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1 **Exploring intraspecific variation in migratory destinations to**
2 **investigate the drivers of migration**

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19

20 **Abstract**

21 Various benefits (e.g. tracking of resources and of climate niche) and costs (e.g. distance
22 travelled) are hypothesized to drive seasonal animal migrations. Until now, these potential
23 factors have been investigated together at the species level, but migratory movements are made
24 at the individual level, leading to intraspecific variability. Here, we use ringing/recovery data
25 from 1308 individuals belonging to thirteen North American bird species to analyse patterns in
26 intraspecific variability of migratory destinations in order to investigate which factors underpin
27 bird migration and how individuals trade-off among multiple factors. Our results suggest that
28 migratory destinations have been shaped by access to resources (most important during the
29 breeding season) and climatic niche tracking (during winter, mostly). However, the benefits of
30 resource surpluses and climate niche tracking appear to be traded off against the cost of
31 migratory distance, which seems to strongly constrain where individuals migrate.

32

33 **Keywords**

34 Bird migration, niche tracking, North American passerines, resource surplus, ringing/recovery
35 data

36 **Introduction**

37 Migration, the geographical redistribution of individuals between seasonal grounds, is
38 widespread among birds (Greenberg and Marra 2005). As seasonal changes in environmental
39 conditions prompt individuals to move, breeding and non-breeding geographical ranges (more
40 or less distinct) emerge for each migratory species. Environmental seasonality therefore acts
41 as a ‘natural experiment’, with analysis of the consequent migratory responses providing
42 insights into the ecological mechanisms driving the geography of species distributions
43 (Somveille et al. 2015). Previous studies aiming at understanding the general drivers of
44 migration have mostly focused on inter-species comparisons (e.g. Hurlbert and Haskell 2003;
45 Nakazawa et al. 2004; Boucher-Lalonde et al. 2013; Dalby et al. 2014; Gómez et al. 2016;
46 Somveille et al. 2015, 2019). Nonetheless, movements are ultimately made by individuals, with
47 species’ seasonal ranges emerging from the sum of these movements. The study of individual-
48 level variation in migratory movement can therefore provide valuable insights into the
49 mechanisms underpinning species’ distributions during the breeding and non-breeding seasons.

50 Previous macroecological studies highlighted three factors that appear to shape migratory
51 destinations in birds. First, migration may allow individuals to track their niche throughout the
52 year (Nakazawa et al. 2004). Indeed, assuming that individuals are adapted to certain
53 environmental conditions, migration could allow them to follow these conditions from one
54 season to the next. Supporting this hypothesis, Gómez et al. (2016) found in New World
55 warblers that migratory species track their climatic niche better than resident species; and
56 Somveille et al. (2019) used a null model to show that avian species’ seasonal grounds across
57 the world are such that they allow them to track a temperature regime throughout the year. At
58 the individual level, Ramos et al. (2015) found evidence for individual specialisation in
59 Bulwer’s petrels *Bulweria bulwerii* migrating between the North and South Atlantic, as

60 populations leapfrog each other during migration to find conditions in the non-breeding season
61 that are similar to the ones they experience in the breeding season.

62 Second, migration may allow individuals to maximise access to resources throughout the year.
63 In locations with high seasonality in resource availability, the number of resident species is
64 constrained by the resources available in the least productive season. Migratory species may
65 thus move in to take advantage of the seasonal surplus of resources available in the most
66 productive season (Herrera 1978). Hurlbert and Haskell (2003) provided support for this
67 hypothesis by showing that the seasonality in resources (as measured by the seasonal difference
68 in Normalized Difference Vegetation Index, NDVI, a remote-sensing measure of greenness)
69 explained 61% of the spatial variation in migratory avian species richness in the United States.
70 Dalby et al. (2014) were also able to explain a good part of the latitudinal gradient in waterfowl
71 species richness during the breeding season using seasonal variability in plant productivity. In
72 particular, they found that annual plant productivity and evapotranspiration explained very little
73 of the gradient, but intra-annual variability explained more of it, emphasizing the importance
74 of seasonality. Thorup et al. (2017) found that red-backed shrikes *Lanius collurio* and
75 nightingales *Luscinia megarhynchos* track seasonal surplus in greenness by migrating (whereas
76 common cuckoos *Cuculus canorus* appear to simply maximise absolute vegetation greenness).
77 All these studies suggest that access to resources is an important driver of migratory
78 destinations.

79 Whether niche tracking or access to resources is more important likely depends on the season,
80 since birds change their needs during the year. Indeed, increased energy requirements for
81 reproduction may result in food resources being more important than climate during the
82 breeding season. In contrast, harsher climatic conditions during the winter may become a
83 restricting factor that shapes wintering grounds. Previous studies found support for such
84 seasonal distinction in migration drivers, including Somveille et al. (2015) for the global

85 variation in seasonal species richness of all migratory birds, and Dalby et al. (2014) for the
86 latitudinal seasonal variation in waterfowl species richness.

87 Third, migratory movement itself can be highly costly to birds, through energetic costs (e.g.
88 Wikelski et al. 2003) and increased mortality risks (Newton 2008), including weather-induced
89 starvation and in-flight losses (see Newton 2007 for a review of weather-related mass mortality
90 events in migrants). On average, the costs of migration are expected to increase with the
91 distance travelled, with a previous study indicating that bird species prefer wintering areas that
92 are more connected to their breeding grounds (Somveille et al. 2015).

93 Overall, any advantages of migration through niche tracking and/or maximised access to
94 resource surplus should be balanced against the costs of migration. We should therefore expect
95 a trade-off between migratory distance and how well individuals track their niche and/or reach
96 energetically advantageous locations. Accordingly, at the species level, Somveille et al. (2019)
97 found a trade-off between migratory distance and resource surplus, as well as a trade-off
98 between migratory distance and thermal niche tracking for short to medium distance migrants.
99 However, how individuals within a species actually perform along such trade-off between the
100 cost of migratory distance and the benefits of migration in terms of niche tracking and resource
101 gain remains unknown.

102 In summary, previous results based on the analyses of the seasonal spatial distribution of
103 migratory species support the hypotheses that: 1) migration allows birds to better track their
104 thermal niche, when compared to resident birds; 2) migration provides access to seasonal
105 surplus of resources; and 3) these benefits should trade off with the costs of migration itself as
106 quantified through migratory distance. However, for these results to emerge at the species level,
107 they should ultimately derive from a translation of costs and benefits at the scale of individual
108 migratory destinations. Within species, there can be substantial variation in the distances

109 travelled (e.g. Prescott 1991, Jenkins et al. 2002, Mathot et al. 2007), reflecting potentially
110 different strategies regarding the above-mentioned trade-offs. Without large-scale individual
111 data, and especially so in species whose breeding and wintering ranges overlap, it is impossible
112 to know how individuals redistribute within the seasonal ranges, and in particular which costs
113 and benefits each individual is exposed to. Here we take advantage of a continental-scale
114 ringing/recovery dataset collated by the USGS Bird Banding Lab to test the three above-
115 mentioned hypotheses for thirteen short- to medium-distance migratory bird species across
116 North America. We focus on migratory individuals within these species. Having identified the
117 costs and benefits of migration, and trade-offs between them, we then investigate where each
118 individual stands along these trade-off.

119 **Data and methods**

120 **Species and individual locations**

121 We used data from the North American ringing scheme (USGS Bird Banding Laboratory,
122 2016), which contains, for each bird, the locations (i.e. longitude and latitude) and dates of
123 ringing and re-sighting events. The spatial precision of the coordinates varies with location, but
124 the coarsest (and the most frequent) is within 10 arc minutes (which, at 40°N, for example,
125 corresponds to 18.5 km in latitude, and 14.2 km in longitude). We chose this dataset because it
126 covers a nearly continental scale (most of North America), and thus encompasses the entire life
127 cycle (i.e. both breeding and non-breeding grounds) of several migratory species with relatively
128 high ringing effort. We focused on species that met two criteria: 1) most of their breeding and
129 non-breeding ranges are within the area covered by the ringing scheme (hence, we excluded
130 species that winter mostly in Central or South America or breed mainly in Northern Canada,
131 where ringing data are very scarce and were not available to us); and 2) more than 10 pairs of
132 observations of migratory individuals (as defined below). We thus selected one species of

133 woodpecker (Yellow-shafted flicker, *Colaptes auratus*) and twelve species of passerines
134 (American crow, *Corvus brachyrhynchos*; Blue jay, *Cyanocitta cristata*; European starling, *Sturnus*
135 *vulgaris*; Brown thrasher, *Toxostoma rufum*; American robin, *Turdus migratorius*; Evening grosbeak,
136 *Coccothraustes vespertinus*; Purple finch, *Haemorhous purpureus*; American goldfinch, *Spinus tristis*;
137 Red-winged blackbird, *Agelaius phoeniceus*; Brown-headed cowbird, *Molothrus ater*; Common
138 grackle, *Quiscalus quiscula*; White-throated sparrow, *Zonotrichia albicollis*). See Appendix S1 Fig. S1
139 for the spatial distribution of records for each season.

140 We defined the breeding season as the months of May to July, and winter as the months of
141 December to February, and only considered ringing/recovery records that took place within
142 these months. We constrained the definition of the seasons to reduce the odds of records
143 corresponding to birds on migration, or to juveniles dispersing but not migrating (exclusion of
144 the month of August). We retained only individuals for which we had at least a ringing/recovery
145 record in each of the two seasons. Whenever several recoveries were available for a given
146 individual in the same season, we used the first record only (i.e., the closest year to the ringing
147 event). We excluded recoveries of dead birds, as there can be mismatches between the dates of
148 death and the dates when the rings are recovered. We thus obtained, for each species, a variable
149 number of individuals, each with a pair of observations: one during the breeding season and
150 one during winter. For each individual, we then calculated migration distance as the great circle
151 distance between these two locations. For some of these species, some populations are partially
152 migratory (i.e., some individuals migrate and some do not; Bonnet-Lebrun et al. 2020a). As
153 our aim was to understand migratory destinations, we focused on migratory individuals only,
154 defined as those moving further than 50 km between seasonal locations (thus excluding resident
155 individuals; Table 1). The 50km threshold was based on the distribution of migratory distances
156 (Fig. S2), as a compromise between the risk of including individuals that are not really
157 migrating and the risk of excluding relevant, short-distance migratory individuals from the

158 study (resulting in low sample sizes). See Fig. S3 for the distribution of ringing/recovery years
159 of ‘migratory’ individuals.

160 We also checked that for each species, and for each season, the distribution of records used in
161 the analysis was broadly representative of the whole distribution of the species, as assessed by
162 visually comparing the distribution of the specific records analysed with the (much larger)
163 dataset of all locations (all ringing and recovery events) for the same species in the same season
164 (Fig. S1). We found no large gaps in the distribution of records analysed, and so no evidence
165 of populations being captured by the ringing scheme during one season only (which would
166 have implied that birds migrate in the opposite season to regions with few observers).

167 Environmental data

168 Temperature has been previously found to play a role in driving bird migration, either as a
169 physiological limit (evidence suggests that migratory birds avoid regions with very cold
170 winters; Somveille et al. 2015), or as an environmental cue that migratory species track
171 between seasons (e.g. Gómez et al. 2016; Somveille et al. 2019). We thus used seasonal mean
172 temperature to characterise the thermal conditions experienced by individuals. We calculated
173 monthly means from the Worldclim database (resolution 30’’; Hijmans et al. 2005), further
174 aggregated to seasonal means using the above definitions of the breeding season (May to July)
175 and winter (December to February). Temperature data were not available for all
176 ringing/recovery years, therefore, to avoid focusing on an unrepresentative year, we averaged
177 values across all available years (1970-2000). We extracted, for each location, the mean
178 temperature of the corresponding season in a 10km buffer (to account for the spatial resolution
179 of individual locations, usually within – and no coarser than - 10’). We then calculated, for each
180 individual, its temperature range as the absolute value of the difference between the mean

181 winter temperature (at the winter location) and the mean temperature during the breeding
182 season (at the breeding location).

183 Following Hurlbert and Haskell (2003) and Somveille et al. (2015, 2019), we used the
184 Normalized Difference Vegetation Index (NDVI) as an indicator of resources (food, nesting
185 sites and roosting sites). This index can be related to the amount and type of vegetation present:
186 positive values of NDVI correspond to vegetated areas, with higher values interpreted as
187 healthier and denser vegetation (Jackson and Huete 1991). We used monthly averages from
188 NASA's Earth Observatory (resolution 0.1°; NASA, 2016). To obtain representative values,
189 we computed monthly means over available years 2006-2015 and, from those, seasonal means
190 following the same approach as for temperature data.

191 For each location, we extracted the mean NDVI for the corresponding season in a 10km buffer.
192 Then for each pair of locations, we calculated the seasonal surplus in resources from one season
193 to the next at each location in each season (as in Somveille et al. 2015):

$$194 \quad \text{Resource_surplus}_{location \in season1} = NDVI_{location \in season1}^{season1} - NDVI_{location \in season1}^{season2}$$

195 We obtained a value of year-round resource surplus per individual by summing the resource
196 surpluses for the respective pair of locations in the corresponding seasons. By definition, a
197 resident individual would have a total annual resource surplus of 0. A positive value means that
198 migration allows individuals to get access to more resources than if they had been resident; a
199 negative value means that migration translates into individuals having access to fewer
200 resources than residency.

201 **Costs and benefits of migrating**

202 For each of the thirteen species in our dataset separately, we asked whether intra-specific
203 patterns of migratory destinations show support for niche tracking and access to resources

204 being drivers of migration, and if so whether those benefits trade off against the costs of travel
205 distance.

206 To test whether migration allows birds to better track their climatic niche, we compared the
207 inter-seasonal temperature range experienced by migrant individuals with the temperature
208 range they would experience if they were residents instead, by remaining either at their non-
209 breeding or at their breeding location. If the climatic niche-tracking hypothesis is true, then the
210 observed temperature range of migrants should be smaller than the alternative of being resident.
211 We tested the significance of the difference using paired *t*-tests and sequential Bonferroni
212 correction with a significance level $\alpha = 0.05$. In all cases, normality of residuals was visually
213 assessed.

214 We tested whether migration allows individuals to increase access to resources compared with
215 remaining in place as residents, by comparing their year-round resource surplus with 0 (the
216 value for residents), using one-sample *t*-tests and sequential Bonferroni correction with $\alpha =$
217 0.05. If this is the case, the year-round resource surplus should be higher than 0.

218 To investigate whether there is a trade-off between migratory distance and the two above-
219 described benefits of migration, we tested the relationship between migratory distance and 1)
220 temperature range between the breeding season and winter, or 2) total annual resource surplus,
221 by fitting a different linear model for each species. If there are such trade-offs, we expect a
222 negative relationship between temperature range and geographical distance, and a positive
223 relationship between resource surplus and geographical distance. We tested these relationships
224 using linear regressions and sequential Bonferroni correction with $\alpha = 0.05$. The normality of
225 residuals and the absence of outliers was visually assessed using standard diagnostic plots.

226 **Observed migratory destinations vs possible alternatives**

227 We investigated how observed migratory destinations (i.e., each individual's pair of breeding

228 and non-breeding locations) performed regarding each cost/benefit in comparison with
229 alternative migration possibilities. For this purpose, we compared the observed migration of
230 each individual with virtual alternative migrations, adapting to the individual level the approach
231 that Somveille et al (2019) developed at the species level.

232 We characterised each individual migration (either observed or virtual) in terms of three axes:
233 1) temperature range (the narrower the range, the higher the benefit of migration in terms of
234 niche-tracking); 2) resource scarcity (one minus standardised year-round resource surplus; the
235 lower the scarcity, the higher the benefit of migration in terms of access to resources); and 3)
236 distance travelled (the shorter the distance, the smaller the cost of migration). For each
237 individual bird in our sample, we evaluated the performance of its migratory destination in
238 each season, and along each axis (hence, 6 comparisons per individual), by comparing the axis
239 value for the observed migration (i.e., given the observed breeding and winter locations) with
240 the values for virtual migrations (i.e., given the observed location for the focal season and
241 simulated locations in the opposite season).

242 Virtual alternative migrations were simulated for any given individual, in any given focal
243 season, by taking its observed location in that season and then selecting possible destinations
244 in the opposite season, regardless of the destinations of conspecifics. We set as possible virtual
245 destinations any location within the study area, constrained to going south for the winter and
246 north for the breeding season (hence, the number of virtual alternative migrations varies
247 depending on the location of individuals and the season). We defined our study area as the
248 region of North America containing most of the records in the North American ringing scheme
249 (and thus likely to have been sampled; see Fig. 1). Note that in this null model, the distance
250 migrated by individuals is only limited to by the shape and size of the study area. We also
251 explored a second null model where virtual individuals were constrained to go no further than
252 the maximum distance travelled by any individual in the dataset, i.e. 2,654.6 km. When not

253 specified, results refer to the first null model. We characterised locations using a hexagonal
254 grid (ISEA discrete global grid, resolution 7, hexagon area $\sim 23,375 \text{ km}^2$, available at
255 <http://bufo.geo.orst.edu/tc/firma/gg/table.html>) covering the study area (i.e. all hexagons in
256 Fig. 1). Each location (observed or virtual) was allocated to the respective hexagon and
257 characterised in terms of temperature and NDVI (calculated as the mean value across the pixels
258 overlapping the hexagon) and position (for calculating distance, this was assumed to be the
259 centroids of hexagon).

260 For each individual, for each season, and for each of the three axes above, we quantified the
261 performance of the observed migration as the proportion of the virtual alternative migrations
262 that had a better rank: thus a score of 0 means that the observed migration performs better than
263 all the virtual alternatives tested; 1 means that it is worse than all alternatives; and 0.5 means
264 that it falls in the middle. For each species and each axis, we tested whether the distribution of
265 scores across all individuals differed significantly from 0.5 using one-sample *t*-tests and
266 sequential Bonferroni correction with $\alpha = 0.05$.

267 In addition, we contrasted visually how each species' observed range in each season compares
268 with the virtual range that would have been obtained if the migratory destinations of individuals
269 were derived by optimising destinations along each of the three axes (as well as along
270 combinations of axes). For this purpose, we took the 10% best-performing (i.e., lower value)
271 virtual alternative migrations obtained for each individual (for a particular focal season and a
272 particular axis) and mapped them into a single density map that we compared with a density
273 map of breeding or winter locations of the migratory individuals under study. The resulting
274 virtual range thus reflects the expected range at the opposite season if all individuals of the
275 species had migrated from their observed locations in the focal season to the locations that give
276 them the best performance along the axis. We also produced virtual maps for the combination
277 of two axes, by selecting the 10% alternative locations with the lowest value in summed scores

278 for the two axes. To identify the best virtual range (i.e. the one that resembles most the empirical
279 range), we computed the Earth Mover's Distance (EMD) using the *move* package (Kranstauber
280 et al. 2019) between each virtual range and the empirical range. The lower the EMD, the more
281 similar the distributions.

282 Data and codes will be made available following acceptance for publication.

283 **Results**

284 **Costs and benefits of migrating**

285 We found that, for all species, the average temperature range between the breeding season and
286 winter is significantly narrower when individuals migrate than it would be if they stayed either
287 at their winter or at their breeding location (Table 1, Fig. S4 and Table S1), consistent with the
288 hypothesis that migration allows individuals to better track their climatic niche. For all species,
289 staying at the breeding location year-round would have led to a significantly greater inter-
290 seasonal temperature range than staying at the winter location year-round (Table 1, Fig. S4 and
291 Table S1).

292 For all species, all or nearly all individuals experienced a surplus in resources at their breeding
293 location (i.e. this location holds more resources in the breeding season than in winter) and a
294 deficit in resources at their winter location (i.e. fewer resources at this location in the winter
295 than in the breeding season; Table 1, Fig. S5 and Table S2). For most species (11 out of 13),
296 the former surplus largely exceeds the later deficit, such that there is on average a significantly
297 total (year-round) positive resource surplus (Table 1, Fig. S5 and Table S2), consistent with the
298 hypothesis that migration allows individuals to increase access to resources. For two species,
299 however (Blue jay and the American goldfinch), the average surplus is not significantly higher
300 than zero. Furthermore, even for those species for which surplus is significantly positive, there
301 is wide individual variation, with some species having a relatively high fraction of individuals

302 for which migration leads to a net deficit in resources throughout the year compared with being
303 resident (e.g. Brown-headed cowbird, Common grackle, Evening grosbeak).

304 For all species (but significantly so after sequential Bonferroni correction for 11 out of 13
305 species), the inter-seasonal temperature range tends to decrease with an increase in the
306 geographical distance travelled (i.e., individuals migrating further tend to track their niche
307 better; Table 1, Table S4 and Fig. S6), consistent with the hypothesis of a trade-off between a
308 benefit of migration for tracking the climatic niche and the costs of travel distance. Similarly,
309 the resource surplus tends to increase with the geographical distance (Table 1, Table S5 and
310 Fig. S7), consistent with the hypothesis of a trade-off between a benefit of migration for
311 increasing access to resources and the costs of travel distance. However, even though most
312 slopes for the relationship between distance and resource surplus are significantly different
313 from zero (apart from the ones for the American goldfinch and the Yellow-shafted flicker – two
314 species with very low sample sizes), the proportion of variance explained by these relationships
315 (R^2) varies greatly between species (Fig. S7) and is consistently lower than the R^2 of the
316 relationships between distance and temperature range (Fig. S6). Finally, the Evening grosbeak
317 is the only species for which the slope of the relationship between distance and resource surplus
318 is negative (significantly so, but with a very small $R^2 = 0.0065$).

319 Observed migratory destinations vs possible alternatives

320 Observed migratory distances were consistently shorter than virtual alternatives (significant for
321 nearly all species, in both seasons; Table 1 and Fig. 2), supporting the hypothesis that the costs
322 of migration affect migratory destinations.

323 Results were less clear for the other two axes analysed. Regarding the breeding locations, for
324 five species observed individual destinations were significantly better than expected in terms
325 of access to resources, but differences were non-significant for seven other species, and

326 significantly worse for another (Table 1 and Fig. 2). In contrast, individuals of all but one
327 species ranked higher than expected regarding temperature range, indicating that they track
328 their climatic niche significantly less than they could, given the considered alternatives.

329 As for winter destinations, for two species individuals appear to maximise niche-tracking, but
330 for five species the reverse is true with six others having non-significant results. As for access
331 to resources, nearly all species (11 out of 13) appear to minimise rather than maximise it (non-
332 significant for the others).

333 Results for the second null model (migratory distance capped to 2,654.6 km, the maximum
334 distance reached by any bird in the study) suggest that, once constrained by distance,
335 individuals of more species maximise niche-tracking and access to resources (Fig. S8). Indeed,
336 observed breeding destinations allowed a better niche tracking for four out of 13 species
337 (significant for only two species) and more access to resources for seven out of 13 species
338 (significant for four species) than virtual alternatives. Compared with alternatives, observed
339 winter destinations allowed a better niche tracking for eight out of 13 species (significant for
340 only three species), and more access to resources for seven out of 13 species (significant for
341 only two species).

342 Contrasts between species' seasonal maps and virtual maps obtained to optimise the three axes
343 analysed (individually or combined) provide a visualisation of the extent to which the different
344 factors may influence the migratory destinations of individuals (Figs. S9-S21). Results are
345 difficult to interpret for species with small sample sizes, so we focus on the four species with
346 more than 100 individuals (Fig. 1; Figs. S12, S14, S15, S20). For example, for the European
347 starling (Fig S12), if the migratory destinations of individuals were simply driven by
348 minimising distance, then the predicted winter distribution would fall further north than
349 observed, whereas the predicted distribution based solely on resource surplus would fall further

350 south; a combination of these two axes provides the closest match between the virtual map and
351 the empirical distribution. The combination of these two axes is also the one that best predicts
352 the winter range of the Common grackle (Fig. 1 and Fig. S20) and the Evening grosbeak (Fig.
353 1 and Fig. S15), while for the American robin distance alone performs best (Fig. 1 and Fig.
354 S14). On the other hand, the best virtual breeding range of the Common grackle (Fig. 1 and
355 Fig. S20) and the American robin (Fig. 1 and Fig. S14) is obtained by combining access to
356 resources and distance, and that of the European starling (Fig. 1 and Fig. S12) and the Evening
357 grosbeak (Fig. 1 and Fig. S15) is obtained by combining niche tracking and distance.

358 **Discussion**

359 Overall, we found support for the hypotheses that migration allows individuals to benefit in
360 terms of access to resources and tracking their climatic niche. In particular, our results suggest
361 that resources tend to be more important during the breeding season, whilst temperature
362 tracking plays a greater role in determining winter destinations. First, our results support the
363 hypotheses that individual birds benefit from migrating both in terms of thermal niche tracking
364 and by increasing access to available resources, compared to the hypothetical alternative of
365 staying in the same location year round. Second, we found that the benefits arising from thermal
366 niche tracking (and, to a lesser extent, from better access to resources) increase with longer
367 migratory distances, thus implying a trade-off between the costs of migration (assumed to
368 increase with distance) and the benefits. However, we also found that, for the short- to medium-
369 distance migrants species studied, when compared to virtual alternatives within the study area,
370 the only consistent signal that emerges is for an effect of travel distance.

371 More specifically, we found that, in general, migration results in a lower between-seasons
372 temperature range, compared with what individuals would have experienced by staying at their
373 breeding or winter grounds. This effect was stronger in winter than in the breeding season,

374 supporting the predictions that avoiding harsh winter temperatures is an important driver of
375 migration (as suggested in Somveille et al. 2015). We also found that, in most species,
376 migratory individuals experience, on average, a positive resource surplus, supporting the
377 hypothesis that access to resources is a driver of migration (Table 1, Fig. S5 and Table S2),
378 consistent with results from Somveille et al. (2019), who found that 91% of migratory bird
379 species experience a net year-round surplus in NDVI. Nonetheless, for some species
380 individuals vary widely in whether they experience a net surplus or a deficit in resources. Those
381 individuals experiencing a deficit in resources therefore get less access to resources than
382 residents (which, by definition, experience a zero net year-round resource surplus).

383 Our results indicate that, even though there are benefits to migrating compared with staying,
384 given the costs incurred by migrating not all migratory destinations are equivalent. Our finding
385 that (on average) the further individuals travel, the more efficient the thermal niche tracking
386 (Table 1, Fig. S6 and Table S3), suggests a trade-off between the benefits of thermal niche
387 tracking and the cost of migratory distance. Somveille et al. (2019) found a similar effect for
388 short to medium-distance migrants (with a travel distance up to ~2000km; the effect found for
389 long-distance migrants was reverse, but none of the species in our dataset fall into this
390 category). Based on results at the species level (Somveille et al. 2019), we might expect longer
391 distance migrants to experience better annual resource surplus, but not necessarily better niche
392 tracking. However, due to unequal ringing/recovery effort across the globe, data to investigate
393 this question are not currently available. Additionally, the further individuals travel, the higher
394 on average their access to a resource surplus (Table 1, Fig. S7 and Table S4) but this relationship
395 is much weaker than for thermal niche tracking (consistently lower R^2 for the corresponding
396 regressions; Fig. S6-S7). Even among those individuals migrating the longest distances, several
397 of them experience a negative total annual resource surplus (Fig. S5 and S6).

398 This suggests that NDVI, our proxy for available resources, might not fully capture the types
399 of resources used by migratory birds. There are a number of reasons why this might be the
400 case. First, there can be other sources of resources not captured by a remote sensing measure
401 of greenness, such as some anthropogenic resources (e.g. bird feeders in gardens, Job and
402 Bednekoff 2011; Bonnet-Lebrun *et al.* 2020a). In addition, the amount of food items specific
403 to the diet of some species (e.g. insects such as ants eaten by Yellow-shafted flickers) might
404 not necessary correlate well with NDVI; and some of these resources might be at a scale that
405 is missed by our hexagonal grid. Moreover, we could not account for competition in this study,
406 even though it is likely to have an effect on the amount of resources available. Indeed, there
407 can be a high surplus in resources from one season to the next at a certain location, but if there
408 are many migrant birds breeding or wintering there, the amount of resources available to each
409 individual will be limited, thus affecting the benefits of migrating to this location.

410 Besides, the environmental data that we used corresponds to seasonal means over multiple
411 years, hence not capturing the inter-annual variability in conditions. Additionally, the years
412 used to calculate these seasonal means did not go as far back as the years from which we had
413 ringing data. This is because even though there are reconstructions through time of climatic
414 data (e.g. NOAA-CIRES 20th Century Reanalysis, available at <http://www.esrl.noaa.gov/psd/>),
415 to our knowledge, these are not available for NDVI data. To obtain comparable results, we
416 therefore used seasonal means both for measures of the climatic niche and of resource surplus.
417 For these reasons, some patterns due to year-to-year variation in resources might not be
418 captured. For instance, resource blooms in certain years have been proposed as an explanation
419 for the irruptive migrations of Evening grosbeaks (Bock and Lepthien 1976, Prescott 1991).
420 This probably goes some way to explain why the Evening grosbeak is among the species for
421 which we were least able to explain individual migratory destinations based on environmental
422 factors (niche tracking and access to resources). Such irruptions happen in several bird species,

423 allowing them to track irregularly fluctuating resources (e.g. boreal finches tracking peaks of
424 tree-seed and fruit crops productivity, owls tracking cycling rodent populations, or waterbirds
425 tracking ephemeral wetlands; Newton 2008).

426 More broadly, drivers of migration are likely to vary between different seasons. For example,
427 Dalby et al. (2014) found that the latitudinal distribution of waterfowl species was driven
428 primarily by variability in plant productivity in the breeding season, but also by potential
429 evapotranspiration (a proxy for ambient energy, related with solar radiation) in the non-
430 breeding season. Similarly, Somveille et al. (2015) found that the distribution of migratory
431 birds' species richness is mainly driven by minimum temperature in winter, but also by
432 resources in the breeding season. Here we found that migrating allows individuals to better
433 track their thermal niche than staying at the winter location year-round, but also to much better
434 track it than staying at the breeding location year-round (Table 1, Fig. S4 and Table S1),
435 suggesting that the benefits in terms of temperature range are more important during winter.
436 We also found that breeding locations do not show a strong signal of optimisation for niche
437 tracking, but do so for access to resources in certain species (Fig. 2 and, to a certain extent, Fig.
438 S8). In contrast, winter locations do not seem to reflect an optimisation in terms of access to
439 resources, but sometimes do so in terms of niche tracking (Fig. 2 and, to a certain extent, Fig.
440 S8). This strongly suggests that drivers of migratory destinations depend on the season.

441 The distance travelled during migration, though, appears as a consistently strong constraint to
442 the migratory destinations across seasons for our study species, over and above niche tracking
443 or access to resources (Figs. 1 and 2). This tendency appears most clearly on the maps of
444 predicted virtual ranges obtained from environmental variables alone, which for many species
445 match poorly the empirical distribution of season records (Figs. S9-S21). This said, this result
446 could be very different for long-distance migrants, which we could not study here given the
447 scarcity of records from South and Central America. Caution is therefore needed when

448 interpreting this result, as short- to medium-distance migrants like the ones in this study
449 represent slightly less than half of all migratory birds (Somveille et al. 2019). Nevertheless, for
450 the species studied here, virtual breeding ranges based on access to resources alone tend to
451 expand further west (and, sometimes, north) than the empirical ranges, and it is only after
452 adding the effect of migratory distance that these predicted ranges more closely resemble the
453 empirical ones. This is likely because there is a wide set of locations which would provide
454 similar access to resources, but some of these locations are too far to be worth the journey. This
455 explanation is supported by the results of the null model constrained by distance (i.e. removing
456 allowable destinations that would be too far away, Fig. S8), in which ranks associated with
457 niche tracking or resources surplus tend to be lower (i.e. individuals perform better along these
458 axes) than in the first null model (with no distance cap). For similar reasons, virtual winter
459 ranges based on niche tracking alone also tend to expand further west than empirical ones.
460 Additionally, virtual winter ranges based on niche tracking only are consistently located further
461 south than empirical ones. This suggests that for most species the observed seasonal ranges of
462 their migratory populations were not shaped by perfectly tracking the climatic niche, or at least
463 that the benefit of doing so does not compensate the cost of migratory distance. Perhaps more
464 importantly than perfectly tracking the niche is for individuals to remain in their thermoneutral
465 zone (see Somveille et al. 2019).

466 Additionally, the lack of perfect match between the virtual predicted ranges and the empirical
467 ones suggest that additional drivers, such as habitat (Barnagaud et al. 2012), including urban
468 areas (Bonnet-Lebrun et al. 2020a) are likely to play a role. The variable quality of the match
469 across species suggests that the nature and strength of these additional drivers are likely to be
470 species-dependent. Species-specific characteristics such as diet might drive the migratory
471 behaviour of some species, such as the irruptive migrations of the Evening grosbeak.

472 Our results indicate that temperature and access to resources shape migratory destinations.
473 Accordingly, there is already evidence that for some species patterns of migration are
474 responding to ongoing climate change (e.g. Eurasian blackbirds *Turdus merula* becoming
475 mainly resident in Great-Britain; Berthold 1993, Main 2000; white storks *Ciconia ciconia*
476 overwintering in higher numbers in Southern Europe; Gilbert et al. 2016; also see Newton
477 2008 for a review) as well as to changes in landuse (e.g. urbanisation; Bonnet-Lebrun et al.
478 2020a).

479 Overall, our results suggest a consistent signal in the drivers of migration that is apparent both
480 in interspecific patterns of migration (Hurlbert and Haskell 2003, Gómez et al. 2016, Somveille
481 et al. 2019) and at the intraspecific level. The fact that we found weaker effects than Somveille
482 et al. (2019) found for species suggests more stochasticity in the redistribution of individuals
483 within the species range than in the redistribution of species themselves. This is not surprising
484 as underlying processes driving individuals' behaviour are expected to be more apparent when
485 large aggregates of individuals are analysed together at the level of the entire species, and
486 indeed we obtained clearer results for the four species with larger numbers of analysed
487 individuals (Fig. 1). We can expect more detailed individual-level data to become available for
488 large numbers of individuals, including from small-sized species, and long-distance migrants,
489 in the near future thanks to improvement in tracking technology. These include the ICARUS
490 project – a large-scale initiative to fit animals with mini GPS transmitters sending data daily
491 via satellite (<https://icarusinitiative.org/>) – and the Motus Wildlife Tracking System – a
492 collaborative research network of radio telemetry stations tracking animals equipped with radio
493 transmitters, spreading out from the Arctic to South America (Taylor et al. 2017). The synergy
494 between individual movement data and high resolution environmental data will shed further
495 light into the factors driving bird migration.

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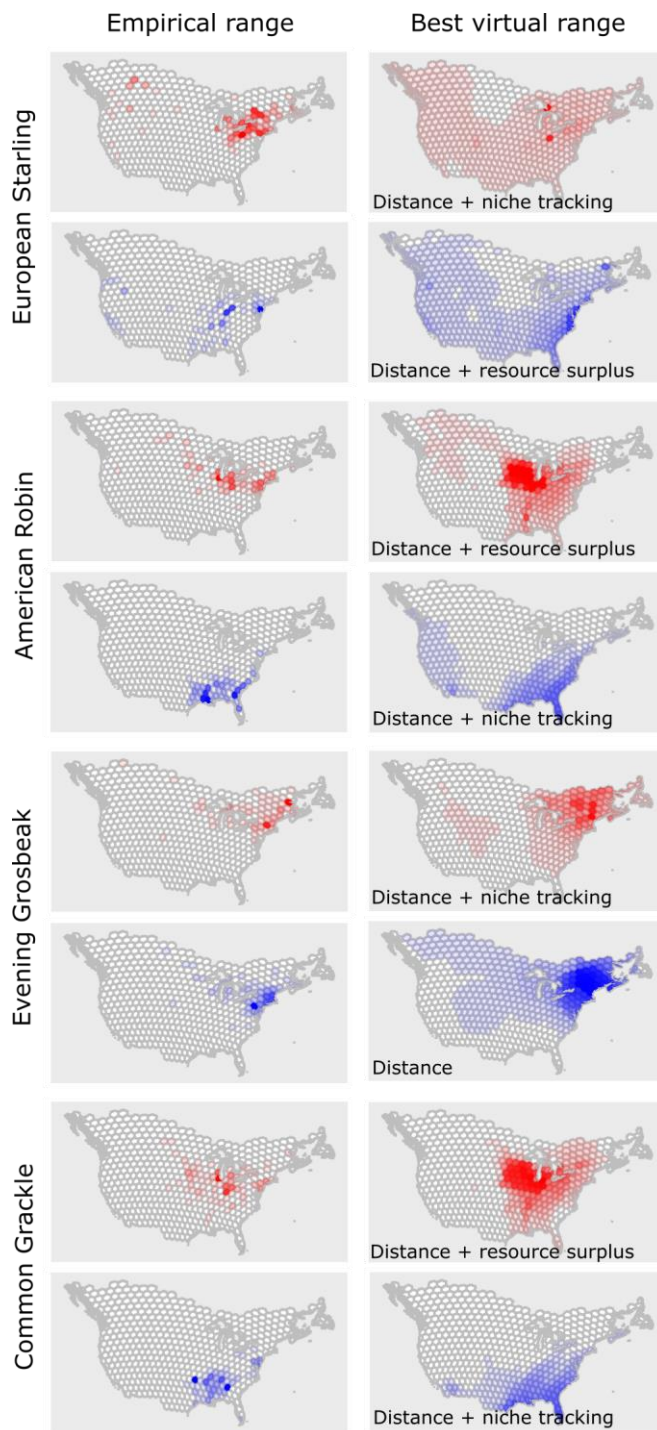
576 **Figure legends**

Figure 1: Contrast between the empirical range and the best virtual range for the four species with the largest number of records. Empirical ranges correspond to the location of ringing records of analysed individuals, either in the breeding season (red) or in the winter (blue). Virtual ranges for either the breeding season (red) or the winter season (blue) are derived from the ringing records in the opposite season, by predicting where those same individuals would have been located if they had migrated while optimising along a single axis (distance, niche tracking or resource surplus) or combination of two axes (see Methods for more details). The map presented in each case is the best one obtained, as assessed through contrast with the empirical range using the Earth Mover's Distance (all maps presented in figures S7 to S19).

Figure 2: Relative position of observed migratory destinations (pairs of breeding and wintering locations) for each species in relation to virtual alternatives (with no constraint on migratory distance), along three axes: migratory distance, niche tracking, and access to resources. In all cases, lower ranks indicate a higher degree of optimisation along the respective axis (for niche tracking: lower temperature differences between breeding and wintering location; for access to resources: lower resource deficit). Blue boxplots: median < 0.05 (individuals perform better along this axis than alternatives), pink boxplots: median > 0.05 (individuals perform worse than alternatives). Dark boxplots: ranks significantly different from 0 (t-test, significance level: 0.05 and sequential Bonferroni correction); light boxplots: ranks not significantly different from 0.

577 **Figures**

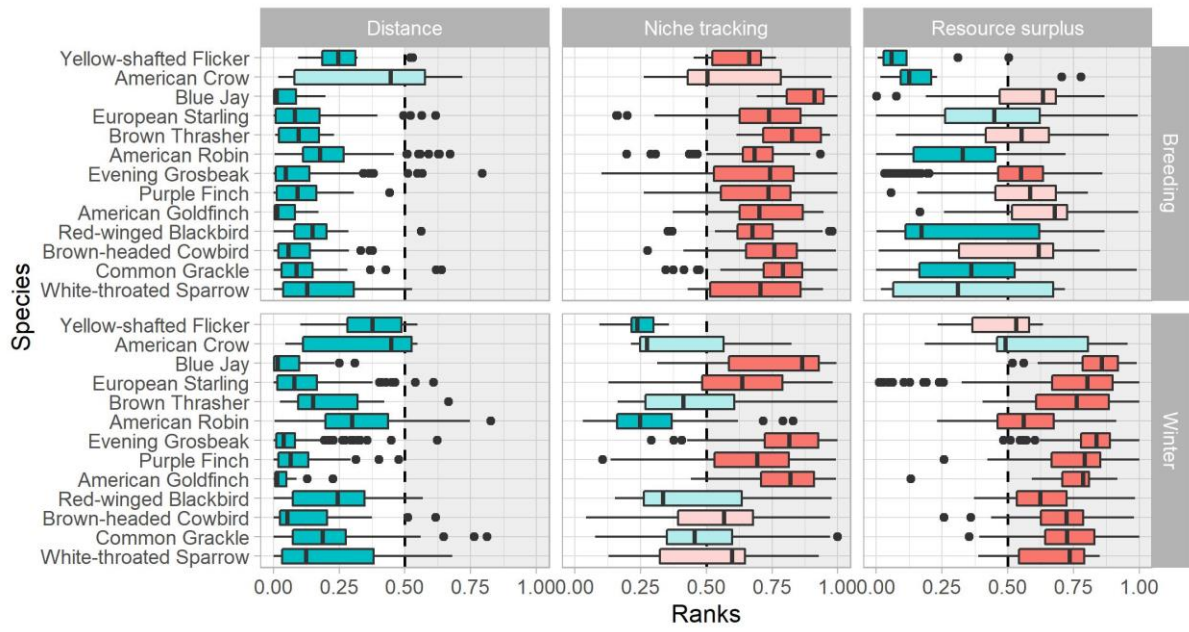
578 **Figure 1**



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581 Figure 2



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Table 1. Overview of results per species. *N* indicates the number of migratory birds sampled. Symbols indicate signal and significance of the statistical tests: blue plus sign for significantly ‘positive’ results (i.e. as expected; after sequential Bonferroni correction, with $\alpha = 0.05$), red minus sign for significantly ‘negative’ results (i.e. against expectations; after sequential Bonferroni correction, with $\alpha = 0.05$); n.s. for non-significant results. See the supplementary materials for detailed results: Figure S3 and Table S1 for niche tracking; Figure S4 and Table S2 for resource surplus; Figures S5-S6 and Tables S3-S4 for the trade-offs.

	N	Niche tracking		Resource surplus			Trade-offs		Individual migratory strategies						
		Migration better than staying at winter location	Migration better than staying at breeding location	Gain at breeding location	Gain at winter location	Year-round: migration better than residency	Distance & niche tracking	Distance & resource surplus	Minimise distance		Maximise niche tracking		Maximise resource surplus		
									Choice of winter location	Choice of breeding location	Choice of winter location	Choice of breeding location	Choice of winter location	Choice of breeding location	
Yellow-shafted flicker <i>Colaptes auratus</i>	11	+	+	+	-	+	<i>n.s.</i>	<i>n.s.</i>	+	+	+	-	<i>n.s.</i>	+	
American crow <i>Corvus brachyrhynchos</i>	12	+	+	+	-	+	+	+	+	+	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	+
Blue jay <i>Cyanocitta cristata</i>	29	+	+	+	-	<i>n.s.</i>	+	+	+	+	-	-	-	-	<i>n.s.</i>
European starling <i>Sturnus vulgaris</i>	178	+	+	+	-	+	+	+	+	+	-	-	-	-	<i>n.s.</i>
Brown thrasher <i>Toxostoma rufum</i>	16	+	+	+	-	+	<i>n.s.</i>	+	+	+	+	<i>n.s.</i>	-	-	<i>n.s.</i>
American robin <i>Turdus migratorius</i>	160	+	+	+	-	+	+	+	+	+	+	-	-	-	+
Evening grosbeak <i>Coccothraustes vespertinus</i>	689	+	+	+	-	+	+	-	+	+	-	-	-	-	-
Purple finch <i>Haemorhous purpureus</i>	62	+	+	+	-	+	+	+	+	+	-	-	-	-	<i>n.s.</i>
American goldfinch <i>Spinus tristis</i>	18	+	+	+	-	<i>n.s.</i>	+	<i>n.s.</i>	+	+	-	-	-	-	<i>n.s.</i>
Red-winged blackbird <i>Agelaius phoeniceus</i>	34	+	+	+	-	+	+	+	+	+	+	<i>n.s.</i>	-	-	+
Brown-headed cowbird <i>Molothrus ater</i>	78	+	+	+	-	+	+	+	+	+	+	<i>n.s.</i>	-	-	<i>n.s.</i>
Common grackle <i>Quiscalus quiscula</i>	177	+	+	+	-	+	+	+	+	+	+	<i>n.s.</i>	-	-	+
White-throated sparrow <i>Zonotrichia albicollis</i>	14	+	+	+	-	+	+	+	+	+	+	<i>n.s.</i>	-	-	<i>n.s.</i>