Effects of urbanisation on bird migration

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.

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 & 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 passerines 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 & 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 & Haskell 2003; Dalby *et al.* 2014; Somveille *et al.* 2015, 2018a, b). More specifically, these studies 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 & Böhning-Gaese 2003; Carnicer & 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 & 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 & Belthoff (1998)).

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

81   Given that anthropogenic activities are affecting both the climate (IPCC, 2014) and the
82   distribution of natural resources (Haberl *et al.* 2014), it is not surprising that there is
83   mounting evidence of human effects on bird migration (Visser *et al.* 2009; Plummer *et al.*
84   2015; Greig *et al.* 2017). One such major effect is by altering land cover, with urbanization in
85   particular creating habitats that are in many ways radically distinct from natural ones. The
86   resulting changes to local environmental conditions may plausibly affect the migratory
87   decisions of urban birds. First, urban areas are often 'heat islands', multiple degrees warmer
88   than surrounding areas (Collier 2006), which may buffer birds against harsh winter
89   temperatures (Shochat *et al.* 2006) and thus increase their probability of remaining over
90   winter. Second, urban areas can provide particular resources, for example through bird
91   feeders, garbage, and garden flowers and fruits (e.g. Robb *et al.* 2008; Greig *et al.* 2017).
92   These may either buffer populations against the low resources of winter, and thus increase the
93   probability of breeding birds remaining over winter, or provide resources in the breeding
94   season that increase the odds that wintering birds remain to breed. Overall, urbanization is
95   thus expected to increase the propensity to residency among migratory birds.

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

109   Some studies investigated the mechanisms behind changes in migratory behaviour. Among
110   these, some highlighted the role of increasing resources on bird migration. For example, bird
111   feeders were found to increase the frequency of wintering Eurasian blackcaps (*Sylvia*
112   *atricapilla*) in urban areas in Britain (Plummer *et al.* 2015) and of Carolina wrens
113   (*Thryothorus ludovicianus*) staying after winter at the northern edge of their range in
114   Michigan (Job & Bednekoff 2011). Also, the use of nectar feeders seems to play a key role in
115   the northwards expansion of wintering Anna's hummingbirds (*Calypte anna*) in the United
116   States (Greig *et al.* 2017), whereas overwintering birds in a population of mainly breeding
117   migrant white storks (*Ciconia ciconia*) rely strongly on landfills (Gilbert *et al.* 2016). Some
118   studies' results support the hypothesis that urban areas buffer migratory birds from winter
119   harshness. For example, a study of ringing records of European blackbirds in the Netherlands
120   found that the fraction of birds migrating away from their breeding areas in the winter was

121 inversely correlated with temperature in rural areas, but found no noticeable effect in urban
122 areas (Vliet *et al.* 2009). The urban 'heat island effect' was also considered a factor
123 explaining the above-mentioned winter range expansion of Anna's hummingbirds in the
124 United States, with the interaction between January minimum temperatures and housing
125 densities being a significant predictor of winter presence (Greig *et al.* 2017).

126 Most of previous studies have however analysed the effects of urbanization on bird migration
127 by focusing on small parts of the range (e.g. Dhondt & Adriaensen 1990; Gilbert *et al.* 2016;
128 Greig *et al.* 2017), and typically only at a specific season (usually winter). Additionally,
129 measures of migratory propensity are oftentimes crude (e.g. contrasts between local bird
130 densities, Tryjanowski et al. 2015; fraction of colour-marked birds, Dhondt & Adriaensen
131 1990; stable isotopes sensitive to only very large differences in migratory distance, Evans *et*
132 *al.* 2012), and can thus mask important differences in migratory behaviour (e.g. local post-
133 breeding dispersion versus long-term migration).

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

Data and Methods

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

155 We focused on migratory species whose entire life cycle is well covered by the NABBP, i.e.,
156 whose breeding and non-breeding ranges (in the Western Hemisphere) fall mainly within the
157 United States and southern Canada. We then searched within each species for individuals
158 seen alive at least twice and in opposite seasons, i.e., one record in the breeding season (May
159 to July), another in the non-breeding season (December to February). Whenever an individual
160 was recorded more than once in a season, we retained only the first record. Using the great
161 circle distance between the breeding and non-breeding locations, we classified each
162 individual into either 'resident' (< 20km) or 'migrant' (>100km; following Fiedler & Pulido
163 (2006); Brown & Miller (2016)). We focused on twelve species for which we were able to
164 obtain a reasonable number of individuals (≥ 50) including a mix of resident and migrant
165 individuals: American Goldfinch (*Spinus tristis*), American Robin (*Turdus migratorius*), Blue
166 Jay (*Cyanocitta cristata*), Brown-headed Cowbird (*Molothrus ater*), Common Grackle
167 (*Quiscalus quiscula*), European Starling (*Sturnus vulgaris*), Evening Grosbeak

168 (*Coccothraustes vespertinus*), House Finch (*Haemorhous mexicanus*), Pine Siskin (*Carduelis*
169 *pinus*), Purple Finch (*Haemorhous purpureus*), Red-winged Blackbird (*Agelaius phoeniceus*)
170 and White-throated Sparrow (*Zonotrichia albicolis*). The eastern House Finch population has
171 been recently introduced and is mostly resident (Able and Belthoff 1998), so we exclude it
172 from the analysis, by removing all House Finch records east of 95°W. Total number of birds
173 and number of residents are presented in Fig. 1). Records span the 1920-2016 period
174 (Appendix A). Ringing/recovery effort, and thus NABBP records, are spatially clustered in
175 regions of higher human density and those with more nature-friendly habitants, but we have
176 no reason to expect ringing/recovery effort to affect the propensity of individuals to migrate.

Environmental data

Winter harshness

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

Breeding resource surplus

190 Following Hurlbert & Haskell (2003) and Somveille *et al.* (2015, 2018a, b), we used values
191 of mean monthly Normalized Difference Vegetation Index (NDVI) as a general indicator of
192 resources (food, nesting sites and roosting sites). For any given location, we first calculated
193 the mean monthly NDVI in the breeding season (May to July) and in the wintering season
194 (December to February) within a buffer of 10km around the location, and then measured the
195 resource surplus in the breeding season (ΔNDVI) as the difference between the former and
196 the latter. Assuming (in a simple way) that resident species use the same resources year-
197 round, this surplus is a measure of the resources available to migratory species (Somveille *et*
198 *al.* 2018a, b). We obtained mean monthly NDVI values from NASA's Earth Observatory
199 (2016; resolution 0.1˚), again averaging across all available years (May 2000 – February
200 2016) to create seasonal means.

Urbanization levels

202 We considered local human population density as a proxy for the level of urbanization. The
203 median ringing/re-sighting year for the pooled species data was 1956 (interquartile: 1946-
204 1968; Appendix A), so we used the closest spatially explicit data on reconstructed population
205 density across North America that we were able to obtain (1970; Center for International
206 Earth Science Information Network – CIESIN – Columbia University, 2017; resolution 30'').
207 We extracted the mean population density in a buffer of 10km around each individual
208 location, and log transformed it using $\log(x+1)$ (Fig. 1C, 1E). A log transformation improved
209 the distribution of this variable, which spans several orders of magnitude.

Testing of hypothesis

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

215 location is (3) higher if breeding resource surplus is higher (i.e., higher local ΔNDVI) and (4)
216 higher if urbanization levels are stronger (i.e., higher local human density).

217 We tested these hypotheses for each species by fitting a binomial Generalised Linear Model
218 (logit link), with the resident (1) vs. migrant (0) status of each individual bird as a response
219 and local environmental conditions (natural: winter temperature, ΔNDVI; anthropogenic:
220 human density) as predictors. We tested hypotheses 1 and 2 by focusing solely on the
221 breeding locations, using as predictors local winter temperature and local (log-transformed)
222 human density, and hypotheses 3 and 4 by focusing on the wintering locations, using local
223 breeding resource surplus (ΔNDVI) and local human density as predictors. Note that we did
224 not model the probability of birds being present at a given location, but rather their
225 probability of remaining as residents at a given location, knowing that they were present in a
226 given season.

227 We standardised variables prior to modelling to allow for the comparison of estimated
228 coefficients, using the following formula: $(x - mean(x))/sd(x)$. We used a backwards stepwise
229 selection procedure using AIC to select the best model, and a sequential Bonferroni
230 correction to deal with the large number of repeated tests across species. All analyses were
231 done in R.3.4.2 (R Core Team 2017). Codes are provided in Appendix S4.

232

Results

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

Probability of remaining at the winter location during the breeding season
243 For five out of twelve species – American Goldfinch, American Robin, Common Grackle,
244 European Starling, and Evening Grosbeak – we found a significant positive effect of the
245 surplus in resources during the breeding season on the probability that individuals remain at
246 their wintering location into the breeding season (Fig. 1D, 2C, Appendix C). This effect was
247 positive but not significant for six other species, and negative but not significant for the
248 remaining species (Red-winged Blackbird) (Fig. 2C, Appendix C). We found a significant
249 effect of local human density on the probability that individuals remain at their wintering
250 location during the breeding season for eight species: American Goldfinch, American Robin,
251 Blue Jay, Common Grackle, European starling, House Finch, Purple Finch, and White-
252 throated Sparrow (Figure 1E, 2D; Appendix C). The effect was non-significant for the other
253 species: positive in two cases, and negative in two (Appendix C).

254

Discussion

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

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

270   It is also possible that this individual variability arose from limitations in our data, for
271   instance in the environmental axes we considered and their proxies. For example, NDVI as a
272   general measure of resources does not necessarily capture the specific resources needed for
273   each species. And human density is a crude proxy for anthropogenic effects (e.g. agricultural
274   areas often have low population densities and yet can provide important resources, Foley *et*
275   *al.* 2011; managed green spaces are often more productive than the surrounding wildlands,
276   Imhoff et al. 2009).

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

287   Despite these limitations, which likely added noise to our data, our results support the
288   predictions that local environmental conditions as we measured them affect the migratory
289   decisions of individuals, in agreement of previous studies at the species level (Somveille et al.
290   2015). In particular, and for all but one species, our results strongly support the hypothesis
291   that winter harshness drives individuals to migrate elsewhere from their breeding locations
292   (Fig 1B, 2A). For most species, we also found support for the hypothesis that high local
293   natural surpluses in summer increase the propensity of individuals to remain as residents in
294   their wintering locations, even if we only found a significant effect in five cases (Fig 1D, 2C).

295   For nine species, results also support the hypothesis that urbanization (measured through
296   human population density) affects the propensity of individual birds to migrate (Fig. 1C, 1E,
297   2B, 2D; Appendices B and C): in four species by increasing the probability that individuals
298   stay over winter in their breeding locations, possibly by buffering them against winter
299   harshness; in eight species by increasing the likelihood that individuals remain during the
300   breeding season in their wintering grounds, possibly by increasing local resources. Our
301   analysis thus adds to the existing evidence that urbanization is contributing to sedentarize at
302   least some migratory species, showing that this effect can happen in either the wintering or
303   the breeding portions of species' ranges.

304   It is not immediately clear why some species appeared in our results to be more responsive to
305   urbanization than others. This could be in part due to limited statistical power, as the species

306 for which we found no effect (Brown-headed Cowbird, Pine Siskin and Red-winged
307 Blackbird) are among the ones with the smallest number of records (respectively 131, 104
308 and 160; but we found an effect – in the winter only – for the White-throated Sparrow and the
309 House Finch, with respectively 69 and 123 records). Species with irruptive migrations (i.e.
310 which move in irregular patterns in the winter tracking blooms in resources), may be less
311 responsive to human density. Indeed, we found that the two irruptive migrants in our sample,
312 Pine Siskins and Evening Grosbeaks, showed no response to human density in their
313 propensity to remain at their winter location (Fig. 2B). However, Evening Grosbeaks seem to
314 respond to human density in their propensity to remain at their breeding location (Fig. 2B).

315 Another explanation may come from species' level of association with anthropogenic
316 resources and infrastructures. Although a review by Archer et al. (2019) found strong support
317 for most species in our sample being synanthropic (medium support for the American
318 Goldfinch, low support for the American Robin, and a lack of data about the White-throated
319 Sparrow), there are known differences between species. For example, North-American
320 populations of European Starlings are highly associated with cities (Alsop 2002), and we
321 found a significant positive effect of human density on the propensity to remain as resident in
322 both seasons (Fig. 1C, 1E, 2B, 2D; Appendices B and C). Similarly, American Goldfinches
323 are common in suburbs, parks and backyards, and tend to visit garden feeders (Alsop 2002),
324 and we found for this species a higher propensity to be resident (in both seasons) in densely
325 human-populated areas (Fig. 2B, 2D). And House Finches in the east of North American are
326 common in human-created habitats (Hill 2002) and were found to have a higher propensity to
327 remain in their wintering location over the summer in densely human-populated areas (Fig.
328 2D). In contrast, we found no effect of human density for Red-winged Blackbirds, whose
329 main habitats (marshes and agricultural fields) are outside densely populated areas (Alsop
330 2002).

331 A higher propensity to remain year-round in urban areas does not obviate the fact that
332 urbanization itself often has substantial impacts on bird diversity, resulting in poorer
333 communities (Lee *et al.* 2004; Biamonte *et al.* 2011). In particular, a meta-analysis showed a
334 lower passerine fledging success in urban areas (Chamberlain et al. 2009). Nonetheless, our
335 results suggest that, at least for some bird species that can cope well with anthropogenic
336 habitats, urban areas can provide conditions that are beneficial enough to outweigh the costs
337 of migration. However, it is possible that the benefits of urban areas only stand up to a certain
338 level of urbanization, in the same way as Tratalos et al. (2017) found a hump-shaped
339 relationship between bird species richness or abundances and household densities in Britain.
340 Sample sizes for some of our study species were too small to allow us for the inclusion of
341 non-monotone effects in our models, so we were unable to test for this additional hypothesis.

342 Additionally, it is unclear whether individual choices to remain in urban areas rather than
343 migrating translate into positive effects at the population level. Indeed, urban areas may be
344 acting as ecological traps – i.e. when organisms choose poor-quality habitats above better
345 alternatives (Gilroy and Sutherland 2006). Urban resources may appear more attractive yet
346 result in worse outcomes; for example, great tits have been shown to prefer larger nesting
347 cavities in urban areas despite this leading to lower fledging success (Demeyrier et al. 2016).
348 Concerns have also been raised about the nutritional value of anthropogenic food (Jones and
349 Reynolds, 2008), the increased risk of disease spread around anthropogenic food sources
350 (Robb et al. 2008; Jones and Reynolds, 2008). Previous studies suggest complex effects: for
351 example, for garden feeders, a review by Robb et al. (2008a) found mostly positive effects on
352 the breeding performance of supplementary-fed birds (e.g. Robb et al. 2008b), but Plummer
353 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.

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Figure legends

Figure 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 Figure 2A by a significant positive effect of the winter temperature at the breeding location on the propensity of individuals to migrate.

Figure 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 urbanisation at the breeding locations. C) Effects of breeding resource surplus at the wintering locations. D) Effects of urbanisation at the wintering locations.

Figures

Figure 1

Figure 2