIESIN – Columbia University, 2017; resolution 30″). We extracted the mean population density in a buffer of 10 km around each individual location, and log transformed it using log(x + 1) (Fig. 1C, E). A log transformation improved the distribution of this variable, which spans several orders of magnitude.

2.2.4. Testing of hypothesis

We tested four hypotheses: that the probability of an individual remaining year-round at its breeding location is (1a) higher if winters are milder (i.e., higher local temperatures during the wintering season) and (1b) higher if urbanization levels are stronger (i.e., higher local human density); and that the probability of an individual remaining year-round at its wintering location is (2a) higher if breeding resource surplus is higher (i.e., higher local ΔNDVI) and (2b) higher if urbanization levels are stronger (i.e., higher local human density).

We tested these hypotheses for each species by fitting a binomial Generalised Linear Model (logit link), with the resident (1) vs. migrant (0) status of each individual bird as a response and local environmental conditions (natural: winter temperature, ΔNDVI; anthropogenic: human density) as predictors. We tested hypotheses 1a and 1b by focusing solely on the breeding locations, using as predictors local winter temperature and local (log-transformed) human density, and hypotheses 2a and 2b by focusing on the wintering locations, using local breeding resource surplus (ΔNDVI) and local human density as predictors. Note that we did not model the probability of birds being present at a given location, but rather their probability of remaining as residents at a given location, knowing that they were present in a given season.

We standardised variables prior to modelling to allow for the comparison of estimated coefficients, using the following formula: $(x - \text{mean}(x))/\text{sd}(x)$. We used a backwards stepwise selection procedure using AIC to select the best model, and a sequential Bonferroni correction to deal with the large number of repeated tests across species. All analyses were done in R.3.4.2 (R Core Team, 2017). Codes are provided in Appendix D.

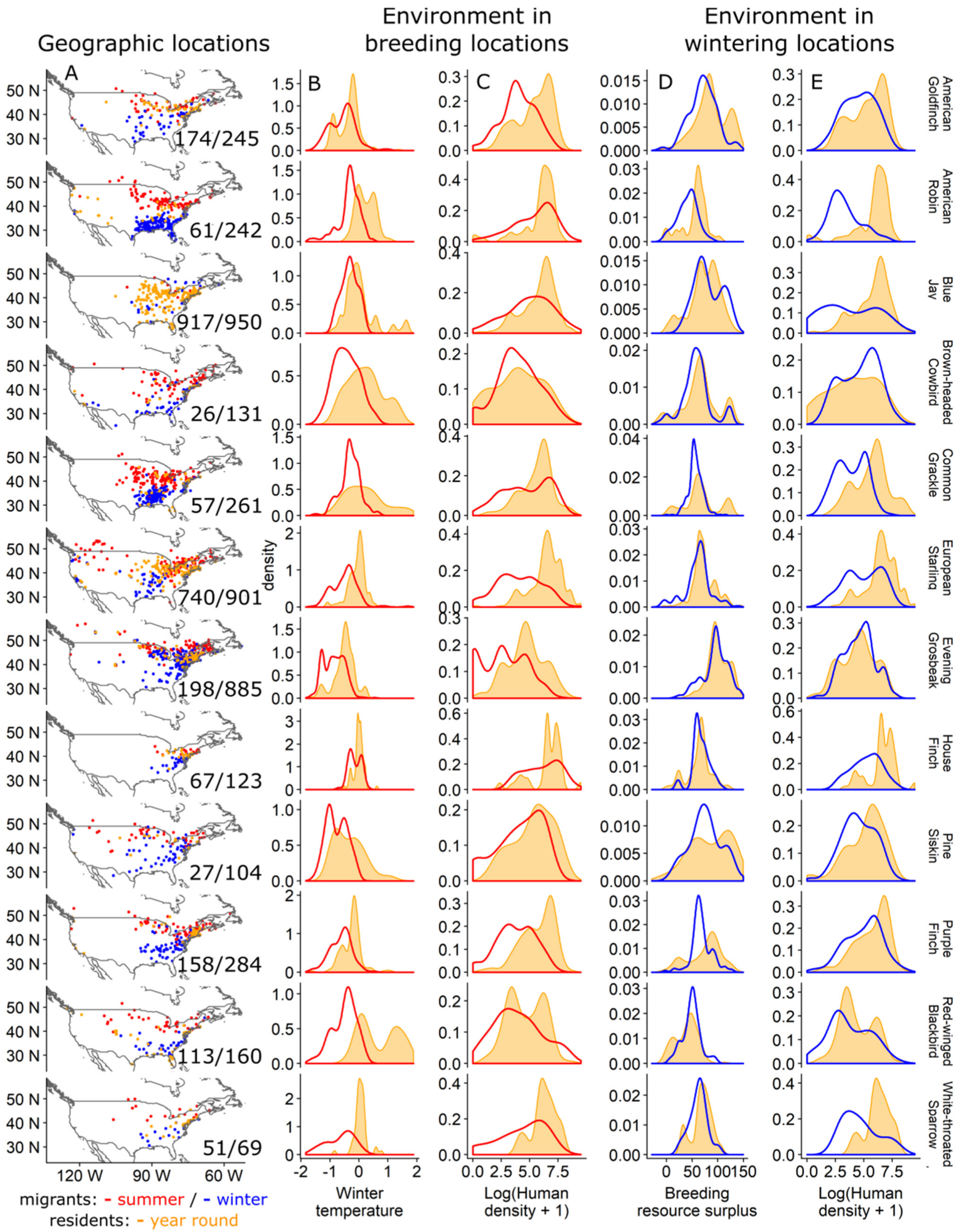
3. Results

3.1. Probability of remaining at the breeding location over winter

We found for eleven out of twelve species a significant positive relationship between the probability that individuals overwinter in their breeding locations and local winter temperature (Figs. 1B, 2A, Appendix B). Human density was significantly positively related with the probability that individuals remain at their breeding locations overwinter for four out of twelve species: American Goldfinch, European Starling, Evening Grosbeak and Purple finch (Figs. 1C, 2B). The effect was positive for five other species, and negative for three but not significantly so after sequential Bonferroni correction (Fig. 2B, Appendix B).

3.2. Probability of remaining at the winter location during the breeding season

For five out of twelve species – American Goldfinch, American Robin, Common Grackle, European Starling, and Evening Grosbeak – we found a significant positive effect of the surplus in resources during the breeding season on the probability that individuals remain at their wintering location into the breeding season (Figs. 1D, 2C, Appendix C). This effect was positive but not significant for six other species, and negative but not significant for the remaining species (Red-winged Blackbird) (Fig. 2C, Appendix C). We found a significant effect of local



(caption on next page)

Fig. 1. Geographic and environmental distribution of bird records, for each of the twelve species analysed. A) Geographical distribution of individuals: residents (in orange) are represented by a single dot. Migrant individuals are represented by two dots: one at their winter location (in blue), another at their breeding location (in red). Numbers indicate sample sizes: number of residents/total number of birds. B) to E) Environmental conditions experienced by individuals, represented as density curves (area under the curve equals one). Each graph indicates the frequency distribution of two sets of individuals: residents (in orange) and migrants (blue for winter migrants; red for summer migrants). B) and C) correspond to environmental conditions in the breeding locations; D) and E) to conditions in the wintering locations. Hence, for example, for the American Robin: in B a strong negative deviation of the red curve (migrants) in relation to the orange curve (residents) indicates that individual birds that migrate away from their breeding locations (i.e. summer migrants, thus in red) tend to be found in locations that experience lower temperatures in the winter than the those occupied by individuals that remain year round (residents, in orange). This is then reflected in Fig. 2A by a significant positive effect of the winter temperature at the breeding location on the propensity of individuals to migrate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

human density on the probability that individuals remain at their wintering location during the breeding season for eight species: American Goldfinch, American Robin, Blue Jay, Common Grackle, European starling, House Finch, Purple Finch, and White-throated Sparrow (Figs. 1E, 2D; Appendix C). The effect was non-significant for the other species: positive in two cases, and negative in two (Appendix C).

4. Discussion

Here we investigated whether natural and anthropogenic conditions affect the propensity of individuals to remain resident in twelve partially migratory North American bird species, using a large scale ringing dataset (USGS Bird Banding Laboratory, 2016).

In all species studied, we found substantial individual variability, with the same conditions under which some individuals migrate apparently tolerated by others year-round. This may reflect true individual variation in migratory strategies within populations. For example, individual differences in propensity to migrate have been related to factors such as sex (Dhondt and Adriaensen, 1990; Perez et al., 2014), dominance status (Ketterson and Nolan, 1979), personality (reaction to a novel object; Nilsson et al., 2010), body size (Belthoff and Gauthreaux, 1991) and physiology (e.g. basal metabolic rates and cost of thermoregulation; Nilsson et al., 2011). Individual strategies can also change over time, for example in response to changing environmental conditions (Shaw and Levin, 2011) or age, an effect that we could not disentangle from individual variability, since we only had one pair of observations per individual.

It is also possible that this individual variability arose from limitations in our data, for instance in the environmental axes we considered and their proxies. For example, NDVI as a general measure of resources does not necessarily capture the specific resources needed for each species. And human density is a crude proxy for anthropogenic effects (e.g. agricultural areas often have low population densities and yet can provide important resources, Foley et al., 2011; managed green spaces are often more productive than the surrounding wildlands, Imhoff et al. 2000).

Apparent individual variability in the propensity to migrate for apparently similar conditions can also arise from the temporal mismatch between the ringing data (see Appendix A for a distribution of records through time) and the explanatory variables (e.g. temperature averaged over 1970–2000, population density in 1970). Furthermore, data limitations meant we were unable to integrate within-season mobility (e.g. Thorup et al., 2017), yearly variation in migratory propensity (e.g. species known for their irruptive migrations: Evening Grosbeak, Bock and Lepthien, 1976; Pine Siskin, Alsop, 2002), and the possibility that among our study species there may have been changes in migratory propensity over time (e.g. migratory populations becoming increasingly resident, Adriaensen et al., 1993; Brown and Miller, 2016; or the opposite, Berthold, 1999).

Despite these limitations, which likely added noise to our data, our results support the predictions that local environmental conditions as we measured them affect the migratory decisions of individuals, in agreement of previous studies at the species level (Somveille et al., 2015). In particular, and for all but one species, our results strongly support the hypothesis that winter harshness drives individuals to

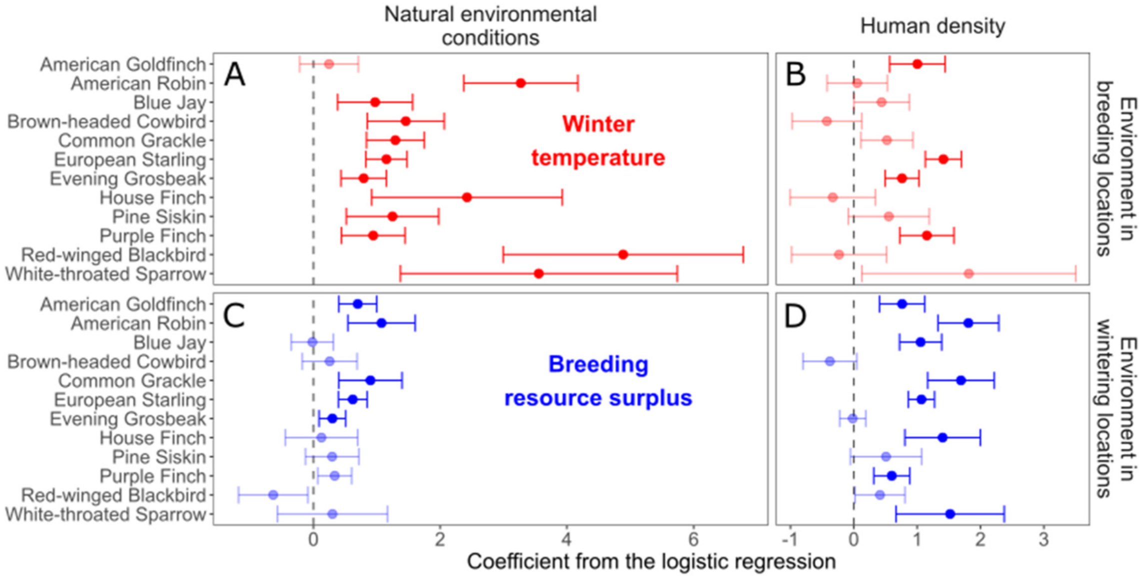


Fig. 2. Migratory response of individuals to environmental conditions, analysed through binomial Generalised Linear Models (GLMs) modelling the propensity of individuals to remain as resident as function of local conditions. Values correspond to estimated coefficients of the GLMs for each species with 95% confidence intervals, with positive values indicating a higher propensity to remain as resident, and negative values a higher propensity to migrate. Transparency: significance after Bonferroni correction, with coefficients significantly different from 0 in dark. A) Effects of winter temperatures at the breeding locations. B) Effects of urbanization at the breeding locations. C) Effects of breeding resource surplus at the wintering locations. D) Effects of urbanization at the wintering locations.

migrate elsewhere from their breeding locations (Figs. 1B, 2A). For most species, we also found support for the hypothesis that high local natural surpluses in summer increase the propensity of individuals to remain as residents in their wintering locations, even if we only found a significant effect in five cases (Figs. 1D, 2C).

For nine species, results also support the hypothesis that urbanization (measured through human population density) affects the propensity of individual birds to migrate (Figs. 1C, E, 2B, D; Appendices B and C): in four species by increasing the probability that individuals stay over winter in their breeding locations, possibly by buffering them against winter harshness; in eight species by increasing the likelihood that individuals remain during the breeding season in their wintering grounds, possibly by increasing local resources. Our analysis thus adds to the existing evidence that urbanization is contributing to sedentarize at least some migratory species, showing that this effect can happen in either the wintering or the breeding portions of species' ranges.

It is not immediately clear why some species appeared in our results to be more responsive to urbanization than others. This could be in part due to limited statistical power, as the species for which we found no effect (Brown-headed Cowbird, Pine Siskin and Red-winged Blackbird) are among the ones with the smallest number of records (respectively 131, 104 and 160; but we found an effect – in the winter only – for the White-throated Sparrow and the House Finch, with respectively 69 and 123 records). Species with irruptive migrations (i.e. which move in irregular patterns in the winter tracking blooms in resources) may be less responsive to human density. Indeed, we found that the two irruptive migrants in our sample, Pine Siskins and Evening Grosbeaks, showed no response to human density in their propensity to remain at their winter location (Fig. 2B). However, Evening Grosbeaks seem to respond to human density in their propensity to remain at their breeding location (Fig. 2B).

Another explanation may come from species' level of association with anthropogenic resources and infrastructures. Although a review by Archer et al. (2019) found strong support for most species in our sample being synanthropic (medium support for the American Goldfinch, low support for the American Robin, and a lack of data about the White-throated Sparrow), there are known differences between species. For example, North-American populations of European Starlings are highly associated with cities (Alsop, 2002), and we found a significant positive effect of human density on the propensity to remain as resident in both seasons (Figs. 1C, E, 2B, D; Appendices B and C). Similarly, American Goldfinches are common in suburbs, parks and backyards, and tend to visit garden feeders (Alsop, 2002), and we found for this species a higher propensity to be resident (in both seasons) in densely human-populated areas (Fig. 2B, D). And House Finches in the east of North American are common in human-created habitats (Hill, 2002) and were found to have a higher propensity to remain in their wintering location over the summer in densely human-populated areas (Fig. 2D). In contrast, we found no effect of human density for Red-winged Blackbirds, whose main habitats (marshes and agricultural fields) are outside densely populated areas (Alsop, 2002).

A higher propensity to remain year-round in urban areas does not obviate the fact that urbanization itself often has substantial impacts on bird diversity, resulting in poorer communities (Lee et al., 2004; Biamonte et al., 2011). In particular, a meta-analysis showed a lower passerine fledging success in urban areas (Chamberlain et al., 2009). Nonetheless, our results suggest that, at least for some bird species that can cope well with anthropogenic habitats, urban areas can provide conditions that are beneficial enough to outweigh the costs of migration. However, it is possible that the benefits of urban areas only stand up to a certain level of urbanization, in the same way as Tratalos et al. (2007) found a hump-shaped relationship between bird species richness or abundances and household densities in Britain. Sample sizes for some of our study species were too small to allow us for the inclusion of non-monotone effects in our models, so we were unable to test for this additional hypothesis.

Additionally, it is unclear whether individual choices to remain in urban areas rather than migrating translate into positive effects at the population level. Indeed, urban areas may be acting as ecological traps – i.e. when organisms choose poor-quality habitats above better alternatives (Gilroy and Sutherland 2007). Urban resources may appear more attractive yet result in worse outcomes; for example, great tits have been shown to prefer larger nesting cavities in urban areas despite this leading to lower fledging success (Demeyrier et al., 2016). Concerns have also been raised about the nutritional value of anthropogenic food (Jones and Reynolds, 2008), the increased risk of disease spread around anthropogenic food sources (Robb et al., 2008a; Jones and Reynolds, 2008). Previous studies suggest complex effects: for example, for garden feeders, a review by Robb et al. (2008a) found mostly positive effects on the breeding performance of supplementary-fed birds (e.g. Robb et al., 2008b), but Plummer et al. (2013) found a negative effect of feeders on the breeding performance of blue tits. To estimate whether remaining as resident in urban areas is actually beneficial would require data on population trends for migratory versus non-migratory individuals, or monitoring their breeding performance, which we did not have access to in this study.

Our results also indicate that, for some species, the effects of urbanization on the propensity to migrate are of similar orders of magnitude as those of variation in natural environmental conditions (as measured by the standardised coefficients of the regressions; Fig. 2). This suggests that recent human activities are changing environmental conditions at scales comparable to those naturally experienced by species over longer-term evolutionary-ecological processes. Based on our results, we predict that the combination of climate change (leading to an increase in average temperatures) and urbanization will converge to decrease the propensity of individuals of many migratory bird species across their current range in temperate areas. But for many of those, it will also lead to their expansion into new higher-latitude breeding grounds. Furthermore, the effects of climate change are spatially and temporally complex, as even though average temperature increase, some areas may experience a higher frequency of extremely cold winters. Climate change can also affect the spatial and temporal distribution of local resources, in particular through the interactions between temperature and precipitation on local primary productivity, which may increase in some areas and decline in others. Finally, humans are affecting the distribution of local resources through land use change, including not only urbanization but also other habitat changes at continental scales (Foley et al., 2005). Overall, our results add to the body of evidence that bird migration is not a fixed behaviour in bird populations, and that it is already being shaped by human activities.

CRediT authorship contribution statement

Anne-Sophie Bonnet-Lebrun: Conceptualization, Formal analysis, Supervision, Visualization, Writing - original draft, Writing - review & editing.**Andrea Manica:**Conceptualization, Supervision, Writing - review & editing.**Ana Rodrigues:**Conceptualization, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to all the volunteers who collected the banding data and to the many employees of the Bird Banding Lab who worked to curate the data. We are grateful to Marius Somveille for insightful discussions on the project, and to Rémi Patin for useful comments on early versions of this manuscript. We also thank Will Cresswell and two additional anonymous referees for their help in improving this manuscript. This project was part of A-S Bonnet-Lebrun's PhD at the University of Cambridge, funded by a Saint John's College Benefactors' Scholarship.

Appendices A-D. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108423.

References

Able, K.P., Belthoff, J.R., 1998. Rapid ‘evolution’ of migratory behaviour in the introduced house finch of eastern North America. Proc. R. Soc. Lond. B Biol. Sci. 265, 2063–2071.

Adriaensen, F., Ulenaers, P., Dhondt, A.A., 1993. Ringing recoveries and the increase in numbers of European great crested grebes Podiceps cristatus. Ardea 81, 59–70.

Alsop, F.J., 2002. Smithsonian Handbooks: Birds of New England. DK, New York.

Archer, J.-M.J., Hostetler, M.E., Acomb, G., Blair, R., 2019. A systematic review of forest bird occurrence in north American forest fragments and the built environment. Landsc. Urban Plan. 185, 1–23.

Belthoff, J.R., Gauthreaux, S.A., 1991. Partial migration and differential winter distribution of house finches in the eastern United States. Condor 374–382.

Berthold, P., 1993. Bird Migration: A General Survey. Oxford University Press, Oxford.

Berthold, P., 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70, 1–11.

Biamonte, E., Sandoval, L., Chacón, E., Barrantes, G., 2011. Effect of urbanization on the avifauna in a tropical metropolitan area. Landsc. Ecol. 26, 183–194.

Bock, C.E., Lepthien, L.W., 1976. Synchronous eruptions of boreal seed-eating birds. Am. Nat. 110, 559–571.

Brown, D., Miller, G., 2016. Band recoveries reveal alternative migration strategies in American robins. Animal Migration 3, 35–47.

Carnicer, J., Diaz-Delgado, R., 2008. Geographic differences between functional groups in patterns of bird species richness in North America. Acta Oecol. 33, 253–264.

Center for International Earth Science Information Network - CIESIN - Columbia University. 2017. Global Population Density Grid Time Series Estimates. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). doi:https://doi.org/10.7927/H47M05W2. .

Chamberlain, D.E., et al., 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151, 1–18.

Chan, K., 2001. Partial migration in Australian landbirds: a review. Emu-Austral Ornithology 101, 281–292.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å., Hansson, L.-A., 2011. The ecology and evolution of partial migration. Oikos 120, 1764–1775.

Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A., et al., 2012. Partial migration in fishes: causes and consequences. J. Fish Biol. 81, 456–478.

Collier, C.G., 2006. The impact of urban areas on weather. Q. J. R. Meteorol. Soc. 132, 1–25.

Dalby, L., McGill, B.J., Fox, A.D., Svenning, J.-C., 2014. Seasonality drives global-scale diversity patterns in waterfowl (Anseriformes) via temporal niche exploitation. Glob. Ecol. Biogeogr. 23, 550–562.

Dällenbach, L.J., Glauser, A., Lim, K.S., Chapman, J.W., Menz, M.H.M., 2018. Higher flight activity in the offspring of migrants compared to residents in a migratory insect. Proc. R. Soc. B 285, 20172829.

Demeyrier, V., Lambrechts, M.M., Perret, P., Grégoire, A., 2016. Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. Anim. Behav. 118, 181–190.

Dhondt, A., Adriaensen, F., 1990. Population dynamics and partial migration of the European Robin (Erithacus rubecula) in different habitats. J. Anim. Ecol. 59, 1077–1090.

Evans, K.L., Newton, J., Gaston, K.J., Sharp, S.P., McGowan, A., Hatchwell, B.J., 2012. Colonisation of urban environments is associated with reduced migratory behaviour, facilitating divergence from ancestral populations. Oikos 121, 634–640.

Fiedler, W., Pulido, F., 2006. S19-3 bird ringing as a means for studying the evolution of avian migration — potentials, limits and prospects. Current Zoology (formerly Acta Zoologica Sinica) 52 (Supp. issue 201), 345–349.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., et al., 2005. Global consequences of land use. Science 309, 570–574.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., et al., 2011. Solutions for a cultivated planet. Nature 478, 337–342.

Gilbert, N.I., Correia, R.A., Silva, J.P., Pacheco, C., Catry, I., Atkinson, P.W., et al., 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (Ciconia ciconia) from a partially migratory population. Movement Ecology 4, 7.

Gilroy, J.J., Sutherland, W.J., 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends Ecol. Evol. 22, 351–356.

Greig, E.I., Wood, E.M., Bonter, D.N., 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. Proc. R. Soc. B 284, 20170256.

Haberl, H., Erb, K.-H., Krausmann, F., 2014. Human appropriation of net primary production: patterns, trends, and planetary boundaries. Annu. Rev. Environ. Resour. 39, 363–391.

Hebblewhite, M., Merrill, E.H., 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120, 1860–1870.

Herrera, C., 1978. On the breeding distribution pattern of European migrant birds: MacArthur’s theme reexamined. Auk 3, 496–509.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hill, G.E., 2002. A Red Bird in a Brown Bag: The Function and Evolution of Colorful Plumage in the House Finch. Oxford University Press, Oxford; New York.

Hurlbert, A.H., Haskell, J.P., 2003. The effect of energy and seasonality on avian species richness and community composition. Am. Nat. 161, 83–97.

Imhoff, M.L, Tucker, C.J., Lawrence, W.T., Stutzer, D.C., 2000. The use of multisource satellite and geospatial data to study the effect of urbanization on primary productivity in the United States. IEEE Trans. Geosci. Remote Sens. 38, 2549–2556.

IPCC, 2014. In: Core Writing Team, Pachauri, R.K., Meyer, L.A. (Eds.), Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland (151 pp).

Job, J., Bednekoff, P.A., 2011. Wrens on the edge: feeders predict Carolina wren Thryothorus ludovicianus abundance at the northern edge of their range. J. Avian Biol. 42, 16–21.

Jones, D.N., Reynolds, S.J., 2008. Feeding birds in our towns and cities: a global research opportunity. J. Avian Biol. 39, 265–271.

Ketterson, E.D., Nolan, V., 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of dark-eyed juncos (Junco hyemalis). Auk 96, 532–536.

Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., et al., 2008. Key conservation issues for migratory land- and waterbird species on the world’s major flyways. Bird Conservation International 18, S49–S73.

Kristensen, M., Thorup, K., 2011. Urbanization Effects on Migration Behaviour of Short-Distance Migratory Birds.

Lee, P.-F., Ding, T.-S., Hsu, F.-H., Geng, S., 2004. Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. J. Biogeogr. 31, 307–314.

Lemoine, N., Böhning-Gaese, K., 2003. Potential impact of global climate change on species richness of long-distance migrants. Conserv. Biol. 17, 577–586.

Main, I.G., 2000. Obligate and facultative partial migration in the blackbird (Turdus merula) and the greenfinch (Carduelis chloris): uses and limitations of ringing data. Die Vogelwarte 40, 286–291.

Møller, A.P., Jokimäki, J., Skorka, P., Tryjanowski, P., 2014. Loss of migration and urbanization in birds: a case study of the blackbird (Turdus merula). Oecologia 175, 1019–1027.

Moreau, R.E., 1952. The place of Africa in the Palaearctic migration system. J. Anim. Ecol. 21, 250.

NASA's Earth Observatory, 2016. Global maps. NASA Available at. http://earthobservatory.nasa.gov/GlobalMaps (downloaded 10 June and 12 July 2016).

Nilsson, A., Nilsson, J.-A., Alerstam, T., Bäckman, J., 2010. Migratory and resident blue tits Cyanistes caeruleus differ in their reaction to a novel object. Die Naturwissenschaften 97, 981–985.

Nilsson, A.L.K., Nilsson, J.-Å., Alerstam, T., 2011. Basal metabolic rate and energetic cost of thermoregulation among migratory and resident blue tits. Oikos 120, 1784–1789.

Partecke, J., Gwinner, E., 2007. Increased sedentariness in European blackbirds following urbanization: a consequence of local adaptation? Ecology 88, 882–890.

Perez, C., Granadeiro, J.P., Dias, M.P., Alonso, H., Catry, P., 2014. When males are more inclined to stay at home: insights into the partial migration of a pelagic seabird provided by geolocators and isotopes. Behav. Ecol. 25, 313–319.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E., Blount, J.D., 2013. Winter food provisioning reduces future breeding performance in a wild bird. Sci. Rep. 3, 1–6.

Plummer, K.E., Siriwardena, G.M., Conway, G.J., Risely, K., Toms, M.P., 2015. Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? Glob. Chang. Biol. 21, 4353–4363.

Podhrázský, M., Musil, P., Musilová, Z., Zouhar, J., Adam, M., Závora, J., et al., 2017. Central European Greylag geese Anser anser show a shortening of migration distance and earlier spring arrival over 60 years. Ibis 159, 352–365.

Pulido, F., Berthold, P., 2010. Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proc. Natl. Acad. Sci. 107, 7341–7346.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL. https://www.R-project.org/.

Robb, G.N., McDonald, R.A., Chamberlain, D.E., Bearhop, S., 2008a. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front. Ecol. Environ. 6, 476–484.

Robb, G.N., McDonald, R.A., Chamberlain, D.E., Reynolds, S.J., Harrison, T.J.E., Bearhop, S., 2008b. Winter feeding of birds increases productivity in the subsequent breeding season. Biol. Lett. 4, 220–223.

Schaefer, H.-C., Jetz, W., Böhning-Gaese, K., 2008. Impact of climate change on migratory birds: community reassembly versus adaptation. Glob. Ecol. Biogeogr. 17, 38–49.

Shaw, A.K., Levin, S.A., 2011. To breed or not to breed: a model of partial migration. Oikos 120, 1871–1879.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. Trends Ecol. Evol. 21, 186–191.

Somveille, M., Manica, A., Butchart, S.H.M., Rodrigues, A.S.L., 2013. Mapping global diversity patterns for migratory birds. PLoS One 8, 1–10.

Somveille, M., Rodrigues, A.S.L., Manica, A., 2015. Why do birds migrate? A macroecological perspective. Glob. Ecol. Biogeogr. 24, 664–674 (n/a-n/a).

Somveille, M., Manica, A., Rodrigues, A.S.L., 2018a. Where the wild birds go: explaining the differences in migratory destinations across terrestrial bird species. Ecography 41, 1–12.

Somveille, M., Rodrigues, A.S.L., Manica, A., 2018b. Energy efficiency drives the global seasonal distribution of birds. Nature Ecology & Evolution 2, 962.

Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., et al., 2017. Resource tracking within and across continents in long-distance bird migrants. Sci. Adv. 3, e1601360.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D., Gaston, K.J., 2007. Bird densities are associated with household densities. Glob. Chang. Biol. 13, 1685–1695.

Tryjanowski, P., Sparks, T.H., Biaduń, W., Brauze, T., Hetmański, T., Martyka, R., et al., 2015. Winter bird assemblages in rural and urban environments: a National Survey. PLoS One 10, e0130299.

USGS Bird Banding Laboratory, 2016. North American Bird Banding and Band Encounter Data Set. Patuxent Wildlife Research Center, Laurel, MD (08/06/2016).

Visser, M.E., Perdeck, A.C., van BALEN, J.H., Both, C., 2009. Climate change leads to decreasing bird migration distances. Glob. Chang. Biol. 15, 1859–1865.

Vliet, J.V., Musters, C.J.M., Keurs, W.J.T., 2009. Changes in migration behaviour of blackbirds Turdus merula from the Netherlands. Bird Study 56, 276–281.