# 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.

**Introduction**

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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 2000*a*;

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 2000*a*; 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 2000*b*; 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).

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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. 2019*a*). 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 2000*a*).

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 2000*b*; 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, Sillett 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 (Sillett 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 2000*a*).

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

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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

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130  breeding and winter ranges (Zurell et al. 2018) is correlated with migration distance and whether

131  it predicts annual survival.

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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 2000*a*; 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

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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

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182    experiences a high density of bird migration, and an active community of birdwatchers generate

183    ample eBird data (Winger et al. 2019*b*). 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 ($\phi$, 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

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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 ($\lambda$) 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 $\lambda$, 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 $\lambda$ 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

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260   *Catharus fuscescens* and *Oporonis 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 ($\phi$) in

273   separate models that included mass as a covariate, after log-transforming $\phi$ and mass.

274

275   **Results**

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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).

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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 ($\phi$; 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-

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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 ($\phi$) was significantly predicted by migratory distance, and

321    migratory distance significantly predicted both winter climate PC1 and niche overlap, $\phi$ 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 $\phi$ 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**

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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

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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

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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 (Sillett

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

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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.

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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. 2019*a*). 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    2019*a*). 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. 2019*a*). 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. 2019*a*). 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 2000*a*; 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

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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. 2019*a*), 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. 2019*b*), 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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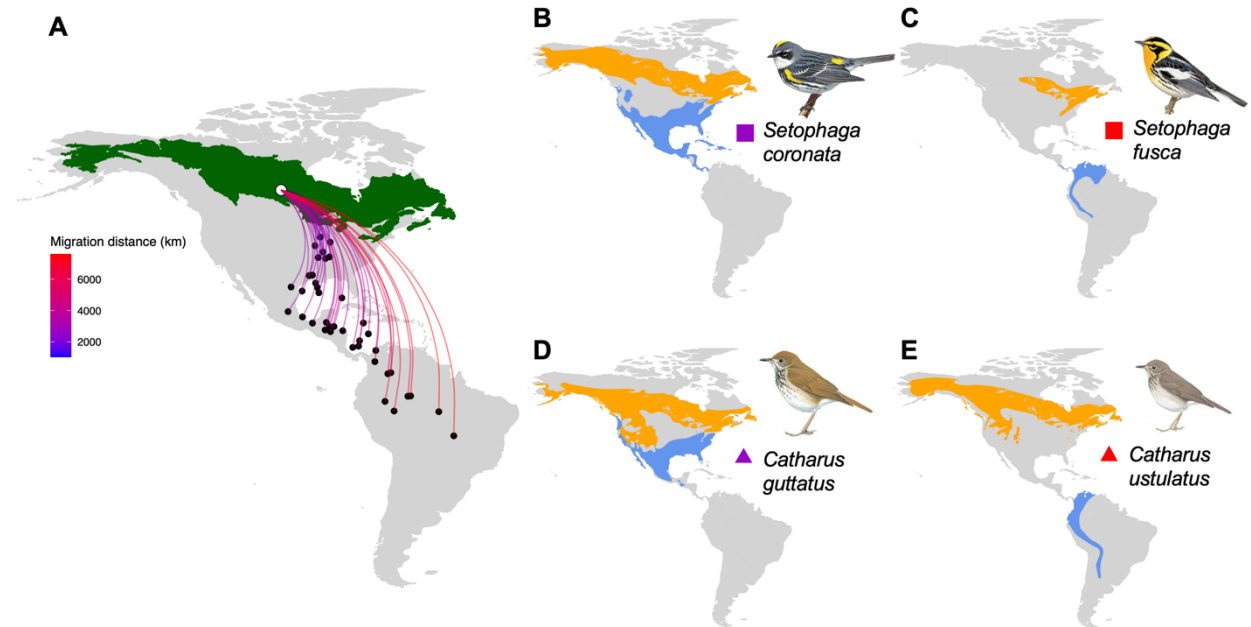740

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**Figures and Tables**



**Figure 1**. A) The 45 species in our study (Table S1) broadly co-occur during the breeding season across the boreal forest belt (green, indicating ecoregions "northern forests", "taiga" and "Hudson plain"; Omernik and Griffith 2014) but winter in disparate locations. Hypothetical migration routes are depicted between a single breeding location and the centroid of the winter ranges of each of 39 migratory species (Methods). B-E) Example species representing short- (B, D) and long- (C, E) distance migratory species in pairs in each of two genera. These example species are highlighted in Figs. 2-4 with the squares (*Setophaga)* and triangles (*Catharus*) colored according to migratory distance in panel A. Species maps from BirdLife International and Naturserve (2014). Illustrations reproduced by permission of Lynx Edicions.

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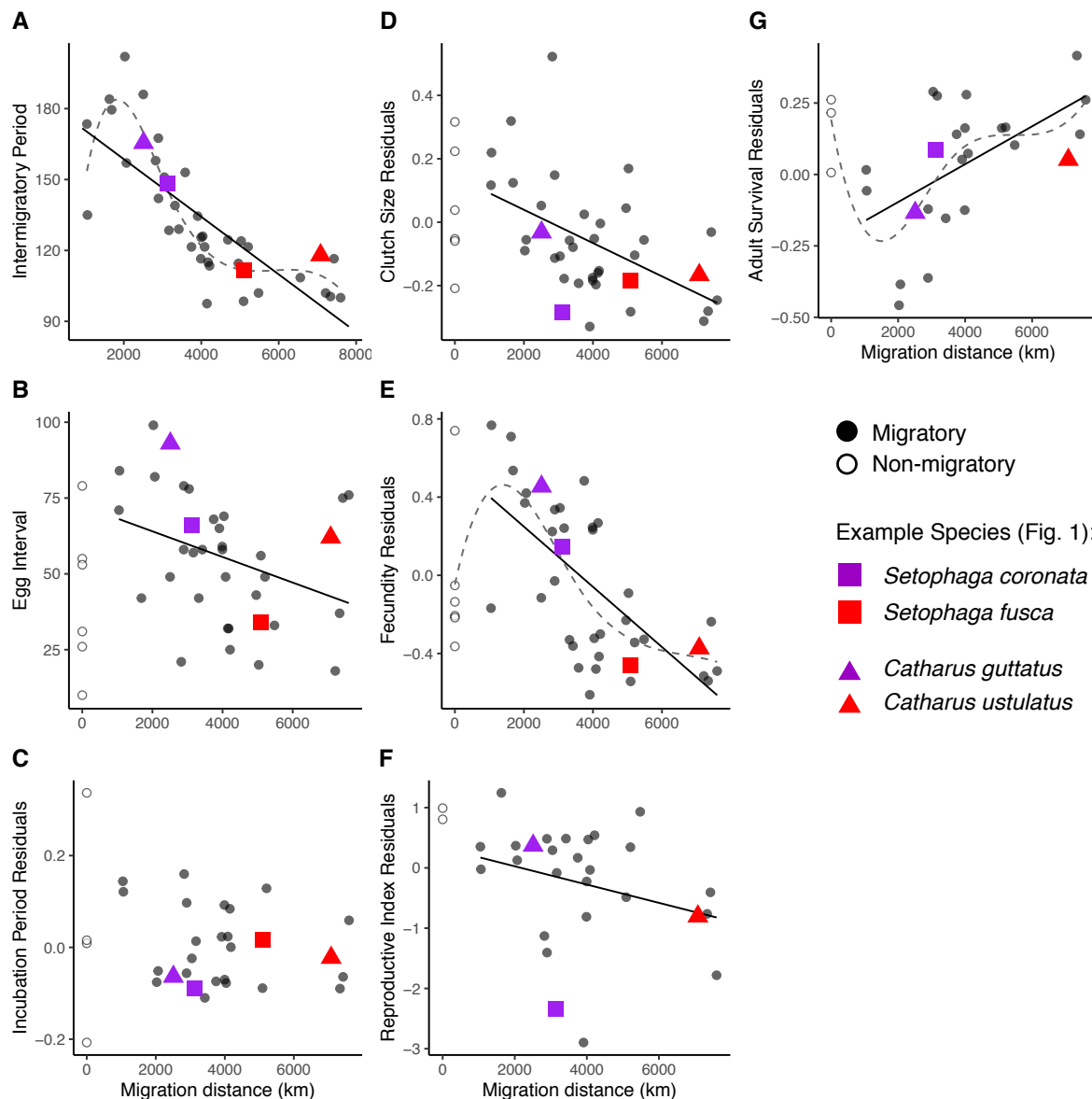
**Figure 2.** Relationships between migration distance and the variables (Table 1) related to breeding time allocation (A, B), developmental duration (C), reproductive output (D, E, F) and survival (F). For visualization purpose, the points shown in (C–G) are the residuals from a phylogenetic size-correction using the phyl.resid function in *phytools* (Revell 2009, 2012) because these panels represent variables thought to scale with body size. The solid line illustrates the linear relationship with migration distance among the 39 migratory species for variables in which migration distance was included in the best fit

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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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**Figure 3.** (A) Longer migrations carry species to winter ranges that are warmer, wetter and greener but (B) have less niche overlap (Zurell et al. 2018) with summer conditions. (C) Adult survival tends to be higher in warmer, wetter and greener winter ranges associated with long migrations (Fig. 2E) but that (D) have less overlap with breeding niches. Survival values are residuals from a phylogenetic size-correction (see Fig. 2). In (B, D) we did not plot the value for Golden-crowned Kinglet (*Regulus satrapa*), a short-distance migrant with a very low outlier value for survival, to more easily visualize the re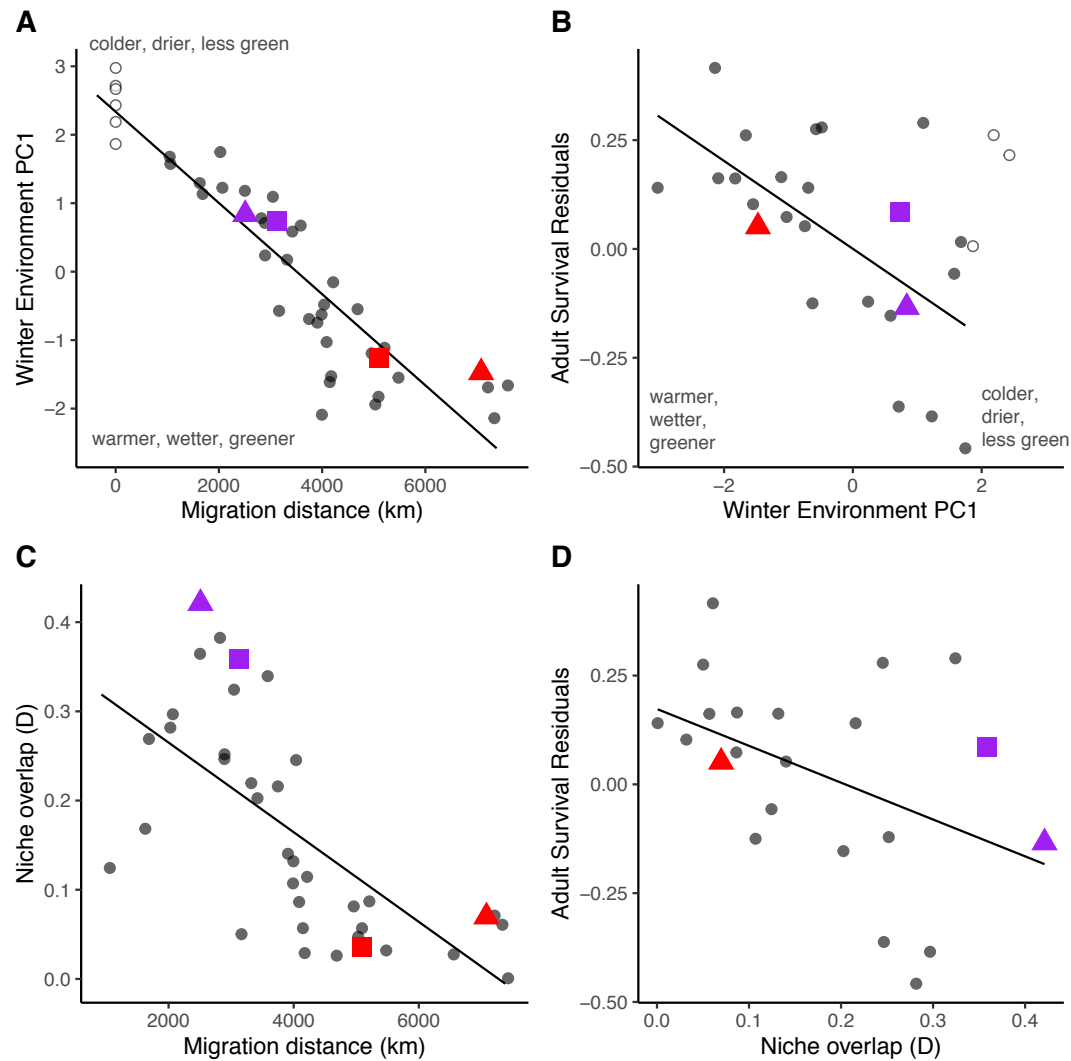lationship among the remaining species. Niche overlap (D) were not calculated for the non-migratory species (Zurell et al. 2018). See Fig. 2 for color legend.
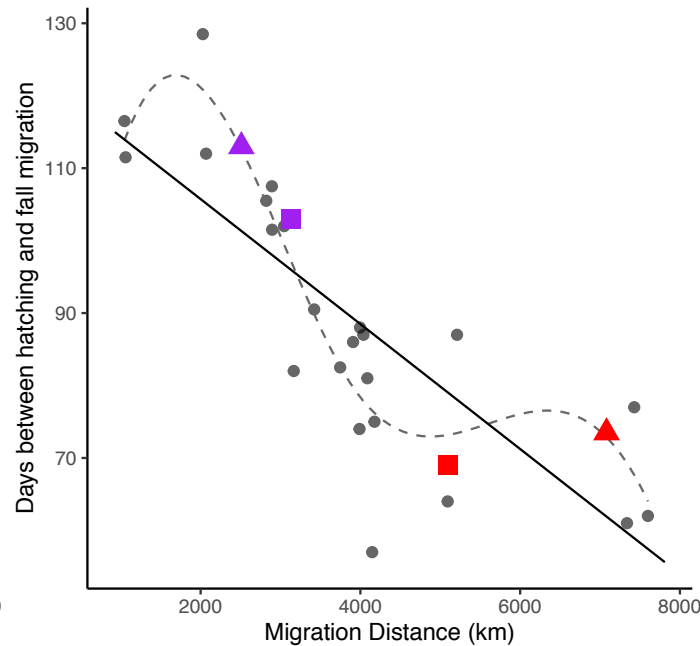
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**Figure 4.** Duration of time between hatching and fall migration across the spectrum of migratory distance. Hatching date was estimated as the median of early dates that nests have been found with eggs in Ontario for each species from *Nidiology* (Peck and James 1983, 1987) plus average incubation period for 27 species with data on incubation period from *Nidiology*. Fall migration was estimated from eBird as the median date when each species passes through Chicago, IL, a stopover site close to the southern edge of the boreal region (see Methods), meant to approximate the beginning of fall migration. Short-distance migrants spend substantially greater time on or near their breeding grounds between hatching and fall migration than long-distance migrants. Data were not available on the durations of the nestling and fledgling stages (post-embryonic development) of each species, but differences in post-embryonic developmental rates are unlikely to fill this extra time. Incubation period was not correlated with migration distance (Fig. 2), and thus the relationship between migration distance and days between clutch initiation and fall migration is nearly identical (not shown). After the fledgling period, birds are thought to undergo prospecting for future breeding sites, an important phase of natal dispersal, which may allow them to settle on their first breeding territory more quickly following spring migration. We propose that hatch year short-distance migrants may use their greater time on the breeding grounds for more extensive 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 ($\phi$) | Apparent annual adult survival ($\phi$) 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 | | | *-26.11* | OLS | 0.68 | 39 |
| Egg Interval | | *-30.14* | *-9.09* | OLS | 0.47 | 41 |
| **Developmental Duration** | | | | | | |
| Incubation Period | 0.07 | | | PGLS | *0.73* | 31 |
| **Reproduction** | | | | | | |
| Clutch Size | *-0.17* | -0.07 | *-0.11* | OLS | 0.45 | 43 |
| Fecundity | *-0.16* | *-0.62* | *-0.33* | OLS | 0.21 | 43 |
| Reproductive Index | | 0.33 | -0.09 | OLS | 0 | 29 |
| **Survival** | | | | | | |
| Annual Adult Survival ($\phi$) | *0.42* | *0.66* | *0.18* | PGLS | *1.03* | 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 ($\phi$) | *0.44* | -0.08 | | 1.04 | 26 |
| Niche Overlap (D) | *-0.11* | 0 | 37 | Annual Adult Survival ($\phi$) | *0.51* | | -0.48 | 1.05 | 22 |

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

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| | | MD | IMP | IP | EI | CS | F | RI | | $\phi$ | PC1 | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parulidae | *Setophaga caerulescens* | 10.09 | 3166 | 128.5 | 12 | 57 | 4 | 8 | | 0.53 | -0.57 | 0.05 |
| Parulidae | *Setophaga castanea* | 12.59 | 5031 | 124 | | 20 | 5.5 | 5.5 | | | -1.94 | 0.047 |
| Parulidae | *Setophaga coronata* | 12.51 | 3126 | 148.5 | 11 | 66 | 3.5 | 7 | 0.03 | 0.47 | 0.73 | 0.358 |
| Parulidae | *Setophaga fusca* | 9.7 | 5096 | 111.5 | 12 | 34 | 4 | 4 | | | -1.26 | 0.036 |
| Parulidae | *Setophaga magnolia* | 8.72 | 4087 | 121.5 | 12 | 49 | 4 | 4 | 0.25 | 0.42 | -1.03 | 0.086 |
| Parulidae | *Setophaga palmarum* | 10.3 | 3322 | 139 | | 42 | 4.5 | 4.5 | | | 0.17 | 0.219 |
| Parulidae | *Setophaga pensylvanica* | 9.64 | 3996 | 125.5 | 11 | 58 | 4 | 8 | 0.21 | 0.47 | -2.09 | 0.132 |
| Parulidae | *Setophaga tigrina* | 11 | 4687 | 124.5 | | | | | | | -0.55 | 0.026 |
| Parulidae | *Setophaga virens* | 8.8 | 3908 | 134.5 | 12 | 65 | 3.5 | 3.5 | 0.01 | 0.41 | -0.74 | 0.14 |
| Icteridae | *Euphagus carolinus* | 59.42 | 2503 | 186 | | 49 | 4 | 4 | | | 1.18 | 0.364 |

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

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

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| Type | logLik | AICc | $\partial$AICc | Weight |
|---|---|---|---|---|
| *Incubation Period* | | | | |
| 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 |
| *Clutch Size* | | | | |
| 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 |
| *Fecundity* | | | | |
| 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 |
| *Reproductive Index* | | | | |
| 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 |
| *Annual Adult Survival ($\phi$)* | | | | |
| 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 PGLSλ 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 ($\phi$) | *0.43* | 0.62 | *0.16* | -1.05 | 28 |

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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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