

The evolution of seasonal migration and the slow-fast continuum of life history in birds

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Abstract

Seasonal migration is a widespread adaptation in environments with predictable periods of resource abundance and scarcity. Migration is frequently associated with high mortality, suggesting that migratory species live on the “fast” end of the slow-fast continuum of life history. However, few interspecific comparative studies have tested this assumption and prior assessments have been complicated by environmental variation among breeding locations. We evaluate how migration distance influences the tradeoff between reproduction and survival in 45 species of mostly passerine birds that breed sympatrically in North American boreal forests but migrate to a diversity of environments and latitudes for the northern winter. We find, after accounting for mass and phylogeny, that longer distance migrations to increasingly amenable winter environments are correlated with reduced annual reproductive output, but also result in increased adult survival compared to shorter-distance migrations. Non-migratory boreal species have life history parameters more similar to long-distance migrants than to shorter-distance migrants. These results suggest that long-distance migration and other highly specialized strategies for survival in seasonal environments impose selection pressures that both confer and demand high adult survival rates. That is, owing to the reproductive cost of long-distance migration, this strategy can only persist if balanced by high adult survival. Our results reveal migratory distance as a fundamental life history parameter that predicts, and is inextricable from, the balance of survival and reproduction. Our study further provides evolutionary context for understanding the annual cycle demography of migratory species and the strategies long-distance migrants use to maximize survival on their journeys.

1 Introduction

2

3 Annual fecundity and age-specific survival represent a fundamental tradeoff along the
4 slow-fast continuum of life history (Stearns 1976; Reznick 1984; Saether 1988; Ricklefs 2000a;
5 Martin 2002). Fecundity and survival operate in tension presumably owing to physiological
6 constraints, though the evolutionary causes of this tradeoff remain debated (Gasser et al. 2000;
7 Zera and Harshman 2001; Ricklefs and Wikelski 2002; Karagicheva et al. 2018). This tradeoff is
8 integral to understanding the evolution of species' behavioral and ecological attributes, because
9 traits that promote survival may come at a cost to fecundity and vice versa (Clark and Martin
10 2007; Sol et al. 2016). However, the clarity of these patterns is often obfuscated by life history
11 variation along ecogeographic gradients, necessitating hypothesis testing frameworks that
12 distinguish between intrinsic constraints on life history and environmental variation in
13 demographic parameters (Ricklefs 2000a; Ricklefs and Wikelski 2002). In this paper, we
14 examine the evolutionary connections between seasonal migration—a widespread adaptation to
15 seasonality in vagile animals—and the slow-fast continuum of life history. We show that the
16 extraordinary long-distance migrations that characterize many temperate-breeding passerine
17 birds are fundamentally shaped by a tradeoff between annual fecundity and adult survival.
18 Further, we show that the migration distance of a species predicts its position along the slow-
19 fast continuum—but in a direction counter to widespread assumptions about migration.

20 Seasonal migration is an annual round-trip between regions dedicated to reproduction
21 and those dedicated to survival (Greenberg and Marra 2005), and as such is intrinsically
22 connected to these two fundamental life history parameters. In birds, long a model for both life
23 history theory (Ricklefs 2000b; Ricklefs and Wikelski 2002; Martin 2004) and migration
24 research, a widespread view about migration and fecundity is that migration evolved in tropical
25 species to increase reproductive output by exploiting seasonally available resources for
26 breeding in the temperate zone while escaping competition in the tropics (Cox 1968, 1985).

27 Migration has also been described as the costliest period of the annual cycle for migratory birds
28 (Sillett and Holmes 2002). These ideas—that migration improves fecundity and is costly to
29 survival—together have suggested (Bruderer and Salewski 2009) that the evolution of seasonal
30 migration shifts migratory species towards the fast end of the slow-fast gradient (higher
31 fecundity at a cost of lower survival; Sibly et al. 2012).

32 An alternative perspective is that migration evolves in seasonal areas to increase
33 survival during the resource-depleted non-breeding season (Salewski and Bruderer 2007;
34 Winger et al. 2019a). Under this view, migration does not evolve out of the tropics per se but
35 rather evolves as a survival strategy in response to seasonality in a breeding range, regardless
36 of the biogeographic origin of a lineage (Salewski and Bruderer 2007). That is, species exhibit
37 migratory behavior in circumstances in which escape from the breeding grounds during a
38 predictable period of resource scarcity improves annual survival and therefore the likelihood of
39 achieving a breeding season the next year. This view casts migration as an adaptive strategy to
40 seasonality analogous to hibernation, as opposed to an exploratory dispersal strategy to
41 improve reproductive success relative to an ancestral tropical condition. If migration evolves to
42 increase survival in the face of seasonality, then species that migrate to more favorable
43 locations in the nonbreeding season might be expected to have higher survival than species
44 that breed in the same seasonal environments but stay closer to their breeding grounds all year.
45 If migration serves to promote annual survival, it should be expected to come at a cost to annual
46 reproductive output (Ricklefs 2000a).

47 Despite the connections between life history theory and hypotheses for the evolution of
48 migration in birds, the relationship between the migratory strategies employed by different
49 species and tradeoffs in survival and fecundity has not been rigorously tested (Bruderer and
50 Salewski 2009). The study of life history tradeoffs in birds has long focused on understanding
51 ecogeographic patterns in reproductive strategies, such as larger clutch sizes in temperate
52 versus tropical breeding birds (Ricklefs 2000b; Martin 2004) or the pace of growth and

53 development across latitudes (Martin 2015). Owing to the general recognition of seasonal
54 migration as a fundamental aspect of avian ecology and behavior, macroecological studies of
55 global variation in avian reproductive output (Jetz et al. 2008; Sibly et al. 2012; Cooney et al.
56 2020) or survival (Muñoz et al. 2018; Bird et al. 2020) often include migratory status as a model
57 covariate, but without an explicit hypothesis for its effect. These studies have often found
58 migration to be associated with a “faster” life history strategy, such as high breeding productivity
59 (Sibly et al. 2012). However, because migratory behavior is strongly correlated with seasonality
60 and breeding latitude, migratory species are likely to exhibit life history conditions associated
61 with breeding at high latitudes, such as relatively large clutch sizes (Jetz et al. 2008). Thus, a
62 direct influence of migratory behavior on the slow-fast continuum may not be revealed by global
63 analyses whose primary axis of variation is latitudinal.

64 A second area of relevant research has focused on seasonal variation in survival of
65 migratory birds to improve full annual cycle population models (Faaborg et al. 2010; Hostetler et
66 al. 2015; Marra et al. 2015). In a highly cited landmark study, Silllett and Holmes (2002)
67 estimated the mortality associated with migration in a boreal-breeding Neotropical migratory
68 songbird, the Black-throated Blue Warbler (*Setophaga caerulescens*). They found that most
69 mortality in this species occurred during migration as opposed to the breeding (summer) or non-
70 breeding (winter) “stationary” periods (Silllett and Holmes 2002). Although the goals of this and
71 similar studies have been to compare seasonal variation in survival rates of individual migratory
72 species, their results have sometimes been generalized to a paradigm that migration, broadly, is
73 a strategy that carries a high survival cost (Newton 2007; Faaborg et al. 2010; Sibly et al. 2012;
74 Somveille et al. 2019). Yet, it has more rarely been asked how the survival costs associated
75 with long-distance migration compare to an alternative strategy of staying closer to the breeding
76 grounds year-round (Greenberg 1980; Sherry and Holmes 1995; Bruderer and Salewski 2009).
77 Though migration clearly requires substantial energy and presents a risk to survival, so does
78 maintaining homeothermy and body condition in regions with cold temperatures or scarce food

79 resources (Ricklefs 1980; Swanson and Garland 2009). Further, recent studies in other
80 migratory species, especially non-passerines, have discovered high rates of adult survival
81 associated with long-distance migration, calling into question the generality of a high mortality
82 cost of migration (Lok et al. 2015; Conklin et al. 2017; Senner et al. 2019).

83 The consequences of migration for tradeoffs between survival and reproduction have
84 been explored somewhat in studies of intraspecific variation in migratory behavior (Ketterson
85 and Nolan 1982; Alves et al. 2013; Ely and Meixell 2015; Lok et al. 2017; Zúñiga et al. 2017;
86 Buchan et al. 2019), but less so in the context of understanding the evolution of species-level
87 life history tradeoffs and hence the position of species along the slow-fast continuum.
88 Greenberg (1980) proposed the time allocation hypothesis to explain the relationship between
89 migration, survival and reproduction. This study suggested that migratory species invest less
90 time in breeding than temperate non-migratory species but compensate for lower fecundity by
91 investing in migrations to locales with resources that support increased winter survival. A small
92 number of studies have subsequently demonstrated that temperate-breeding migratory species
93 have lower annual fecundity than temperate residents or short-distance migrants (Mönkkönen
94 1992; Böhning-Gaese et al. 2000; Bruderer and Salewski 2009). Research on other taxa has
95 also found that migration distance may be positively, and counterintuitively, correlated with adult
96 survival rates (Conklin et al. 2017) or longevity (Møller 2007). However, most previous
97 interspecific comparisons have tested the relationship between migratory behavior and either
98 survival and reproduction in isolation—rather than the tradeoffs among these parameters—and
99 have often not been able to control for environmental heterogeneity among breeding locations
100 that could influence demographic parameters (Ricklefs 2000a).

101 Here, we assess the influence of seasonal migration on the slow-fast continuum of life
102 history in a geographically and ecologically circumscribed system: small-bodied, mostly
103 passerine birds breeding in the boreal forests of eastern and central North America (Fig. 1). This
104 system is well-suited to assessing the impact of migratory behavior on life history because of

105 the high diversity of similarly-sized species that breed at the same latitudes and in the same
106 habitat but spend the nonbreeding season in drastically different regions (from year-round
107 residents that do not leave the frozen boreal region in the winter to long-distance migrants that
108 migrate to South America; Fig. 1). By integrating multiple published long-term datasets on
109 population demographic parameters from the boreal region, we test how variation in migratory
110 distance influences species' life history. First, we test the time allocation hypothesis (Greenberg
111 1980; Bruderer and Salewski 2009) that long-distance migratory species invest less time during
112 the annual cycle in reproduction than co-distributed short-distance migrants or residents.
113 Second, we test whether increased migratory distance and decreased time allocated to
114 reproduction is associated with reduced annual fecundity. Third, we assess the influence of
115 migration distance on annual adult survival and predict that if longer-distance migrations reduce
116 fecundity, these migrations should also be associated with increased annual survival.

117 If migratory distance away from boreal breeding grounds influences survival, this
118 relationship may be mediated by disparate conditions experienced on the wintering grounds.
119 Are the costs of long-distance migration offset by benefits of more distant wintering grounds
120 (Somveille et al. 2018)? To address this question, we test whether interspecific variation in
121 migratory distances is correlated with macroecological proxies for winter environment
122 (temperature, precipitation and primary productivity) and whether these variables influence
123 annual survival. Survival could also be influenced by the climatic similarity of migratory species'
124 breeding and winter ranges during their summer and winter, respectively, which affects the
125 breadth of conditions to which they must adapt throughout the year. Winter ranges of migratory
126 birds tend to occur in areas that are climatically more similar to the breeding grounds than
127 expected by chance, suggesting that "niche tracking" underlies migratory movements at
128 macroecological scales (Gómez et al. 2016; Zurell et al. 2018; Somveille et al. 2019). To test
129 whether niche tracking provides a survival benefit, we test how niche overlap between the

130 breeding and winter ranges (Zurell et al. 2018) is correlated with migration distance and whether
131 it predicts annual survival.

132

133 **Methods**

134 *Study system.*— Our study system comprises 39 migratory and 6 non-migratory species
135 of birds (41 passerine species from 11 families and 4 woodpecker species) breeding in forested
136 habitats in the boreal forest belt of eastern and central North America (Fig. 1, Table S1).
137 Together, these species comprise a regional community of breeding birds in the northern spring
138 and summer but they spend the northern winter in disparate locales. Because body size is an
139 important axis of the slow-fast continuum (Ricklefs 2000a; Martin 2004), we focused on small-
140 bodied birds that can reproduce beginning at ~1 year of age. Most species ranged from 6-33
141 grams (median 11 grams), but 7 species were larger (50-87 g). In exploratory analyses, we
142 found similar results when restricting analyses to the set of species < 33 grams.

143 We included species that breed in bog, spruce-fir and mixed forested habitats
144 throughout the boreal and hemiboreal region (Fig 1). To control for latitude, we excluded
145 species primarily restricted to more northern treeline habitats of the taiga (e. g., *Catharus*
146 *minimus*, *Setophaga striata*) and those primarily restricted to more southerly latitude (e. g.,
147 *Piranga olivacea*, *Setophaga pinus*) even if their breeding ranges overlapped marginally with
148 our region. We included species whose ranges extend beyond the boreal region if the species
149 breeds broadly throughout the boreal forest (e.g., *Picoides villosus*, *Vireo olivaceus*) and had
150 available data from boreal populations. We included species with regular seasonal migrations
151 and those known to be primarily non-migratory but excluded species that primarily undergo
152 facultative irruptive or nomadic movements (e.g., *Sitta canadensis*, *Loxia leucoptera*) due to the
153 difficulty of defining migratory patterns or breeding periods.

154 *Live history predictors: mass and migration.*— Mass data were obtained from Dunning
155 (2008) or Billerman et al. (2020). We used a binary predictor, migratory status, to indicate

156 whether or not a species engages in regular seasonal migration. We estimated migration
157 distance as the geodesic distance between the centroids of the breeding and wintering range of
158 each species, including any year-round portions in both the breeding and wintering range when
159 calculating centroids (BirdLife International and Naturserve 2014). To ensure that our migration
160 distance estimate was as accurate as possible for populations breeding in the boreal forest belt,
161 we used only the portions of breeding ranges overlapping with boreal forest ecoregions
162 (Omernik and Griffith 2014; Level I ecoregions “northern forests,” “taiga,” and “Hudson plain”;
163 Fig. 1) in the calculation of breeding range centroid. We also excluded any portions of wintering
164 ranges within or west of the Rocky Mountains because these areas are generally used by more
165 western breeding populations (Kelly and Hutto 2005; Kardynal and Hobson 2017). Geographic
166 calculations were made using geospatial packages in R (Bivand and Rundel 2019; Bivand et al.
167 2019; Hijmans 2019).

168 *Life history outcome variables.*— We gathered published data related to time allocation
169 for breeding, developmental duration, annual reproductive output and annual adult survival
170 (Table 1). The data we compiled was collected mainly within the boreal region (Fig. 1) to control
171 for latitudinal variation in demographic parameters.

172 We estimated the number of days each species invests in breeding. Comparable data
173 on the full breeding cycle (from establishment of territories and building of nests through
174 fledging of chicks) was not available for the boreal region for many species, so we used three
175 proxies.

176 First, we estimated the amount of time each species spends on or near its breeding
177 grounds by using eBird data (Sullivan et al. 2009) to calculate the interval of time between
178 spring and fall migratory passage through Chicago, IL, USA. Migratory passage through
179 Chicago is a reasonable proxy for time spent on the breeding grounds for the migratory species
180 in this study because Chicago is near to but not within the boreal region (approximately 350 km
181 to the southern edge of the boreal forest), it is a stopover location common to all the species, it

182 experiences a high density of bird migration, and an active community of birdwatchers generate
183 ample eBird data (Winger et al. 2019b). We analyzed eBird data from Cook County, IL from
184 2000-2017. For each species in each year and season (spring and fall), we calculated the date
185 with the most eBird records for that species and considered this to be the date of “peak
186 migration”. We calculated the average number of days between the median peak spring and
187 median peak fall migration dates across all years for each species. This “intermigratory period”
188 serves as a proxy for the relative amount of time species spend on or near their breeding
189 grounds.

190 Second, we gathered data specific to the boreal region on the egg laying period. We
191 used data from *Breeding Birds of Ontario: Nidiology and Distribution* (Peck and James 1983,
192 1987), henceforth “*Nidiology*.” *Nidiology* summarizes nearly 85,000 nest records of birds
193 breeding in Ontario, Canada, collected mostly by the Ontario Nest Records Scheme initiated in
194 1956. We used this volume because it is more specific to boreal latitudes and more consistent
195 in information than more general sources on breeding birds (Billerman et al. 2020). We used
196 *Nidiology*’s records of the earliest and latest egg dates to calculate the number of days over
197 which each species lays or incubates eggs (“egg interval”; Table 1).

198 Third, we used *Nidiology* to calculate the average individual incubation period for each
199 species (“incubation period”; Table 1). Egg interval represents the temporal breadth of the
200 breeding cycle for a species in the boreal region, whereas incubation period represents an
201 individual-level and embryonic developmental duration.

202 We calculated average clutch size from the range of clutch sizes listed in *Nidiology* for
203 each species. We calculated annual fecundity as (average clutch size) x (maximum number of
204 successful broods) per season. *Nidiology* did not contain information on number of broods, so
205 we referred to Billerman et al. (2020) for information on number of broods. Data on incidence of
206 double brooding were not available; we marked species as double brooders if species accounts
207 indicated that an additional brood may be raised following a successful first brood.

208 We also compiled data on reproductive output from the Vital Rates of North American
209 Birds project (henceforth, *Vital Rates*; Desante et al. 2015) for 29 species with available data.
210 *Vital Rates* provides estimates of demographic parameters derived from widely implemented
211 constant-effort capture-mark-recapture surveys from 1992-2006, as part of the Monitoring Avian
212 Productivity and Survivorship (MAPS) program. We used *Vital Rate*'s Reproductive Index, an
213 estimate of the number of young birds produced per adult annually, calculated using effort-
214 corrected generalized linear mixed models (Desante et al. 2015). *Vital Rates* presents estimates
215 of Reproductive Index from different geographic regions using Bird Conservation Regions (Bird
216 Studies Canada and NABCI 2014) to delineate boundaries for study sites according to biomes.
217 We calculated mean Reproductive Index for our species by prioritizing BCRs 8 and 12, which
218 broadly overlap with eastern and central boreal forests, and substituting mean estimates BCRs
219 6, 7, 13, or 14 when necessary. We did not include any parameters that *Vital Rates* flagged as
220 not usable due to unreliable model estimates.

221 We similarly estimated annual adult survival from boreal-specific regions using *Vital*
222 *Rates*' Adult Apparent Survival Probability (ϕ , Cormack-Jolly-Seber estimation), which is "an
223 estimate of the annual probability that a resident bird that was alive and present at the station in
224 year t will also be alive and present in year $t+1$ " (Desante et al. 2015).

225 *Modeling.*— We used linear models to test hypotheses on the relationship between
226 seasonal migration and life history. For clutch size, we used average clutch sizes, meaning that
227 these data were not integer counts. We modeled the relationship between the intermigratory
228 period (of migratory species only) and migration distance, and between egg interval and both
229 migratory status and migration distance. For the 5 life history outcome variables related to
230 developmental duration, reproductive output and survival (Table 1) we also assessed the
231 influence of body size. For these 5 variables we fit three models: One model with mass as a
232 predictor, a second model with migration status and migration distance as predictors, and a third
233 model with all three predictors. We log-transformed mass and the outcome variables because

234 many biological processes scale non-linearly with body size, and centered and standardized
235 migration distance. For each outcome variable, we compared the three models with the second-
236 order Akaike Information Criterion (AICc) using *MuMIn* (Bartón 2019) to assess the relative
237 performance of migration and mass as predictors. Models for different outcome variables
238 contain slightly different subsets of species based on the availability of data on the outcome
239 variable (Tables 1, S1).

240 We tested whether the data were best modeled using Phylogenetic Generalized Least
241 Squares (PGLS) or Ordinary Least Squares (OLS) by fitting an OLS full model (using all
242 relevant predictors) and then using the function *phylosig* from *phytools* (Revell 2012) to test for
243 phylogenetic signal (λ) in the model's residuals (Revell 2010). Although controlling for shared
244 phylogenetic ancestry is important in comparative analyses, PGLS has the potential to reduce
245 model accuracy when a model's residuals do not have phylogenetic signal (Revell 2010). For a
246 phylogeny, we built a consensus tree with data from *birdtree.org* (Jetz et al. 2012), using
247 procedures described in Pegan and Winger (2020). For models with significant λ , we performed
248 PGLS modeling with the *gls* function in *nlme* (Pinheiro et al. 2019), including a correlation
249 structure of expected phylogenetic covariance among species according to a Brownian motion
250 model (function "corBrownian" in *ape*; Paradis and Schliep 2019). For response variables that
251 did not have significant phylogenetic signal in model residuals, we used OLS. We also present
252 PGLS analyses of all outcome variables (Table S3) for which we jointly estimated Pagel's λ and
253 the model using "corPagel" in *ape* (Revell 2010; Paradis and Schliep 2019).

254 *Winter climate and niche tracking.*— To test whether differences in annual survival
255 across species with different migratory distances are associated with differences in winter
256 conditions, we assessed winter climate and primary productivity across the winter ranges of
257 each species. We used eBird (Sullivan et al. 2009) records for each species from November to
258 February (all years) and retained all points that fell within a species' typical winter range
259 (BirdLife International and Naturserve 2014) to exclude extralimital vagrants. We excluded

260 *Catharus fuscescens* and *Oporornis agilis* due to a paucity of winter eBird records. We
261 downloaded month-level climate data (Fick and Hijmans 2017) at 30s resolution and NDVI data
262 (Pinzon and Tucker 2014), averaged from the years 2000-2010. We filtered rasters to contain
263 one eBird record per grid cell to mitigate spatial bias and used these points to calculate species-
264 level means for winter temperature, precipitation, and normalized difference vegetation index
265 (NDVI). We then conducted a principal components analysis to reduce temperature,
266 precipitation, and NDVI to a single species-level value (PC1, representing winter climate) and
267 assessed the correlation between migratory distance and winter climate PC1.

268 We also assessed the relationship between migratory distance and an estimate of the
269 overlap of breeding and non-breeding season climatic niches from Zurell et al. (2018). Niche
270 overlap represents the similarity between the conditions (climate and NDVI) encountered in the
271 breeding range during breeding months, and the winter range during winter months. Finally, we
272 analyzed the effect of winter climate PC1 and niche overlap on annual adult survival (ϕ) in
273 separate models that included mass as a covariate, after log-transforming ϕ and mass.

274

275 **Results**

276

277 In most cases, models with migration variables (distance or status) had lower AICc
278 scores (Table S2) than models containing only mass as a predictor, and migration variables
279 were significantly ($p < 0.05$) associated with most life history outcome variables after controlling
280 for mass (see Table 2 for details), indicating that migration explains mass-specific variation in
281 each outcome variable.

282 For two life history outcome variables (incubation period and annual adult survival), we
283 highlight results of phylogenetic generalized least squares regression (PGLS). For the
284 remaining variables, we present the results of OLS regression because we found that PGLS
285 was not justified based on lack of phylogenetic signal in the model residuals (Methods).

286 *Migration distance and life history.*— Among the migratory species in our study, the
287 variables representing time allocation in breeding were significantly negatively associated with
288 migration distance (Table 2). The analysis of intermigratory period indicates that long distance
289 migratory species arrive later and spend significantly less time on or near their breeding
290 grounds before departing earlier for fall migration than short-distance migratory species (Table
291 2, Fig. 2). For an increase in migration distance of one standard deviation, or about 2000 km,
292 our best model predicts a decrease in intermigratory period of about 26 days. This pattern was
293 corroborated by egg interval, which predicted an egg laying period about 9 days shorter per
294 standard deviation increase in migration distance.

295 This shortening of the breeding season does not seem to be associated with faster
296 embryonic developmental rates for longer-distance migrants, as incubation period was not
297 strongly correlated with migratory distance (Fig. 2) and the best model for incubation period
298 contained only mass as a predictor (Tables 2, S2).

299 Average clutch size and annual fecundity were both significantly negatively associated
300 with migratory distance (Fig. 2, Table 2). Reproductive Index (Desante et al. 2015) further
301 suggested that the number of young fledged per adult trends negatively (but not significantly so)
302 with increasing migratory distance across species (Fig. 2, Table 2). Apparent annual adult
303 survival index (ϕ ; Desante et al. 2015) was significantly positively associated with migratory
304 distance (Table 2, Fig. 2).

305 *Migratory status and life history.*— In contrast to the relationships between migration
306 distance and life history variation among the 39 migratory species, in which longer distance
307 migrations were associated with “slower” life history values, non-migratory behavior (which
308 involved 6 species that are year-round residents in a harsh winter environment with scarce
309 resources) was associated with a shorter egg interval, lower clutch size and fecundity, and
310 higher annual survival (Table 2, Fig. 2) than migratory species overall. That is, non-migratory
311 species were more similar in survival and reproduction to long-distance migrants than to short-

312 distance migrants, resulting in non-linear relationships with migration distance and some
313 variables (Fig. 2).

314 *Winter climate and niche tracking.*—Migratory distance was significantly associated with
315 winter climate PC1, indicating that species that migrate longer distances from the boreal region
316 spend the winter in locations that are warmer, wetter and greener (Table 3, Fig. 3). However,
317 migratory distance was also strongly negatively related to niche overlap (Zurell et al. 2018),
318 indicating that longer-distance migrants have winter climates more dissimilar to their summer
319 environments than do short-distance migrants (Table 3, Fig. 3).

320 Although adult survival (ϕ) was significantly predicted by migratory distance, and
321 migratory distance significantly predicted both winter climate PC1 and niche overlap, ϕ was not
322 significantly predicted by either winter climate PC1 or niche overlap (Fig. 3, Table 3).
323 Nevertheless, the trend of the relationship between ϕ and winter climate PC1 suggests that
324 wintering in the warmer, wetter and greener environments associated with longer migrations
325 may improve survival (Fig. 3, Table 3). Tracking a climatic niche throughout the year, however,
326 did not improve survival.

327

328 **Discussion**

329

330 Although there has been widespread interest in the consequences of life table
331 parameters for the population demographics of migratory species (Sherry and Holmes 1995;
332 Ricklefs 1997; Clark and Martin 2007; Faaborg et al. 2010), relatively little attention has been
333 paid to the tradeoffs among these parameters across species with different migratory strategies
334 and the evolutionary forces that shape them. Our focused analysis of demographic parameters
335 from the boreal region shows that across 45 species of small-bodied, co-distributed birds
336 breeding in similar habitats, seasonal migration has important and under-explored

337 consequences for the trade-off between annual fecundity and survival. Further, these dynamics
338 help explain the evolutionary dynamics underlying seasonal migration.

339 In support of the time allocation hypothesis (Greenberg 1980), our results indicate that
340 migratory distance is negatively associated with temporal investment in breeding. As expected,
341 migratory species that winter closer to their boreal breeding grounds migrate earlier in the spring
342 and later in the fall and can be found incubating eggs during a longer time window than longer-
343 distance migrants that winter closer to the equator, indicating a temporal constraint on breeding
344 associated with longer-distance migration (Fig. 2). Long-distance migrants do not appear to
345 compensate for this shorter breeding window through faster embryonic developmental times,
346 which showed little relationship with migratory distance (Table 2, S2).

347 Our results further show that longer-distance migratory species have reduced clutch size
348 and annual fecundity, as well as fewer fledged juveniles per adult (Desante et al. 2015), relative
349 to shorter-distance migrants (Fig. 2). The relationship between annual fecundity and migration
350 distance is consistent with, but stronger than, the relationship between clutch size and
351 migration, because long-distance migrants in our study are not known to raise more than one
352 successful brood in a single year (Table S1, Fig. 2). In some short-distance migratory species in
353 our study the incidence of double brooding is likely low, but comparable data on incidence of
354 multiple broods was lacking. Thus, future field studies are needed to determine whether the
355 relationship between migration distance and reproductive output is closer to the curve for clutch
356 size versus the steeper curve shown when maximum annual brood number is considered (Fig.
357 2).

358 Theory predicts that a decrease in annual fecundity across species should be
359 associated with an increase in survival. By looking to the products of a long-term mark-
360 recapture study with data specific to the boreal region (Desante et al. 2015), we found that
361 migration distance trends positively with apparent annual adult survivorship in boreal-breeding
362 birds. This is particularly striking given that the longest-distance migrants in our system undergo

363 migrations of nearly 8000 km to equatorial forests (Fig. 1, Table S1) and migration is thought to
364 be the costliest period of the annual cycle for survival in Neotropical migratory songbirds (Silllett
365 and Holmes 2002). Yet, our results indicate that these long migrations provide a survival benefit
366 compared to migrating shorter distances to higher latitude temperate and subtropical wintering
367 latitudes (Fig. 2).

368 We further found that migratory distance and, to a lesser extent, annual adult survival
369 were positively correlated with wintering in warmer, wetter and greener environments (Fig. 3).
370 By contrast, the degree to which winter climate was similar to breeding climate (niche overlap)
371 was negatively correlated with migratory distance. These results suggest that among the
372 migratory species in our study, maximum survival is afforded to species that migrate the longest
373 distances to humid equatorial forests, despite the energetic costs of long-distance migration and
374 the fact that these long migrations lead to relatively greater differences in breeding season
375 versus winter season climatic conditions. The importance of winter habitat for the annual cycle
376 of migratory birds has been well documented within species, such as those whose individuals
377 winter in habitats of differing quality (Norris et al. 2004; Faaborg et al. 2010; Rushing et al.
378 2016). However, the connection between migration distance, winter climate and annual survival,
379 and its key evolutionary tradeoff with fecundity, has not been well elucidated in a
380 macroecological comparative context. The specific macroecological conditions correlated with
381 migration distance and winter survival in our study species, which are mainly forest-dwelling
382 landbirds, are not likely to be generally applicable across migratory taxa with other habitat
383 preferences and resource bases, but nevertheless these results speak broadly to the
384 importance of winter resources for survival and reproduction.

385 Whereas long-distance migration is frequently described as costly to survival, our results
386 show that the true cost of the longest migrations among migratory species in a temperate
387 breeding community is a reduction in annual reproductive output. Temperate-breeding
388 songbirds that endure migration of thousands of kilometers each year occupy a slower position

389 on the slow-fast continuum of life history than their close relatives who migrate shorter distances
390 but attempt to survive the winter closer to their breeding grounds. Species with shorter
391 migrations to temperate or subtropical regions operate on the faster end of the slow-fast
392 continuum, with relatively higher annual fecundity and lower adult survival rates. Aspects of this
393 dynamic have been suggested previously in separate studies of survival or reproduction
394 (Böhning-Gaese et al. 2000; Møller 2007; Bruderer and Salewski 2009; Conklin et al. 2017).
395 However, a focused phylogenetic comparative analysis capable of revealing the evolutionary
396 tradeoffs among these highly integrated life history variables has been lacking and thus the true
397 relationship between long-distance migration, survival and fecundity has not been widely
398 appreciated.

399 Our study also reveals meaningful distinctions between non-migratory species and
400 short-distance migrants. We found that non-migratory boreal species had levels of reproductive
401 output and survival more similar to long-distance migrants than to short-distance migrants (Fig.
402 2). Except for Canada Jay (*Perisoreus canadensis*), all non-migratory species in our study
403 (Table S1) are cavity-nesting chickadees (Paridae) or woodpeckers (Picidae), and all six
404 species have specialized adaptations for surviving harsh boreal winters such as food-caching
405 (Sherry 1989; Waite and Reeve 1993), social cooperation, or the ability to excavate grubs from
406 trees. Our results therefore suggest a compelling pattern wherein the most specialized, extreme
407 adaptations—required either to survive the harshest winters *in situ* or perform the longest
408 migrations—exert strong selection pressures (Sol et al. 2010, 2016) that optimize annual adult
409 survival at the cost of annual fecundity.

410 These results are consistent with emerging knowledge from field studies of some of the
411 most extreme long-distance migratory birds, “long-jump” scolopacid sandpipers and godwits that
412 breed in the high arctic and perform extreme flights to reach their wintering grounds (Conklin et
413 al. 2017). In these species, there is increasing evidence that adult annual survival and longevity
414 is surprisingly high given their remarkable annual journeys (Leyrer et al. 2013; Senner et al.

415 2019; Swift et al. 2020). This suggests that extreme long-distance migration selects strongly—
416 potentially during the first year of life—for high quality individuals who as adults are capable of
417 repeating these extraordinary feats every year, thus narrowing the “individual quality spectrum”
418 to the highest quality individuals (Conklin et al. 2017). Our results provide an evolutionary life
419 history framework for interpreting the high annual survival of these extreme long-distance
420 migrants. Given the reproductive cost of long-distance migration, extreme migration can only be
421 a successful evolutionary strategy if individual adult survival is high, thus placing these species
422 on the slow end of the slow-fast continuum.

423 This perspective provides further evolutionary context for some surprising behaviors of
424 migratory species. For example, one of the species in our study, the Veery (*Catharus*
425 *fuscescens*), is a long-distance migrant breeding in temperate forests and wintering in
426 Amazonia. A recent study (Heckscher 2018) found that Veeries shorten their breeding season in
427 years with hurricane activity along their migratory route, putatively due to their perception of
428 distant, future weather conditions. In other words, the evolution of their migration pattern—and
429 the weather-detecting sensory systems that enable it—are so finely tuned to survival probability
430 that some adult individuals will forego reproductive attempts to ensure a successful migration
431 (Heckscher 2018). Our study shows that this species’ adaptive capacity to respond to subtle
432 environmental conditions that threaten future survival during migration is representative of a
433 point along a life history continuum wherein longer, more difficult migrations maximize annual
434 survival at the cost of annual reproduction.

435 *Life history tradeoffs and the evolution of migration.*— The evolution of seasonal
436 migration in birds has often been explained as an out-of-the-tropics process wherein species
437 improve reproductive success by escaping the competition in the crowded tropics (Cox 1968,
438 1985; Rappole and Jones 2002). Support for the out-of-the tropics models has come in part
439 from studies showing higher fecundity in temperate migrants versus tropical residents, which
440 has been interpreted to mean that the evolution of migration facilitates greater reproductive

441 success (reviewed in Salewski and Bruderer 2007; Winger et al. 2019a). A signature of this
442 pattern is visible in some global studies where migration trends positively with fecundity
443 variables (Jetz et al. 2008; Sibly et al. 2012). Although the tropical origins of long-distance
444 migration have been contested in some lineages (Winger et al. 2014), other migratory lineages
445 are ultimately of tropical biogeographic origin (Bruderer and Salewski 2008; Winger et al.
446 2019a). We have argued that even in lineages of tropical origin, migration does not evolve out of
447 the tropics as a consequence of long-distance dispersal to improve reproductive success
448 (Winger et al. 2019a). Rather, migration evolves when species expanding their ranges through
449 normal dispersal processes encounter higher seasonality in a breeding location, often at a
450 higher latitude, or when breeding populations face increases in seasonality through time *in situ*
451 (Salewski and Bruderer 2007). The adaptive benefits of philopatry (returning to breed in similar
452 locations as one was reared; Davis and Stamps 2004) select for individuals that return to their
453 breeding grounds in spring (Winger et al. 2019a). From this perspective, migration is an
454 adaptive survival strategy that allows for persistence in seasonal areas, regardless of the
455 biogeographic origin of a lineage.

456 Our study lends support to this survival hypothesis by demonstrating the relationship
457 between migration, reproduction and survival among a community of species that experiences
458 high seasonality in the breeding range. Overall, the annual fecundity of the migratory species in
459 our study is likely greater than that of close tropical-breeding relatives, since it varies along a
460 strong latitudinal gradient in clutch size (Ricklefs 2000a; Clark and Martin 2007). However,
461 annual fecundity is also relatively high among the non-migratory species that occupy temperate
462 latitudes. Thus, the evolution of migration promotes fecundity only insofar as it promotes
463 survival and persistence of populations in highly seasonal environmental conditions where
464 annual fecundity—and mortality—are generally higher than in the tropics. In other words, the
465 colonization of temperate, seasonal environments moves populations towards a “faster” life
466 history compared to tropical species (Martin 2015), where high fecundity trades off with high

467 mortality. The evolution of long-distance migration mitigates this high annual mortality by
468 bolstering winter survival, but at a necessary cost to annual fecundity, thereby ‘slowing down’
469 life history. The longer the migration, the slower the life history.

470 We suggest that the evolution of seasonal migration should be regarded as a
471 fundamental life history tradeoff intimately connected to environmentally driven patterns of
472 survival and fecundity, as opposed to a unique strategy with a deterministic benefit for
473 reproductive output.

474 *Opportunities for further research.*—Our analyses of data compiled from published
475 sources highlight the potential for further insights to be gained from focused field studies. First,
476 reliable data on longevity across our study species is important to understand lifetime
477 reproductive success as opposed to annual patterns. Second, although annual survival is
478 thought to be age-independent in adult birds (Ricklefs 1997), age-specific life tables of survival
479 and fecundity will improve our understanding of how migratory behavior influences the slow-fast
480 continuum and the consequences for population demography (Saether and Bakke 2000). Data
481 on juvenile survival rates, while much more difficult to study due to the likelihood of conflating
482 mortality with natal dispersal, will help illuminate the differences in selection pressures facing
483 species across the migratory spectrum (Conklin et al. 2017)

484 An important mystery highlighted by our study concerns the post-breeding, pre-migratory
485 periods, which is in general the most poorly understood period of the avian annual cycle (Clark
486 and Martin 2007). Even if post-embryonic developmental rates are longer in shorter-distance
487 migrants, short-distance migrants still spend substantially greater time post-development on or
488 near their breeding sites before fall migration than do long-distance migrants (Fig. 4). That is,
489 short-distance migrants have a “faster” life history despite an annual schedule that is less
490 temporally constrained. What do hatch-year birds in short-distance migratory and resident
491 species—which will not breed until the following spring—do with their “extra” time (Fig. 4)?

492 One possibility is that shorter-distance migratory species and residents invest more time
493 in the prospecting phase of dispersal (Reed et al. 1999), wherein they use the pre-migratory
494 period to search nearby breeding locations for future breeding sites (Cormier and Taylor 2019).
495 By contrast, long-distance migratory species, with constrained time for prospecting, may be
496 under greater selection to return to familiar breeding locations (Winger et al. 2019a), which
497 could counterintuitively constrain dispersal distances in longer-distance migrants. This
498 possibility is important to investigate because annual survival estimates based on mark-
499 recapture could be unreliable if adult dispersal rates differ systematically across species.

500 *Implications for the conservation of migratory birds.*—Our study shows that at its core,
501 migration is a survival strategy that evolves when the benefits of escaping the breeding region
502 during the resource-poor season outweigh the risks of long-distance journeys. Yet, this strategy
503 is only likely to be beneficial when suitable habitat is available on the wintering grounds and
504 throughout migration (Conklin et al. 2017). It is obvious that the pace at which anthropogenic
505 habitat destruction has occurred on the Neotropical wintering grounds and at stopover sites for
506 the long-distance migrants in our study far exceeds the ability of these species to adjust their
507 delicately balanced life history strategies. Other major disruptions to migration, such as from
508 artificial light (Loss et al. 2015; Winger et al. 2019b), may further tip the scales against long-
509 distance migration as an effective strategy. Biologists have warned for decades that long-
510 distance migratory species are among the species most at risk of population decline in the
511 Anthropocene (Robbins et al. 1989; Rosenberg et al. 2019). Our study, by highlighting that
512 lowered fecundity is a cost of the heightened survival afforded to long-distance migrants,
513 provides an evolutionary context for understanding the importance of habitat conservation and
514 safe passage for migratory birds throughout their journeys.

515

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517

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523 **References**

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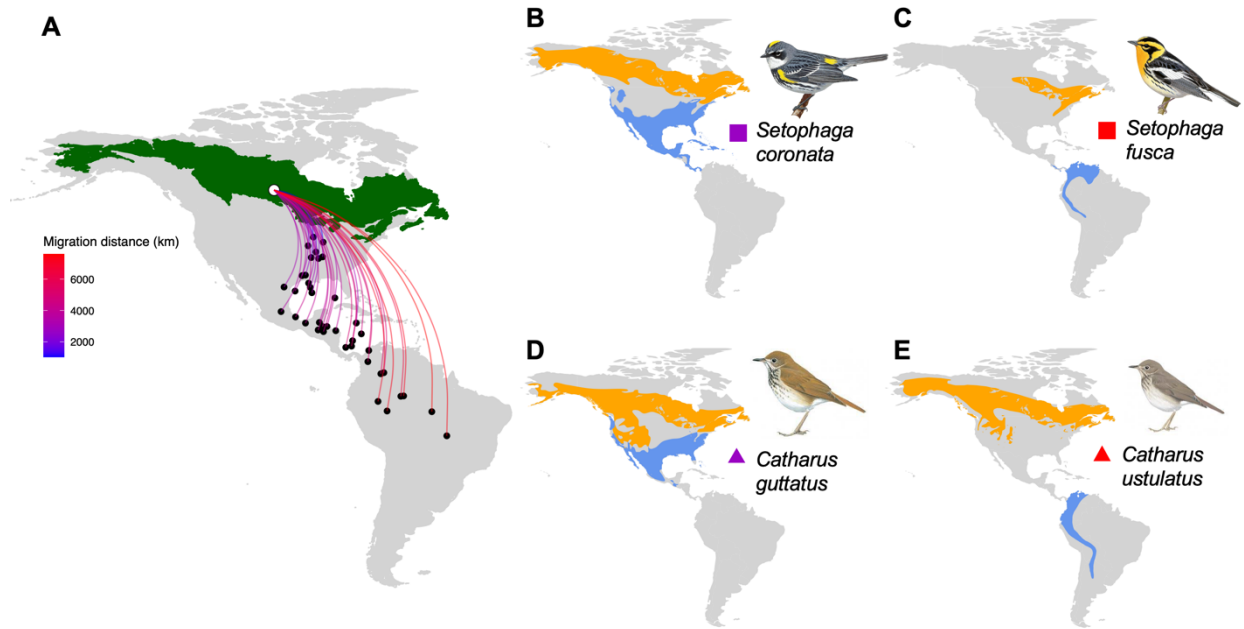
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742 **Figures and Tables**



743 **Figure 1.** A) The 45 species in our study (Table S1) broadly co-occur during the breeding season
744 across the boreal forest belt (green, indicating ecoregions “northern forests”, “taiga” and “Hudson plain”;
745 Omerik and Griffith 2014) but winter in disparate locations. Hypothetical migration routes are depicted
746 between a single breeding location and the centroid of the winter ranges of each of 39 migratory species
747 (Methods). B-E) Example species representing short- (B, D) and long- (C, E) distance migratory species
748 in pairs in each of two genera. These example species are highlighted in Figs. 2-4 with the squares
749 (*Setophaga*) and triangles (*Catharus*) colored according to migratory distance in panel A. Species maps
750 from BirdLife International and Naturserve (2014). Illustrations reproduced by permission of Lynx
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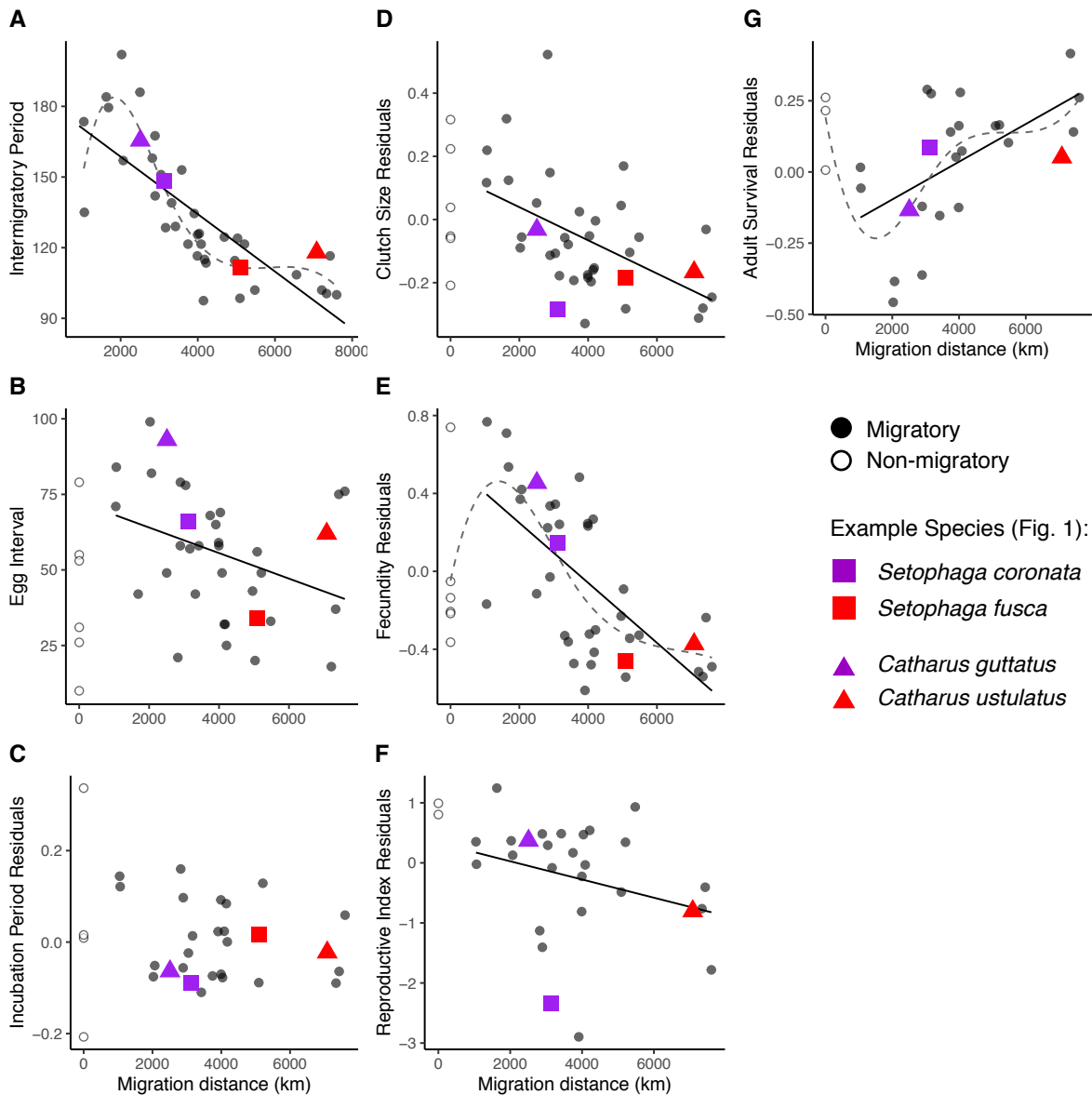
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760 **Figure 2.** Relationships between migration distance and the variables (Table 1) related to breeding time
 761 allocation (A, B), developmental duration (C), reproductive output (D, E, F) and survival (F). For
 762 visualization purpose, the points shown in (C–G) are the residuals from a phylogenetic size-correction
 763 using the `phyl.resid` function in *phytools* (Revell 2009, 2012) because these panels represent variables
 764 thought to scale with body size. The solid line illustrates the linear relationship with migration distance
 765 among the 39 migratory species for variables in which migration distance was included in the best fit

766 model (Table 2; all variables except incubation period, C). We include a cubic spline (dashed line) for
767 plots with obvious non-linear patterns. For fecundity (E) and survival (G), this spline highlights that non-
768 migratory species are more similar to long-distance migrants than to short-distance migrants, but that a
769 relatively linear trend describes the relationship with these variables and migration distance across the
770 migratory species. The splines also reveal that the steepest decline in annual fecundity (E) with migration
771 distance mirror the steepest decline in intermigratory period (A), both occurring between migration
772 distances of approximately 2000-4000km. Colored squares and triangles refer to the example species
773 illustrated in Fig. 1, when data were available for each outcome variable. In (G) we did not plot the value
774 for Golden-crowned Kinglet (*Regulus satrapa*), a short-distance migrant with a very low outlier value for
775 survival, to more easily visualize the relationship among the remaining species.

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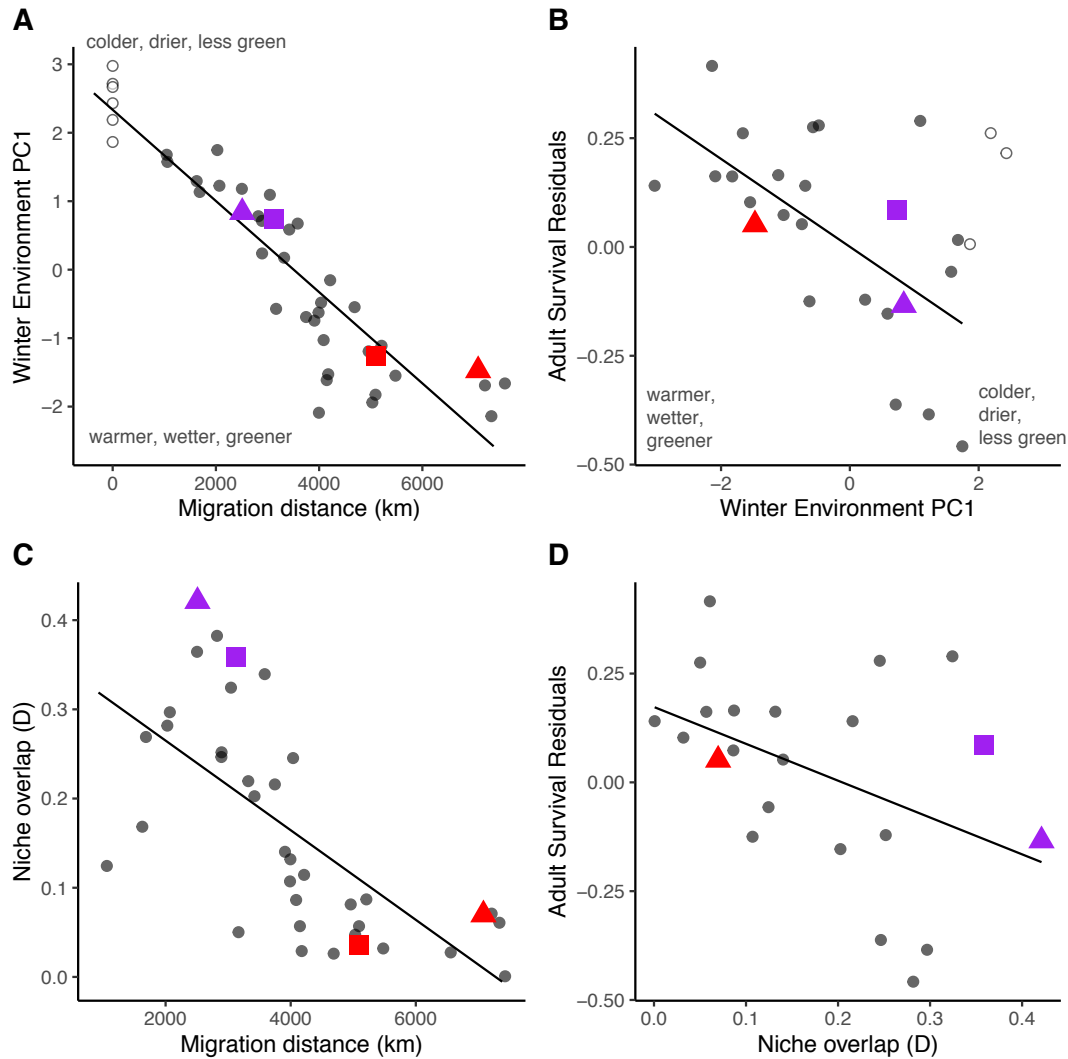
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788 **Figure 3.** (A) Longer migrations carry species to winter ranges that are warmer, wetter and greener but

789 (B) have less niche overlap (Zurell et al. 2018) with summer conditions. (C) Adult survival tends to be

790 higher in warmer, wetter and greener winter ranges associated with long migrations (Fig. 2E) but that (D)

791 have less overlap with breeding niches. Survival values are residuals from a phylogenetic size-correction

792 (see Fig. 2). In (B, D) we did not plot the value for Golden-crowned Kinglet (*Regulus satrapa*), a short-

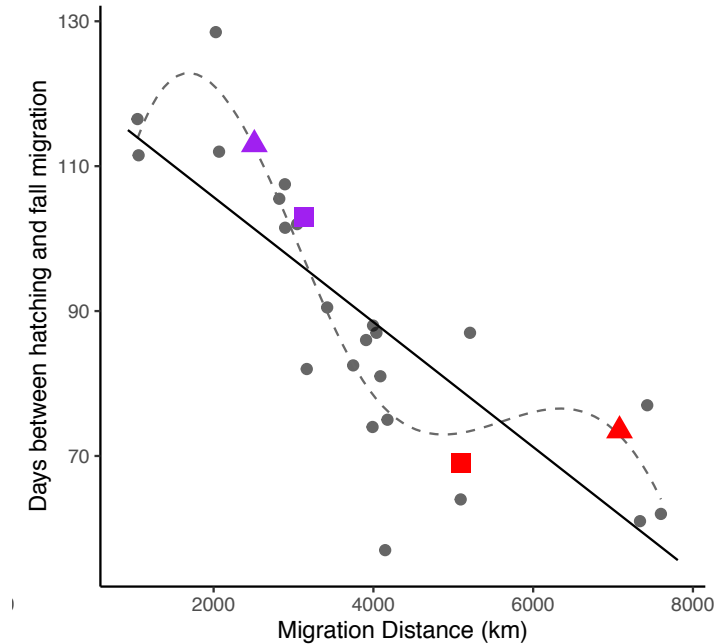
793 distance migrant with a very low outlier value for survival, to more easily visualize the relationship among

794 the remaining species. Niche overlap (D) were not calculated for the non-migratory species (Zurell et al.

795 2018). See Fig. 2 for color legend.

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799 **Figure 4.** Duration of time between hatching and fall migration across the spectrum of migratory distance.

800 Hatching date was estimated as the median of early dates that nests have been found with eggs in
801 Ontario for each species from *Nidiology* (Peck and James 1983, 1987) plus average incubation period for
802 27 species with data on incubation period from *Nidiology*. Fall migration was estimated from eBird as the
803 median date when each species passes through Chicago, IL, a stopover site close to the southern edge
804 of the boreal region (see Methods), meant to approximate the beginning of fall migration. Short-distance
805 migrants spend substantially greater time on or near their breeding grounds between hatching and fall
806 migration than long-distance migrants. Data were not available on the durations of the nestling and
807 fledgling stages (post-embryonic development) of each species, but differences in post-embryonic
808 developmental rates are unlikely to fill this extra time. Incubation period was not correlated with migration
809 distance (Fig. 2), and thus the relationship between migration distance and days between clutch initiation
810 and fall migration is nearly identical (not shown). After the fledgling period, birds are thought to undergo
811 prospecting for future breeding sites, an important phase of natal dispersal, which may allow them to
812 settle on their first breeding territory more quickly following spring migration. We propose that hatch year
813 short-distance migrants may use their greater time on the breeding grounds for more extensive
814 prospecting.

815 **Table 1: Description of outcome variables**

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Variable	Description	Source
Time Allocation		
Intermigratory Period	Interval between peak median spring and fall migration through Chicago, IL	(Sullivan et al. 2009)
Egg Interval	Breadth of dates that nests with eggs have been found in Ontario; represents breadth of the breeding cycle for a species in the boreal region.	(Peck and James 1983, 1987)
Developmental Duration		
Incubation Period	Average of individual incubation periods in Ontario; represents individual-level embryonic developmental rate.	(Peck and James 1983, 1987)
Reproduction		
Clutch Size	Average of clutch size ranges from Ontario	(Peck and James 1983, 1987)
Fecundity	Average clutch size x maximum number of successful broods per year	(Peck and James 1983, 1987; Billerman et al. 2020)
Reproductive Index	Estimated fledglings per adult from long-term capture-mark-recapture study in boreal region	(Desante et al. 2015)
Survival		
Annual Adult Survival (ϕ)	Apparent annual adult survival (ϕ) from long-term capture-mark-recapture study in boreal region	(Desante et al. 2015)

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819 **Table 1:** Summary of life history variables used in study and their data sources. See Methods for further
820 details.

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830 **Table 2: Results of best-fit models**

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Response	Mass	Migratory Status (Nonmigratory)	Migration Distance	Method	λ	n
Time Allocation						
Intermigratory Period			<i>-26.11</i>	OLS	0.68	39
Egg Interval		<i>-30.14</i>	<i>-9.09</i>	OLS	0.47	41
Developmental Duration						
Incubation Period	0.07			PGLS	<i>0.73</i>	31
Reproduction						
Clutch Size	<i>-0.17</i>	-0.07	<i>-0.11</i>	OLS	0.45	43
Fecundity	<i>-0.16</i>	<i>-0.62</i>	<i>-0.33</i>	OLS	0.21	43
Reproductive Index		0.33	-0.09	OLS	0	29
Survival						
Annual Adult Survival (ϕ)	<i>0.42</i>	<i>0.66</i>	<i>0.18</i>	PGLS	<i>1.03</i>	28

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833 **Table 2:** Summary of best-fit models for each life history variable. Variables without coefficients were not
834 included in the best-fit model (see Table S2 for AICc model comparison results). Coefficients with $p <$
835 0.05 are italicized and bold and considered statistically significant in the text. Migration distance was
836 centered and standardized. Mass was log-transformed and outcome variables whose best model
837 included mass were also log-transformed. “Method” notes whether the model type was OLS or PGLS,
838 based on significance of λ at $p < 0.05$ in a test of phylogenetic signal of model residuals (see Methods).
839 Column “n” shows the number of species used in each model, based on data availability (Table S1).
840 Across 39 migratory species, migration distance shows a significant negative relationship with breeding
841 season length (intermigratory period and egg interval), clutch size and fecundity but a significant positive
842 relationship with annual adult survival. By contrast, the 6 non-migratory species have a shorter egg
843 interval, lower fecundity and higher survival (Fig. 3).

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848 **Table 3: Results of climate and niche overlap models**

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Response	Migration Distance	λ	n	Response	Mass	Winter Climate PC1	Niche Overlap (D)	λ	n
Winter Climate PC1	-1.40	0	43	Annual Adult Survival (ϕ)	0.44	-0.08		1.04	26
Niche Overlap (D)	-0.11	0	37	Annual Adult Survival (ϕ)	0.51		-0.48	1.05	22

850

851 **Table 3:** Results of models testing how migration distance predicts winter climate (left panel) and how
852 winter climate predicts adult survival (right panel). Coefficients with $p < 0.05$ are italicized and bolded.
853 Models on the left use OLS whereas those on the right, which had significant values of λ (see Methods),
854 use PGLS. Column “n” shows the number of species used in each model, based on data availability
855 (Table S1). Winter climate is represented by a principle component value ranging from -2 (warmer, wetter,
856 greener) to 2 (cooler, drier, less green). Niche overlap estimates comes from (Zurell et al. 2018), using
857 their estimate that includes climate and NDVI and ranges from 0 to 0.42 in our dataset. Longer distance
858 migrations are associated with wintering in warmer, wetter, and greener locations that show little niche
859 overlap with the boreal breeding range. These conditions trend similarly with survival, but their effects are
860 not significant in models with mass (Fig. 3).

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871 **Table S1: Species and trait data used in analyses**

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Family	Species	Mass	MD	IMP	IP	EI	CS	F	RI	ϕ	PC1	D
Picidae	<i>Picoides dorsalis</i>	53.3	0			10	4	4			2.98	
Picidae	<i>Picoides arcticus</i>	74	0			31	3.5	3.5			2.67	
Picidae	<i>Picoides villosus</i>	70.36	0		11	53	3.5	3.5	0.97	0.68	1.86	
Picidae	<i>Sphyrapicus varius</i>	50.3	2892	167.5	12.5	58	4.5	4.5	0.56	0.43	0.71	0.247
Tyrannidae	<i>Contopus cooperi</i>	32.9	7213	102		18	3	3			-1.69	0.071
Tyrannidae	<i>Empidonax alnorum</i>	12.79	7337	100.5	11	37	3.5	3.5	0.13	0.65	-2.14	0.061
Tyrannidae	<i>Empidonax flaviventris</i>	11.6	4147	97.5	13	32	4	8			-1.61	0.057
Tyrannidae	<i>Empidonax minimus</i>	10.3	3989	116.5	13	59	4	8	0.12	0.36	-0.63	0.107
Vireonidae	<i>Vireo olivaceus</i>	16.7	7599	100	13	76	3.5	3.5	0.05	0.6	-1.66	
Vireonidae	<i>Vireo philadelphicus</i>	12.2	4176	115	12	32	4	4			-1.53	0.029
Vireonidae	<i>Vireo solitarius</i>	16.6	2895	142	13.5	79	4	8		0.41	0.24	0.252
Corvidae	<i>Perisoreus canadensis</i>	73	0		19	55	3	3			2.71	
Corvidae	<i>Cyanocitta cristata</i>	86.8	1061	135	15.5	84	4.5	9	0.36	0.67	1.57	0.124
Regulidae	<i>Regulus calendula</i>	6.68	2822	158	13.5	21	8.5	8.5			0.78	0.382
Regulidae	<i>Regulus satrapa</i>	6.23	1628	184		7	14			0.05	1.29	0.168
Certhiidae	<i>Certhia americana</i>	8.4	1047	173.5	13.5	71	5.5	5.5		0.39	1.68	
Troglodytidae	<i>Troglodytes hiemalis</i>	8.9	1686	179.5		42	5.5	11			1.13	0.269
Paridae	<i>Poecile atricapillus</i>	10.8	0		12	79	6.5	13	0.61	0.54	2.19	
Paridae	<i>Poecile hudsonicus</i>	9.8	0		12	26	6	6		0.5	2.43	
Turdidae	<i>Catharus fuscescens</i>	31.2	7428	116.5	12	75	4	4	0.21	0.63	-3.03	0.001
Turdidae	<i>Catharus guttatus</i>	31	2510	165.5	12	93	4	8		0.48	0.84	0.421
Turdidae	<i>Catharus ustulatus</i>	30.8	7081	118	12.5	62	3.5	3.5	0.14	0.57	-1.47	0.07
Passerellidae	<i>Junco hyemalis</i>	19.89	2027	202	11.5	99	4	8		0.31	1.75	0.282
Passerellidae	<i>Melospiza lincolni</i>	17.4	3046	151	12	78	4	8	0.39	0.62	1.09	0.324
Passerellidae	<i>Zonotrichia albicollis</i>	25.9	2068	157	12	82	4	8	0.35	0.35	1.23	0.297
Parulidae	<i>Cardellina canadensis</i>	10.42	5479	102		33	4.5	4.5	0.69	0.45	-1.55	0.032
Parulidae	<i>Cardellina pusilla</i>	6.9	4214	113.5		25	5	5			-0.15	0.114
Parulidae	<i>Geothlypis philadelphia</i>	12.61	5093	98.5	11	56	3.5	3.5	0.17	0.51	-1.83	0.057
Parulidae	<i>Mniotilta varia</i>	10.74	4038	126	11	69	4.5	4.5	0.43	0.55	-0.48	0.245
Parulidae	<i>Oporornis agilis</i>	15.2	6558	108.5							-1.55	0.027
Parulidae	<i>Leiostyris celata</i>	9	3585	153		4	4				0.67	0.339
Parulidae	<i>Leiostyris peregrina</i>	10.02	4960	114.5		43	5	5			-1.19	0.081
Parulidae	<i>Leiostyris ruficapilla</i>	8.73	3422	129	10.5	58	4.5	4.5	0.43	0.34	0.59	0.203
Parulidae	<i>Parkesia noveboracensis</i>	17.8	5210	121.5	14	49	4	4	0.41	0.55	-1.11	0.087
Parulidae	<i>Seiurus aurocapilla</i>	19.4	3747	121.5	11.5	68	4.5	9	0.35	0.55	-0.69	0.216

Parulidae	<i>Setophaga caerulescens</i>	10.09	3166	128.5	12	57	4	8	0.53	-0.57	0.05	
Parulidae	<i>Setophaga castanea</i>	12.59	5031	124		20	5.5	5.5		-1.94	0.047	
Parulidae	<i>Setophaga coronata</i>	12.51	3126	148.5	11	66	3.5	7	0.03	0.47	0.73	0.358
Parulidae	<i>Setophaga fusca</i>	9.7	5096	111.5	12	34	4	4		-1.26	0.036	
Parulidae	<i>Setophaga magnolia</i>	8.72	4087	121.5	12	49	4	4	0.25	0.42	-1.03	0.086
Parulidae	<i>Setophaga palmarum</i>	10.3	3322	139		42	4.5	4.5		0.17	0.219	
Parulidae	<i>Setophaga pensylvanica</i>	9.64	3996	125.5	11	58	4	8	0.21	0.47	-2.09	0.132
Parulidae	<i>Setophaga tigrina</i>	11	4687	124.5						-0.55	0.026	
Parulidae	<i>Setophaga virens</i>	8.8	3908	134.5	12	65	3.5	3.5	0.01	0.41	-0.74	0.14
Icteridae	<i>Euphagus carolinus</i>	59.42	2503	186		49	4	4		1.18	0.364	

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875 **Table S1:** Species and data used in analyses. MD: Migration distance (km); IMP: intermigratory period
 876 (days); IP: incubation period (days); EI: egg interval (days); CS: average clutch size; F: fecundity; RI:
 877 Reproductive Index; ϕ : Annual Adult Survival; PC1: first principal component of PCA of temperature,
 878 precipitation and NDVI on winter ranges; D: niche overlap value (Zurell et al. 2018). See Table 1 and
 879 Methods for descriptions and data sources for variables.

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893 **Table S2: Results of AICc model comparison**

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Type	logLik	AICc	Δ AICc	Weight
<i>Incubation Period</i>				
mass	26.98	-47.1	0.00	0.85
migration	26.02	-42.5	4.57	0.09
mass+migration	27.07	-41.7	5.32	0.06
<i>Clutch Size</i>				
mass+migration	18.45	-25.3	0.00	0.98
mass	11.79	-17.0	8.32	0.02
migration	9.88	-10.7	14.57	0.001
<i>Fecundity</i>				
mass+migration	-9.76	31.1	0.00	0.78
migration	-12.31	33.7	2.55	0.22
mass	-20.76	48.1	17.0	0.00
<i>Reproductive Index</i>				
migration	-38.05	85.8	0.00	0.54
mass	-40.07	87.1	1.33	0.28
mass+migration	-37.61	87.8	2.06	0.19
<i>Annual Adult Survival (ϕ)</i>				
mass+migration	-5.82	24.4	0.00	0.84
mass	-10.70	28.4	4.03	0.11
migration	-10.07	29.9	5.52	0.05

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896 **Table S2:** Results of model selection for each life history variable in which models with mass and
 897 migration variables were compared. For all response variables except incubation period, models with
 898 migration predictors (status and distance) outperform those without. Model selection was performed on
 899 models using either OLS or PGLS depending on the phylogenetic significance of the residuals of a full
 900 model (Table 2). Outcome variables and mass were log-transformed.

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906 **Table S3: Results of PGLS λ models**

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Response	Mass	Migratory Status (Nonmigratory)	Migration Distance	λ	n
Time Allocation					
Intermigratory Period			-21.20	0.80	39
Egg Interval	-28.64		-8.92	0.46	41
Developmental Duration					
Incubation Period	0.06	0.005	-0.02	0.74	31
Reproduction					
Clutch Size	-0.15	-0.16	-0.065	0.77	43
Fecundity	-0.16	0.67	-34.6	0.23	43
Reproductive Index	-0.71	-0.01	-0.76	-1.86	29
Survival					
Annual Adult Survival (ϕ)	0.43	0.62	<i>0.16</i>	-1.05	28

908

909 **Table S3:** Summary of full PGLS models for each life history variable. For each response, we fit a PGLS
 910 model which optimizes an estimate of λ simultaneously with model fitting (Revell 2010). The trends are
 911 consistent with those reported in Table 2 using OLS, though not all trends are significant in PGLS.
 912 Coefficients with $p < 0.05$ are italicized and bolded.

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