

RESEARCH ARTICLE

Migration distance is a fundamental axis of the slow-fast continuum of life history in boreal birds

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Submission Date: February 6, 2021; Editorial Acceptance Date: May 11, 2021; Published July 7, 2021

ABSTRACT

Seasonal migration is intrinsically connected to the balance of survival and reproduction, but whether migratory behavior influences species' position on the slow-fast continuum of life history is poorly understood. We found that boreal-breeding birds that migrate long distances exhibit higher annual adult survival and lower annual reproductive investment relative to co-distributed boreal species that migrate shorter distances to winter closer to their breeding grounds. Our study uses "vital rates" data on reproductive output and survivorship compiled from the literature for a species assemblage of 45 species of mostly passerine birds. These species breed sympatrically in North American boreal forests but migrate to a diversity of environments for the northern winter. After controlling for body size and phylogeny, migration distance and apparent annual adult survival are positively related across species. Both migration distance and survival are positively correlated with wintering in environments that are warmer, wetter, and greener. At the same time, longer migrations are associated with reduced time spent on the breeding grounds, lower clutch sizes, and lower fecundity (clutch size \times maximum number of broods per year). Although seasonal migration is often associated with high mortality, our results suggest that long-distance migration imposes 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 study supports the idea that migration evolves to promote survival of species breeding in seasonal environments. In boreal birds, the evolution of the longest migrations yields the highest survival, but at an inherent cost to annual fecundity. Our results therefore reveal migratory distance as a fundamental axis of the slow-fast continuum that predicts, and is inextricable from, the balance of survival and reproduction.

Keywords: fecundity, life history, seasonal migration, slow-fast continuum, survival, vital rates

La distancia de migración es un eje fundamental del continuo lento-rápido de la historia de vida de las aves boreales

LAY SUMMARY

- A trade-off between investment in survival and reproduction is among the most fundamental patterns in nature.
- Seasonal migration allows animals to move between areas used specifically for reproduction or survival.
- Migration is frequently thought to involve high mortality, suggesting that the longest-distance migrations should be costliest to survival.
- We show that, counterintuitively, birds that breed in boreal North America and migrate long distances for the winter are more likely to survive to the following year than birds that migrate shorter distances.
- Long-distance migrants also lay fewer eggs each year than short-distance migrants.
- Our study reveals how the evolution of a remarkable behavioral adaptation—long-distance migration—simultaneously shapes and is shaped by the fundamental balance of reproduction and survival.

RESUMEN

La migración estacional está intrínsecamente relacionada con el balance entre supervivencia y reproducción, pero no se comprende bien si el comportamiento migratorio influye en la posición de las especies en el continuo lento-rápido de la historia de vida. Encontramos que las aves de reproducción boreal que migran largas distancias exhiben una mayor supervivencia anual de los adultos y una menor inversión reproductiva anual en relación con las especies boreales con una distribución similar pero que migran distancias más cortas para pasar el invierno más cerca de sus

zonas de reproducción. Nuestro estudio utiliza datos de “índices vitales” sobre desempeño reproductivo y supervivencia recopilados de la literatura para un ensamble de 45 especies de aves, en su mayoría paseriformes. Estas especies se reproducen en simpatría en los bosques boreales de América del Norte, pero migran a una diversidad de ambientes durante el invierno del norte. Después de controlar por el tamaño corporal y la filogenia, la distancia de migración y la supervivencia anual aparente de los adultos se relacionan positivamente para este ensamble de especies. Tanto la distancia de migración como la supervivencia se correlacionan positivamente con la invernada en ambientes más cálidos, húmedos y verdes. Al mismo tiempo, las migraciones más prolongadas se asocian con un menor tiempo de permanencia en las zonas de reproducción, con menores tamaños de nidadas y con menor fecundidad (tamaño de nidadada \times número máximo de nidadadas por año). Aunque la migración estacional a menudo se asocia con una alta mortalidad, nuestros resultados sugieren que la migración de larga distancia impone presiones de selección que confieren y exigen altas tasas de supervivencia de los adultos. Es decir, debido al costo reproductivo de la migración de larga distancia, esta estrategia solo puede persistir si se equilibra con una alta supervivencia de los adultos. Nuestro estudio apoya la idea de que la migración evoluciona para promover la supervivencia de las especies que se reproducen en ambientes estacionales. En las aves boreales, la evolución de las migraciones más largas produce la mayor supervivencia, pero a un costo inherente a la fecundidad anual. Por lo tanto, nuestros resultados revelan que la distancia de migración es un eje fundamental del continuo lento-rápido que predice y es inseparable del balance entre supervivencia y reproducción.

Palabras clave: continuo lento-rápido, fecundidad, historia de vida, migración estacional, supervivencia, tasas vitales

INTRODUCTION

Annual fecundity and age-specific survival represent a fundamental trade-off along the slow-fast continuum of life history (Stearns 1976, Reznick 1984, Bennet and Harvey 1988, Saether 1988). Fecundity and survival operate in tension presumably owing to physiological and energetic constraints, though the evolutionary causes of this trade-off remain debated (Gasser et al. 2000, Zera and Harshman 2001, Ricklefs and Wikelski 2002, Sibly et al. 2012). This trade-off is integral to understanding the evolution of species' behavioral and ecological attributes, because traits that promote survival may come at a cost to fecundity and vice versa (Martin 1995, Ricklefs 2000a, Jeschke and Kokko 2009, Robinson et al. 2010, Sol et al. 2016). However, these patterns are often obfuscated by life history variation along ecogeographic gradients, necessitating hypothesis testing frameworks that distinguish between intrinsic constraints on life history and environmental variation in demographic outcomes (Ricklefs 2000a). In this article, we examine the evolutionary connections between seasonal migration and the slow-fast continuum of life history.

Seasonal migration is an annual round trip between regions dedicated to reproduction and those dedicated to survival (Winger et al. 2019a) and as such is intrinsically connected to these 2 fundamental life history parameters. In birds, long a model for both migration research (Alerstam 1993, Greenberg and Marra 2005) and life history theory (Ricklefs 2000b, Martin 2004, Pincheira-Donoso and Hunt 2017), a widespread view about migration and fecundity is that migration evolved in tropical species to increase reproductive output by exploiting seasonally available resources for breeding in the temperate zone while escaping competition in the tropics (Cox 1968, 1985). Migration is also thought to carry a high risk of mortality (Newton 2007, Diehl et al. 2014). These ideas—that migration improves

fecundity and is costly to survival—together have led to predictions that the evolution of seasonal migration shifts migratory species toward the faster end of the slow-fast gradient, with higher fecundity but diminished annual survival (Clark and Martin 2007, Sibly et al. 2012, Jahn et al. 2020).

An alternative perspective is that migration evolves in seasonal areas to increase survival during the resource-depleted nonbreeding season (Salewski and Bruderer 2007, Winger et al. 2019a). Under this view, migration does not evolve out of the tropics per se but rather evolves as a survival strategy in response to seasonality in a breeding range, regardless of the biogeographic origin of a lineage (Salewski and Bruderer 2007). That is, species exhibit migratory behavior in circumstances in which escape from the breeding grounds during a predictable period of resource scarcity improves annual survival and therefore the likelihood of achieving a breeding season the next year. This view casts migration as an adaptive strategy to seasonality analogous to hibernation, as opposed to an exploratory dispersal strategy to improve reproductive success relative to an ancestral tropical condition (Winger et al. 2019a). If migration evolves to increase survival in the face of seasonality, then species that migrate long distances to more favorable locations in the nonbreeding season might be expected to have higher survival than species that breed in the same seasonal environments but stay closer to their breeding grounds all year. If migration serves to promote annual survival, it should be expected to come at a cost to annual reproductive output (Ricklefs 2000a, Martin 2004).

Despite the connections between life history theory and hypotheses for the evolution of migration in birds, the relationship between the migratory strategies employed by different species and the balance of annual survival and fecundity has not been rigorously tested (Bruderer and Salewski 2009). The study of avian life history trade-offs

has long focused on understanding ecogeographic patterns in reproductive strategies, such as larger clutch sizes in temperate vs. tropical breeding birds (Moreau 1944, Lack 1947, Ricklefs 2000b, Martin 2004, Jetz et al. 2008, Griebeler et al. 2010). Owing to the general recognition of seasonal migration as a fundamental aspect of avian ecology and behavior, macroecological studies of global variation in avian reproductive output (Jetz et al. 2008, Sibly et al. 2012, Cooney et al. 2020) or survival (Muñoz et al. 2018, Bird et al. 2020, Scholer et al. 2020) often include migratory status as a model covariate, typically by using a categorical predictor (e.g., migratory vs. nonmigratory). These global studies have often found migration to be associated with a “faster” life history strategy, such as high breeding productivity, faster development, or diminished survival (Sibly et al. 2012, Cooney et al. 2020, Minias and Włodarczyk 2020, Soriano-Redondo et al. 2020). However, because migratory behavior is strongly correlated with seasonality and breeding latitude, migratory species are likely to exhibit life history conditions associated with breeding at high latitudes. Thus, given the relative paucity of migratory species breeding at low latitudes and nonmigratory species at high latitudes, a direct influence of migratory behavior on the slow-fast continuum may not be revealed by global analyses whose primary axis of life history variation is latitudinal.

A second area of relevant research has focused on modeling seasonal variation in survival rates of individual migratory species throughout their annual cycles (Faaborg et al. 2010a, Hostetler et al. 2015, Marra et al. 2015). These studies have often demonstrated that most mortality occurs during migration as opposed to the breeding (summer) or nonbreeding (winter) “stationary” periods, highlighting the cost of migration (Sillett and Holmes 2002, Lok et al. 2015, Rockwell et al. 2017, Rushing et al. 2017). It has more rarely been asked how total annual survival varies across species with different migratory strategies or distances (Greenberg 1980, Sherry and Holmes 1995, Sandercock and Jaramillo 2002). Migration clearly requires substantial energy and presents a risk to survival, but so does maintaining homeothermy and body condition in regions with cold temperatures or scarce food resources (Wikelski et al. 2003, Swanson and Garland 2009, Stager et al. 2016, Carneiro et al. 2021). Additionally, recent studies in some migratory species, especially non-passerines, have discovered surprisingly high rates of adult survival associated with extreme long-distance migration, calling into question the generality of a high mortality cost of migration (Leyrer et al. 2013, Conklin et al. 2017, Senner et al. 2019, Swift et al. 2020). How does the mortality risk associated with long-distance migration compare to an alternative strategy of staying closer to temperate-breeding grounds year-round, and what relationship do these costs have with reproductive output and the slow-fast continuum?

Greenberg (1980) proposed the time allocation hypothesis to explain how survival and reproduction vary across temperate-breeding species with different migratory strategies. This hypothesis suggested that long-distance migratory species invest less time in breeding than short-distance migrants or temperate residents, but compensate for lower fecundity by investing in migrations to locales with resources that support increased winter survival. Consistent with this hypothesis, a handful of subsequent studies have found evidence that temperate-breeding long-distance migratory species may have lower annual fecundity than temperate residents or short-distance migrants (Mönkkönen 1992, Martin 1995, Böhning-Gaese et al. 2000, Möller 2007, Bruderer and Salewski 2009). However, most previous interspecific comparisons have tested the relationship between migratory behavior and either survival and reproduction in isolation—rather than the relationships among these parameters in the same set of species—and have often not controlled for environmental heterogeneity among breeding locations that could bias demographic parameters.

Here, we assess the influence of migration distance on the slow-fast continuum of life history using published datasets on life history parameters. We use as a model system a sympatric species assemblage of small-bodied, mostly passerine birds that breed in the boreal forests of eastern and central North America (Figure 1). Our boreal study system is well-suited to isolating the impact of migratory distance on life history because of the high diversity of similarly sized species that breed at the same latitudes and in the same habitat but spend the nonbreeding season in drastically different regions (Figure 1). This study design allows us to hold breeding latitude and habitat constant as migratory distance changes. We test 3 predictions that we derive from time allocation hypothesis (Greenberg 1980). First, we test if long-distance migratory species invest less time during the annual cycle in reproduction than co-distributed short-distance migrants or residents. Second, we test whether increased migratory distance and decreased time allocated to reproduction are associated with reduced annual fecundity. Third, we test the prediction that if longer-distance migrations reduce fecundity, these migrations should also be associated with increased annual survival.

A relationship between migratory distance and annual survival could be mediated by several mechanisms, including disparate conditions experienced on the wintering grounds. Indeed, the importance of winter environment for survival and reproduction of migratory birds has been well documented within species (Johnson et al. 2006, Rushing et al. 2016). However, broad-scale environmental predictors of winter survival are more poorly understood in an interspecific comparative context. Are the costs of long-distance migration offset by benefits of lower-latitude wintering grounds (Somveille et al. 2018)? To address this

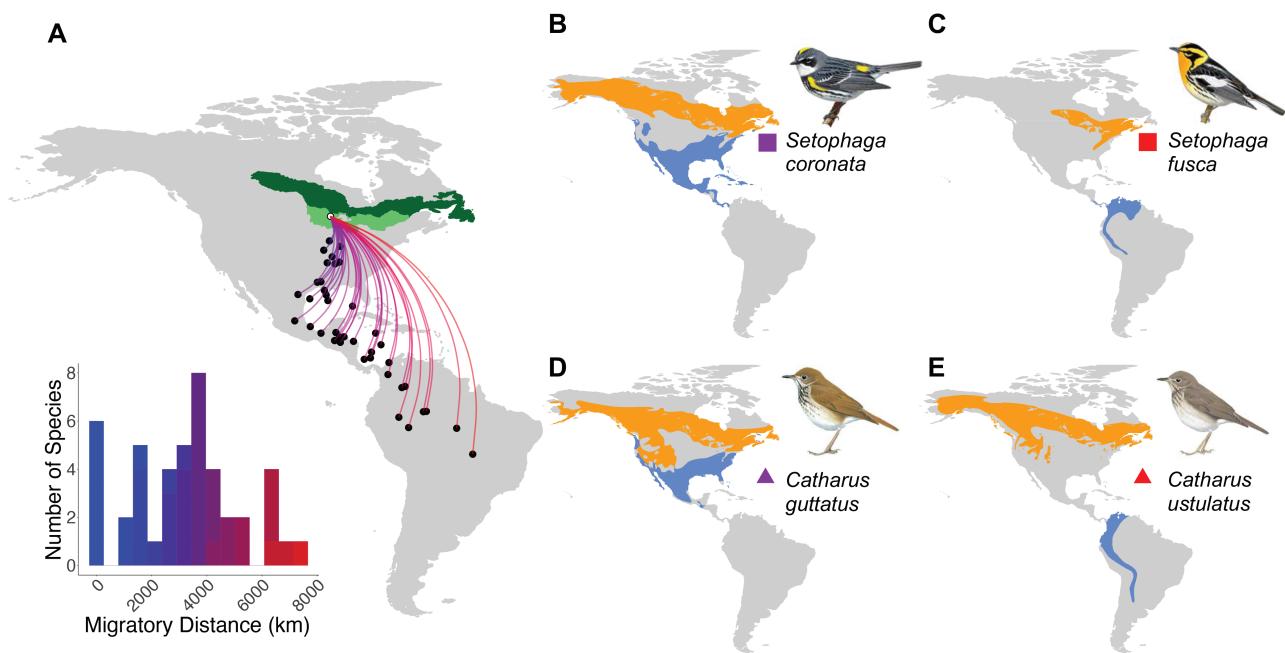


FIGURE 1. (A) The 45 species in our study (Supplementary Material Table S1) broadly co-occur during the breeding season in the North American boreal forest belt but winter in disparate locations. Dark green shading shows BCR 8 (Boreal Softwood Shield) and light green shading BCR 12 (Boreal Hardwood Transition), representing the subregion of the boreal belt from which most of the reproductive and survival data were compiled (see Methods). Hypothetical migration routes are depicted between a single breeding location (Gunflint Trail, MN, USA) and the centroid of the winter ranges of each of the 39 migratory species, with a color scale corresponding to migration distances depicted in the histogram (see Methods). (B–E) Example species representing short-distance (B and D) and long-distance (C and E) migratory species pairs in each of 2 genera. These example species are highlighted in Figures 2 and 3 with the squares (*Setophaga*) and triangles (*Catharus*) colored according to migratory distance in (A). Species maps from BirdLife International and NatureServe (2014); *Setophaga coronata* and *Catharus ustulatus* maps illustrate subspecies *S. c. coronata* and *C. u. swainsoni*, respectively. Illustrations reproduced by permission of Lynx Edicions. All BCRs are shown in Supplementary Material Figure S1.

question, we test whether interspecific variation in migratory distances is correlated with macroecological proxies for winter environment and whether these variables influence annual survival. Survival could also be influenced by the climatic similarity of migratory species' breeding and winter ranges during their summer and winter, respectively, which affects the breadth of conditions to which they must adapt throughout the year. Winter ranges of migratory birds have been shown to occur in areas that are climatically more similar to the breeding grounds than expected by chance, suggesting that "niche tracking" underlies migratory movements at macroecological scales (Gómez et al. 2016, Zurell et al. 2018, Somveille et al. 2019). To test whether niche tracking provides a survival benefit, we test how niche overlap between the breeding and winter ranges (Zurell et al. 2018) is correlated with migration distance in our study system and whether it predicts annual survival.

METHODS

Study System

Our study system comprises 45 species of birds (41 passerine species from 11 families and 4 woodpecker species)

breeding in forested habitats throughout the boreal forest belt of eastern and central North America (Figure 1, Supplementary Material Table S1). Because body size is an important axis of the slow-fast continuum (Ricklefs 2000a, Martin 2004, Bromham 2011), we focused on small-bodied birds (<100 g) that can reproduce beginning at ~1 year of age. Together, these species comprise a regional community of sympatric breeding birds in the northern summer but they spend the northern winter in disparate locales.

We included species that breed in bog, spruce-fir, and mixed forested habitats throughout the boreal and hemiboreal regions (Figure 1). The boreal biome is geographically broad, so we focused specifically on the ecoregions corresponding to adjacent Bird Conservation Regions (BCRs) 8 (Boreal Softwood Shield) and 12 (Boreal Hardwood Transition; Figure 1, Supplementary Material Figure S1, Bird Studies Canada and NABCI 2014). Focusing our study on a sympatric species assemblage required us to exclude some species that overlapped marginally with our study region so as to obtain data from as geographically and ecologically consistent a region as possible. Therefore, we excluded species primarily restricted to more northern treeline habitats of the taiga (e.g., Gray-cheeked Thrush [*Catharus minimus*] or Blackpoll Warbler [*Setophaga*]

striata]) and those primarily restricted to more southerly latitude (e.g., Scarlet Tanager [*Piranga olivacea*], Pine Warbler [*Setophaga pinus*]), as their available data were largely from outside the study region. We included species whose ranges extend beyond the boreal region if the species breed broadly throughout the boreal forest (e.g., Hairy Woodpecker [*Dryobates villosus*] or Red-eyed Vireo [*Vireo olivaceus*]) and had available data from our study region. We included species with regular seasonal migrations and those known to be primarily nonmigratory but excluded species that primarily undergo facultative irruptive or nomadic movements (e.g., Red-breasted Nuthatch [*Sitta canadensis*] or White-winged Crossbill [*Loxia leucoptera*]) due to the difficulty of defining migratory patterns or breeding periods.

Life History Outcome Variables

We gathered published data from the study region related to time allocation for breeding, annual reproductive output, and annual adult survival (Table 1). To test time allocation in breeding, we estimated the relative number of days each species invests in breeding. Comparable data on the full breeding cycle (i.e. from spring establishment of territories through fledging of chicks) were not available for the boreal region for many species, so we used 2 proxies. First, we estimated the amount of time each species spends on or near its breeding grounds by using eBird data (Sullivan et al. 2009) to calculate the interval of time between spring and fall migratory passage through Chicago, IL. Migratory passage through Chicago is a reasonable proxy for time spent on the breeding grounds for the migratory species in this study because Chicago is near to but not within the boreal region (~350 km to the southern edge of the boreal forest), it is a stopover location common to all the species, it experiences a high density of bird migration, and an active community of birdwatchers generate ample eBird data (Winger et al. 2019b). We analyzed eBird data from Cook County, IL from 2000 to 2017. For each species in each year and season (spring and fall), we calculated the date with the most eBird records for that species and considered this to be the date of “peak migration.” We calculated the average number of days between the median peak spring and median peak fall migration dates across all years for each species. This “intermigratory period” serves as a proxy for the relative amount of time species spend on or near their breeding grounds.

The intermigratory period is expected to be correlated with the length of the breeding period, but it also includes nonbreeding activities such as molt (Tonra and Reudink 2018) and movements through to be related to dispersal (Cormier and Taylor 2019). Therefore, as a second proxy for breeding season length, we gathered data specific to the study region on the length of the egg-laying period, using records of early and late egg dates to calculate the number

of days over which each species lays or incubates eggs (“egg interval”). We used data from *Breeding Birds of Ontario: Nidiology and Distribution* (Peck and James 1983, 1987), henceforth “Nidiology.” Nidiology summarizes nest records of birds breeding in Ontario, Canada, collected mostly by the Ontario Nest Records Scheme initiated in 1956 (sample sizes for our study species are given in Supplementary Material Table S2). We used this volume because it is more specific to boreal habitat and latitudes and more consistent in information than more general sources on breeding birds (such as *Birds of the World*; Billerman et al. 2020). For our study species, these nests were largely from the region of Ontario corresponding to BCRs 8 and 12 (Supplementary Material Figure S1).

We used all clutch sizes listed in Nidiology to calculate the average clutch size for each species. We calculated the interquartile mean (mean of the middle 50% of clutches) so that means would not be biased by incomplete or depredated clutches or unusually large clutches. Three species (Orange-crowned Warbler [*Leiothlypis celata*], Cape May Warbler [*Setophaga tigrina*], and Connecticut Warbler [*Oporornis agilis*]) had few nest records in Nidiology (Supplementary Material Table S2), so we referred to Billerman et al. (2020) to verify clutch sizes from our study region. We calculated annual fecundity as (average clutch size) × (maximum number of successful broods) per season. Nidiology did not consistently contain information on the number of broods, so we coded species as double brooders if Billerman et al. (2020) indicated that an additional brood may be raised following a successful first brood in or near boreal latitudes. We excluded information from different subspecies or geographic regions, as brood number can vary geographically, and we ignored re-nesting after predation or unsuccessful nesting. Some species we marked as double brooders may do so relatively rarely. However, data on the incidence of double brooding were not available for most species, as such information demands intensive study (Nagy and Holmes 2005). Thus, our measure of annual fecundity should be considered closer to a maximum annual fecundity.

We extracted data on annual adult survival from the “Vital Rates of North American Birds” project (henceforth, *Vital Rates*; DeSante et al. 2015) for 28 species with available data. *Vital Rates* provides estimates of demographic parameters derived from widely implemented constant-effort capture–mark–recapture surveys from 1992 to 2006, as part of the Monitoring Avian Productivity and Survivorship program. We used *Vital Rates’* Adult Apparent Survival Probability (ϕ), which is “an estimate of the annual probability that a resident bird that was alive and present at the station in year t will also be alive and present in year $t + 1$ ” (DeSante et al. 2015). These survival estimates are produced from ad hoc length-of-stay transient Cormack–Jolly–Seber models that correct for the

potential presence of transient individuals (Pradel et al. 1997, Nott and DeSante 2002, Hines et al. 2003, Saracco et al. 2012).

Vital Rates provides estimates of ϕ for different geographic regions delineated by BCRs. We used *Vital Rates'* “fully model-averaged” estimate of ϕ (parameter TM_PhiR in downloadable data tables), which represents a model-averaged estimate for each BCR based on model sets where ϕ is allowed to vary geographically (DeSante et al. 2015). To best match the geographic locations of the Ontario nest data drawn from *Nidiology* (above), we prioritized BCRs 8 and 12 (Figure 1, Supplementary Material Figure S1 and Table S1). For 13 species, model estimates were available for BCR 12 but not BCR 8. Seven species had estimates for both BCRs 8 and 12, and we used the mean value. *Vital Rates* treats Alder Flycatcher (*Empidonax alnorum*; included in our study) and Willow Flycatcher (*Empidonax trailli*; not included in our study) as a single taxon with combined data because they are difficult to distinguish. For Alder Flycatcher, we therefore used the BCR-specific (nonmodel-averaged) estimate of ϕ from BCR 8, where Willow Flycatcher does not breed; this ϕ value was nearly identical to a model-averaged value from BCRs 8 and 12. Seven species did not have data from BCR 8 or 12, and we used the model estimates for adjacent, latitudinally similar boreal regions (BCRs 6, 13, or 14). Exploratory analyses in which we used only data from BCR 12 showed similar patterns. We did not include any parameters that *Vital Rates* flagged as not usable due to unreliable model estimates.

Predictor Variables

Migration distance. We estimated migration distance as the geodesic distance between the centroids of the breeding and wintering range of each species, including any year-round portions in both the breeding and wintering range when calculating centroids (BirdLife International and Naturserve 2014). Geographic calculations were made using geospatial packages in R (Bivand and Rundel 2019, Bivand et al. 2019, Hijmans 2019). To ensure that our migration distance estimates were representative of populations breeding in the boreal belt, we used only the portions of breeding ranges overlapping BCRs 8 and 12 to calculate breeding range centroids. We also excluded any portions of wintering ranges within or west of the Rocky Mountains because these areas are generally used by more western breeding populations (Kelly and Hutto 2005, Kardynal and Hobson 2017).

Migratory status. There are few species that are year-round residents of the boreal region. Furthermore, any species that does not migrate away from the boreal region in winter must have other specialized adaptations for dealing with harsh winter conditions (Winger et al. 2019a), which could in turn influence life history trade-offs. Therefore, in

addition to migratory distance, we included a binary predictor for migratory status (migratory or nonmigratory). However, there were only 6 nonmigratory species that met our criteria for inclusion, and 5 of these species are cavity nesters from only 2 lineages (Paridae and Picidae; Supplementary Material Table S1). In contrast, only one of the remaining 39 migratory species in our dataset is an obligate cavity nester (Yellow-bellied Sapsucker [*Sphyrapicus varius*]). Cavity nesting may affect species' fecundity and survival (Martin and Li 1992). Thus, we emphasize that in our dataset the migratory status predictor should be considered nearly equivalent to controlling for cavity-nesting behavior. That is, a limitation of our study is that any effects of cavity nesting vs. nonmigratory status on life history are not easily distinguished.

Mass. For the 3 outcome variables related to reproductive output and survival (Table 1), we included log-transformed body mass as a predictor variable in addition to the migration predictors, because reproductive output and survival scale allometrically with avian body size even across the small range of body masses in our study; we also logged the outcome variable in these cases (Ricklefs 2000a, McCarthy et al. 2008, Sibly et al. 2012). We used mass data obtained from Dunning (2008) or Billerman et al. (2020), with species' mean values weighted by sample size reported for each sex. We centered and standardized migration distance.

Analysis of Life History Variables

Modeling approach. We used linear models to examine how migratory behavior is correlated with each outcome variable. Models for different outcome variables contain slightly different subsets of species based on the availability of data on the outcome variable (Table 2). We first tested whether the data were best modeled using phylogenetic generalized least squares (PGLS) or ordinary least squares (OLS) by fitting an OLS model with all relevant predictors and then using the function *phylosig* from phytools (Revell 2012) to test for phylogenetic signal (λ) in the model's residuals (Revell 2010). Although controlling for shared phylogenetic ancestry is important in comparative analyses, PGLS has the potential to reduce model accuracy when a model's residuals do not have a phylogenetic signal (Revell 2010). For a phylogeny, we built a consensus tree with data from birdtree.org (Jetz et al. 2012), using procedures described in Pegan and Winger (2020). For models with significant λ , we performed PGLS modeling with the *gls* function in *nlme* (Pinheiro et al. 2019), including a correlation structure of expected phylogenetic covariance among species according to a Brownian motion model (“corBrownian” in ape; Paradis and Schliep 2019). For response variables that did not have significant phylogenetic signals in model residuals, we used OLS. We

TABLE 1. Summary of outcome variables used in the study and their data sources. See Methods for further details and [Supplementary Material Table S1](#) for values.

Outcome variable	Description	Predictor variables assessed	Source
Time allocation			
Intermigratory period	Interval between peak median spring and fall migration through Chicago, IL	Migration distance	eBird (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	Migration distance, migratory status	(Peck and James 1983, 1987)
Reproduction			
Average clutch size	Interquartile mean of clutch sizes from Ontario nest records	Mass, migration distance, migratory status	(Peck and James 1983, 1987)
Fecundity	Average clutch size \times maximum number of successful broods per year	Mass, migration distance, migratory status	(Peck and James 1983, 1987, Billerman et al. 2020)
Survival			
Annual adult survival (ϕ)	Apparent annual adult survival (ϕ) from long-term capture–mark–recapture study in the boreal region	Mass, migration distance, migratory status	(DeSante et al. 2015)

TABLE 2. Summary of full models for each time allocation and life history variable for all species in the dataset. Intermigratory period and egg interval are not expected to be influenced by mass, so this predictor is omitted from these models. Intermigratory period can only be calculated for migratory birds, so the migratory status predictor is omitted from this model. Values reported under each predictor are the coefficient and the standard error (in parentheses) for that predictor from the model. “Method” notes whether the model type was OLS or PGLS (based on the significance of λ) and n is the number of species used in each model. Coefficients and values of λ with $P < 0.05$ are italicized and bold. Mass was log-transformed and response variables in models with mass were also log-transformed. Migration distance shows a negative relationship with breeding season length (intermigratory period and egg interval), clutch size, and fecundity, but has a positive relationship with annual adult survival.

Response	Mass	Migratory status (nonmigratory)	Migration distance	Adjusted R^2	Method	λ	n
Time allocation							
Intermigratory period			-20.27 (3.18)		PGLS	0.72	39
Egg interval		-29.61 (12.34)	-8.85 (4.37)	0.093	OLS	0.43	41
Reproduction							
Clutch size	-0.17 (0.037)	-0.065 (0.10)	-0.11 (0.032)	0.41	OLS	0	45
Fecundity	-0.18 (0.070)	-0.59 (0.19)	-0.32 (0.061)	0.42	OLS	0	45
Survival							
Annual adult survival	0.46 (0.15)	0.67 (0.32)	0.19 (0.062)		PGLS	1.02	28

also present PGLS analyses of all outcome variables ([Supplementary Material Table S3](#)) for which we jointly estimated Pagel’s λ and the model using “corPagel” in *ape* ([Revell 2010, Paradis and Schliep 2019](#)).

In addition to assessing the correlation among variables in full models as described above, we took a separate information-theoretic approach to assess the importance of mass and migration as predictors for the 3 outcome variables related to reproduction and survival ([Table 1](#)). For each variable, we fit 4 models: a null intercept-only model, a model with only mass as a predictor, a model with migration predictors, and a model with mass and migration predictors. For each outcome variable, we used the second-order Akaike Information Criterion (AIC_2) to assess the relative performance of models with *MuMin* ([Bartón 2019](#)).

Visualization of relationships. Our modeling approaches facilitated nuanced hypothesis testing of the importance of body size and phylogeny for understanding the relationship between migration and life history. We used a simpler approach to visualize the relationships. For the 3 variables pertaining to reproduction and survival ([Table 1](#)), we performed a phylogenetic size correction on each outcome variable using the *phyl.resid* function in *phytools* ([Revell 2012](#)) and plotted the residuals against migratory distance ([Figure 2](#)).

Analysis of Winter Environment and Niche Tracking

To test whether the annual survival of species that migrate different distances is mediated by differential conditions experienced on the wintering grounds, we quantified winter climate and primary productivity across the winter ranges

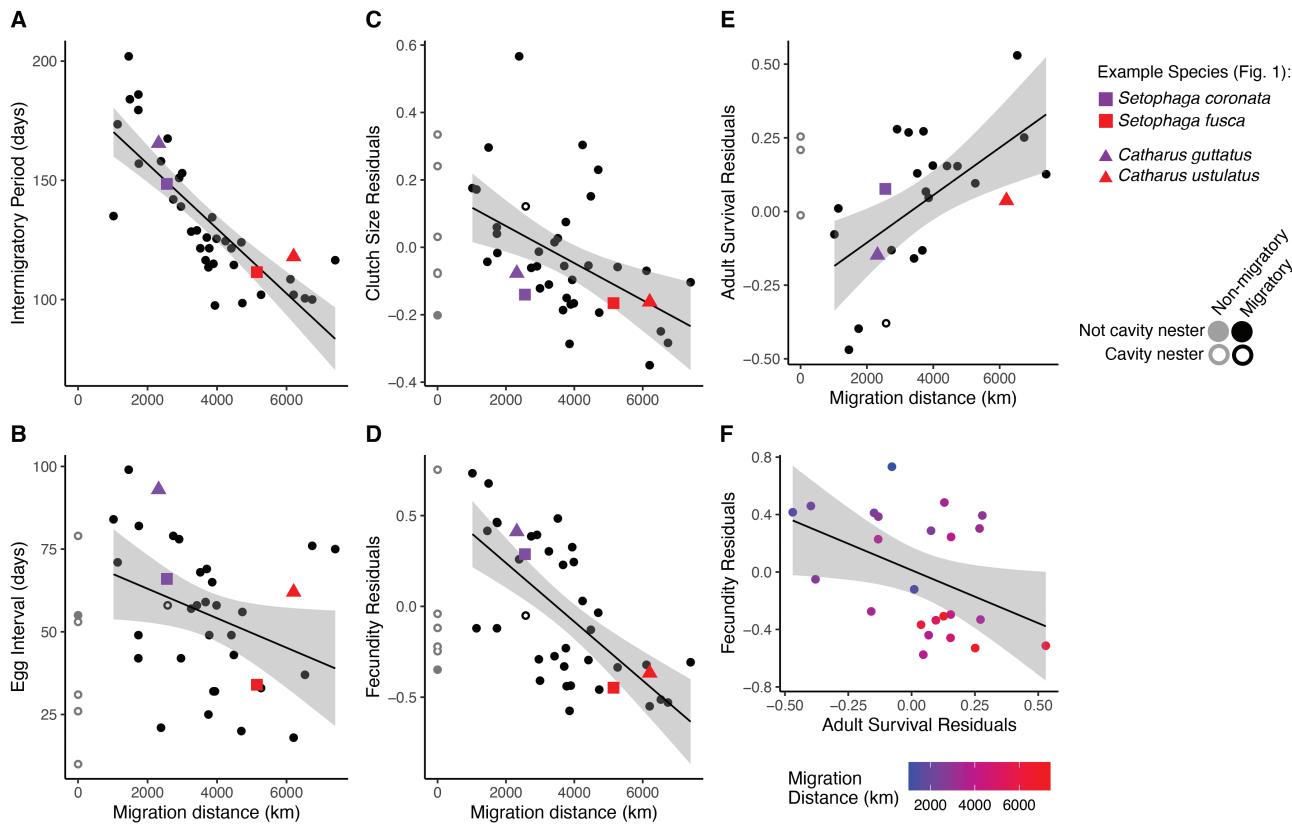


FIGURE 2. (A–E) Relationships between migration distance and the outcome variables (Table 1) corresponding to breeding time allocation (A and B), reproductive output (C and D), and survival (E). The points shown in (C–E) are the residuals from a phylogenetic size-correction of each y-axis variable (see Methods). Black lines in (A–E) show linear relationships of y-axis variables and migration distance among the migratory species (migration distance >0). Among the migratory species, the time devoted to breeding (A and B) and reproductive output (C and D) scales negatively with migration distance, whereas survival (E) scales positively. In contrast, nonmigratory species (which are mostly cavity nesters) fall outside the trends for egg interval, clutch size, fecundity, and survival. Corresponding statistical tests are given in Tables 2 and 3. Colored squares and triangles refer to the example species illustrated in Figure 1, when data were available for each outcome variable. (F) Phylogenetic size-corrected residuals of annual fecundity and annual adult survival are negatively correlated along an axis of migration distance among migratory species ($n = 24$). In panels (E) and (F), we did not plot the value for Golden-crowned Kinglet (*Regulus satrapa*), a short-distance migrant with a low outlier value for survival, to more easily visualize the relationship among the remaining species; figures with this species are shown in Supplementary Material Figure S3.

of each species. We used eBird (Sullivan et al. 2009) records for each species from November to February (all years) and retained all points that fell within a species' typical winter range (BirdLife International and NaturaServe 2014), with western portions cropped as described above to exclude extralimital vagrants. We excluded Veery (*Catharus fuscescens*) and Connecticut Warbler (*Oporornis agilis*) due to a paucity of winter eBird records. We downloaded month-level climate data (Fick and Hijmans 2017) at 30-s resolution and normalized difference vegetation index (NDVI) data (Pinzon and Tucker 2014), averaged from the years 2000–2010. We filtered rasters to contain one eBird record per grid cell to mitigate spatial bias and used these points to calculate species-level means for winter temperature, precipitation, and NDVI. We conducted a principal components analysis (*prcomp* function in R; R Core Team 2018) to reduce temperature, precipitation, and NDVI

to a single species-level value (PC1, representing winter climate).

To assess whether species that migrate longer distances experience more favorable climates, we assessed the correlation between migratory distance and winter climate PC1 with linear models as described above. We then assessed the relationship between annual adult survival (ϕ) and winter climate PC1 directly in a separate model that included mass as a covariate, after log-transforming ϕ and mass to account for allometric relationships discussed above. Using the same modeling approach, we also assessed the relationships between both migratory distance and ϕ and an estimate of the overlap of breeding and nonbreeding season climatic niches calculated by Zurell et al. (2018). This estimate of niche overlap represents the similarity between the conditions (climate and NDVI) encountered in the breeding range

TABLE 3. Results of model comparison for the outcome variables related to reproduction and survival. Under each response variable, models are ordered by AIC_c with the best-fit model appearing first. Numbers reported under each predictor are the coefficient and the standard error (in parentheses) for that predictor from each model. Models for clutch size and fecundity were fit with OLS, whereas the survival model used PGLS (Table 2). Models with migration predictors outperformed those without.

Type	Mass	Migratory status (nonmigratory)	Migratory distance	logLik	AIC_c	ΔAIC_c	w_i
Reproduction							
Clutch size							
Mass + migration	-0.17 (0.37)	-0.065 (0.098)	-0.11 (0.032)	20.29	-29.0	0.00	0.99
Mass	-0.14 (0.039)			13.18	-19.8	9.28	0.01
Migration		-0.22 (0.11)	-0.11 (0.039)	10.45	-11.9	17.14	0.00
Null				6.71	-9.1	19.91	0.00
Fecundity							
Mass + migration	-0.18 (0.070)	-0.59 (0.19)	-0.32 (0.061)	-8.76	29.1	0.00	0.88
Migration		-0.75 (0.19)	-0.32 (0.064)	-12.04	33.1	4.02	0.12
Mass	-0.17 (0.081)			-20.52	47.6	18.58	0.00
Null				-22.73	49.7	20.69	0.00
Survival							
Annual adult survival							
Mass + migration	0.46 (0.15)	0.67 (0.32)	0.19 (0.062)	-6.10	24.9	0.00	0.89
Mass	0.45 (0.17)			-11.57	30.1	5.21	0.066
Migration		0.72 (0.37)	0.19 (0.072)	-10.81	31.5	6.43	0.036
Null				-14.87	34.2	9.28	0.009

during breeding months and the winter range during winter months.

RESULTS

As expected from life history theory (Martin 2004, Bromham 2011), body mass (6.23–86.8 g, mean = 22.3 g) was negatively correlated with both average clutch size (2.8–8.2 eggs, mean = 4.3 eggs) and annual fecundity (clutch size \times maximum brood number; 2.8–12.6 eggs, mean = 5.7 eggs). Likewise, mass was positively correlated with annual survival (ϕ = 0.05–0.68, mean = 0.48; Tables 2 and 3). Our results further revealed relationships between migration predictors and most outcome variables.

Migration Distance and Life History

Among the 39 migratory species, intermigratory period was strongly negatively correlated with migration distance (Figure 2A, Table 2). Our results indicate that long-distance migratory species arrive later in spring and spend less time on or near their breeding grounds before departing earlier on fall migration than short-distance migratory species (Supplementary Material Figure S2). For an increase in migration distance of one standard deviation, or \sim 2,000 km, the model predicted a decrease in intermigratory period of \sim 20 days. This pattern was corroborated by egg interval (Figure 2B, Table 2), which trended negatively with migration distance (though less strongly so than intermigratory period).

Among migratory species, clutch size and annual fecundity were both negatively correlated with migration distance (Figure 2C and D, Table 2). The relationship was

stronger for annual fecundity because only short-distance migrants were double brooders (Figure 2D, Supplementary Material Table S1). Model comparison indicated that migration distance was included in the best models for both clutch size and fecundity and these models showed a notable improvement over models that did not contain migration (Table 3). Apparent annual adult survival (ϕ ; Desante et al. 2015) was positively associated with migratory distance (Figure 2E, Table 2), and model comparison revealed that migration distance improved the fit of the survival model (Table 3). Fecundity and survival are negatively correlated with each other, with long-distance migrants exhibiting low fecundity and high survival (n = 24, P = 0.045, R^2 = 0.132; Figure 2F).

Migratory Status and Life History

In contrast to the relationships between migration distance and life history variation among the migratory species, in which longer-distance migrations were associated with “slower” life history values, nonmigratory status (which involved 6 species that are year-round residents in the boreal region) was associated with lower clutch size and fecundity, and higher annual survival (Figure 2, Table 2). Thus, the nonmigratory species were more similar in survival and reproduction to the “slow” traits exhibited by long-distance migrants than to the fast traits exhibited by short-distance migrants (Figure 2). These patterns should be interpreted with caution due to the small sample size for nonmigrants and the fact that 5 of 6 of these species are cavity nesters. Regardless, the life history traits of the nonmigratory species appear distinct from the linear trends exhibited across migratory species (Figure 2).

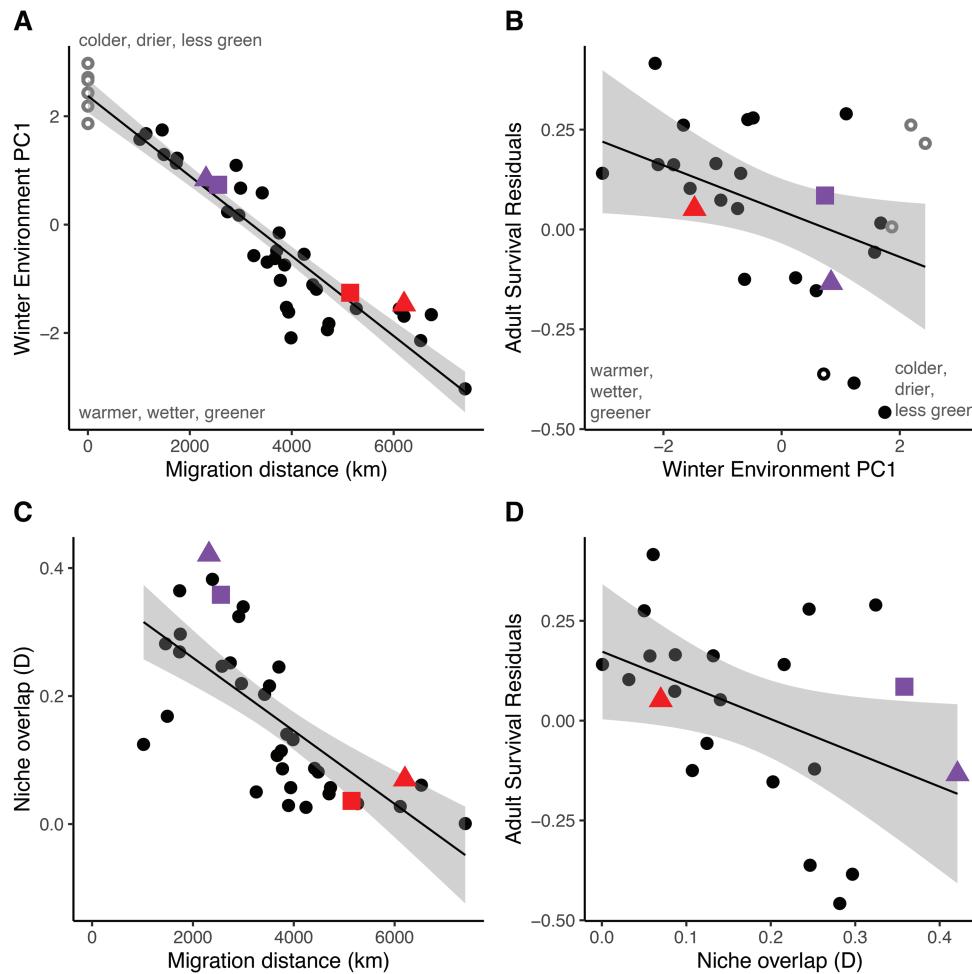


FIGURE 3. Relationship between migration distance (A and C) or annual adult survival (B and D) and environmental conditions in the winter range (A and B) and niche overlap (C and D). The symbol scheme follows Figure 2. Axes are organized according to tests performed in Table 4. (A) Longer migrations carry species to winter ranges that are warmer, wetter, and greener but (B) have less niche overlap with summer conditions. (C) Adult survival tends to be higher in warmer, wetter, and greener winter ranges associated with long migrations but that (D) have less overlap with breeding niches, but both relationships have considerable noise (Table 4). Survival values (B and D) are residuals from a phylogenetic size correction (Figure 2). In panels (B) and (D), we did not plot the value for Golden-crowned Kinglet (*Regulus satrapa*), a short-distance migrant with a low outlier value for survival, to more easily visualize the relationship among the remaining species; figures with this species are shown in Supplementary Material Figure S3. Niche overlap values are from Zurell et al. (2018) and were only calculated for migrants.

Winter Environment and Niche Tracking

For the principal component analysis of winter environmental variables, PC1 explained 80.71% of the variance, PC2 explained 17.67%, and PC3 1.61% (see Supplementary Material Table S4 for PC loadings). Migratory distance was related to winter climate PC1 such that species that migrate longer distances from the boreal region spend the winter in locations that are warmer, wetter, and greener (Figure 3A, Table 4, Supplementary Material Table S4). However, migratory distance was also strongly negatively related to niche overlap, indicating that longer-distance migrants have winter climates more dissimilar to their summer environments than do short-distance migrants (Figure 3C). Adult survival (ϕ) was negatively but weakly correlated

with winter climate PC1, suggesting that wintering in the warmer, wetter, and greener environments associated with longer migrations may improve survival (Figure 3B, Table 4). Tracking a climatic niche throughout the year, however, did not improve survival, as survival is negatively correlated with niche overlap (Figure 3D, Table 4).

DISCUSSION

Body mass, phylogeny, and breeding latitude are the most commonly invoked axes of the slow-fast continuum in birds (Ricklefs 1980, Sibly et al. 2012, Cooney et al. 2020). By controlling for body mass and phylogeny in our analyses and holding breeding latitude constant, our study reveals

TABLE 4. Results of models relating winter range conditions to migration distance and annual adult survival. Numbers reported under each predictor are the coefficient and the standard error (in parentheses) for that predictor. n is the sample size for each model. Coefficients with $P < 0.05$ are italicized and bold. The left side shows the effect of migration distance (predictor variable) on winter climate and niche overlap from OLS models. Winter climate is represented by a principal component value ranging from -2 (warmer, wetter, greener) to 2 (cooler, drier, less green); see [Supplementary Material Table S4](#) for principal component loadings. Niche overlap estimates come from [Zurell et al. 2018](#) (climate + NDVI estimate) and range from 0.42 to nearly 0 in our dataset. Long-distance migration is associated with wintering in warmer, wetter, and greener ranges that show little niche overlap with the breeding range. The right side shows the effect of winter climate or niche overlap (predictors) on annual adult survival from PGLS models. These conditions trend positively with survival ([Figure 3](#)), but their effects are not significant in models with mass.

Response	Migration distance	λ	n	Response	Mass	Winter climate	Niche overlap	λ	n
Winter climate	-1.49 (0.09)	0	43	Annual adult survival	0.46 (0.16)	-0.097 (0.049)		1.04	27
Niche overlap	-0.11 (0.018)	0	37	Annual adult survival	0.54 (0.18)		-0.55 (0.43)	1.05	23

that migration distance is also a major axis of the slow-fast continuum of life history in a sympatric breeding assemblage of migratory birds ([Figure 2](#)). Our results reveal under-explored interactions between life history evolution and seasonal migration, while also helping to explain the evolutionary dynamics underlying migration as an adaptive strategy for seasonality.

Migration Distance and the Slow-Fast Continuum

In support of the time allocation hypothesis ([Greenberg 1980](#)), our results indicate that migration distance is negatively associated with a temporal investment in breeding. Migratory species that winter closer to their boreal breeding grounds migrate earlier in the spring and later in the fall ([Figure 2A](#), [Supplementary Material Figure S2](#)) and can be found incubating eggs during a longer time window than longer-distance migrants that winter closer to the equator ([Figure 2B](#)), indicating a temporal constraint on breeding associated with longer-distance migration. This temporal constraint results in a reduction in annual fecundity in long-distance migrants, as, unlike short-distance migrants, long-distance migrants in our study are not known to raise more than one successful brood in a single year ([Figure 2D](#), [Supplementary Material Table S1](#)). Yet, our results also show that clutch size scales weakly negatively with migratory distance ([Figure 2C](#)), suggesting that annual fecundity may be reduced in long-distance migrants by dynamics beyond the number of breeding attempts ([Böhning-Gaese et al. 2000](#)). As our data were compiled from the literature and reflect central tendencies for clutch size and maximum values for brood number, field studies on the trade-off of brood size and success among individuals ([Cornell and Williams 2016](#)) and the frequency of double brooding ([Nagy and Holmes 2005](#)) are required to understand the strength of the relationship between migration distance and annual fecundity within and among species.

Migration is often found to be the costliest period of the annual cycle for survival in migratory songbirds ([Sillett and](#)

[Holmes 2002](#), [Rockwell et al. 2017](#), [Rushing et al. 2017](#)), and thus it is intuitive to predict that longer migrations are costlier to survival than shorter migrations ([Taylor and Norris 2007](#), [Lok et al. 2015](#)). In contrast, we found that among migratory species, migration distance trends positively with apparent annual adult survival ([Figure 2E](#)). This is particularly striking given that the longest-distance migrants in our system undergo migrations of more than 7,000 km ([Figure 1](#), [Supplementary Material Table S1](#)). Notably, these results are consistent with a recent study that used radar estimates of the seasonal migratory biomass of North American birds to demonstrate that Neotropical migrants had higher overwinter survival than temperate-wintering migrants despite their longer migration distances ([Dokter et al. 2018](#)).

[Conklin et al. \(2017\)](#) suggested that extreme long-distance migrants may experience counterintuitively high adult survival because long-distance migration selects strongly for high-quality individuals who are capable of repeating these extraordinary feats every year, thus narrowing the “individual quality spectrum” and reducing annual adult mortality. Our study lends support to this hypothesis by revealing how survival trades off with fecundity along an axis of migratory distance: Extreme long-distance migration can only be a successful evolutionary strategy if adult survival is high enough to balance the reduction in annual reproductive output inherent to long migrations. That is, long-distance migration constrains the time devoted to breeding, reducing annual fecundity and thereby demanding high annual adult survival.

Yet, life history trade-offs are not one-way causal relationships. It is likely also true that long-distance migration confers high survival but, in so doing, inherently demands a reduced investment in annual reproduction ([Ricklefs 2000a](#)). Our results lend support to this dynamic by suggesting that maximum survival is afforded to species that migrate the longest distances to humid equatorial forests, despite the energetic costs of long-distance migration and the fact that these long migrations lead

to relatively greater differences in breeding season vs. winter season climatic conditions (Figure 3). However, we note that if long-distance migration inherently selects for high survival owing to its negative impact on fecundity (as discussed above), it is challenging to disentangle the specific influence of winter environment on survival when both parameters are correlated with migration distance (Figure 3). Additionally, the specific macroecological conditions that are correlated with migration distance and winter survival in our study species are not likely to be generally applicable across migratory taxa with other habitat preferences and resource bases, such as waders (Piersma et al. 1993, Remeijer et al. 2020). Despite these complexities, our results speak broadly to the importance of winter resources for conferring survival benefits to the species that seek them through long-distance migration (Dokter et al. 2018).

In summary, our study shows that temperate-breeding species that endure migration of thousands of kilometers each year occupy a slower position on the slow-fast continuum of life history than their close relatives who migrate shorter distances but attempt to survive the winter closer to their breeding grounds where winter conditions are poorer. This perspective provides evolutionary context for some surprising behaviors of migratory species. One of the species in our study, the Veery, is a long-distance migrant breeding in temperate forests and wintering in Amazonia. A recent study (Heckscher 2018) found that Veeries may curtail breeding in years with hurricane activity along their migratory route. That is, the evolution of their migration pattern—and the weather-detecting sensory systems that enable it—is so finely tuned to survival probability that some adult individuals will forego reproductive attempts to ensure a successful migration (Heckscher 2018). Our study suggests that this species' adaptive capacity to respond to subtle environmental conditions that threaten future survival during migration is representative of a point along a life history continuum wherein longer, more difficult migrations maximize annual survival at the cost of annual reproductive output.

Migratory Status and the Slow-Fast Continuum

It is more challenging to interpret how migratory status (nonmigratory vs. migratory behavior) influences life history due to the inherently limited sample of nonmigratory birds in our boreal system. Interestingly, we found that some nonmigratory boreal species have levels of reproductive output and survival more similar to long-distance migrants than to short-distance migrants, resulting in nonlinear associations with life history characters as migration distance increases from zero (Figure 2). This result contrasts earlier evidence that temperate resident species may have lower survival and higher fecundity than migrants (Greenberg 1980, Sherry and Holmes 1995).

However, because 5 of the 6 nonmigratory species are cavity nesters, it is difficult to disentangle potential life history influences of cavity nesting (Martin and Li 1992) from nonmigratory status. This relationship is further complicated because the fecundity and survival of cavity nesters may differ depending on whether they are primary excavators: nonexcavating species are thought to have "faster" life histories than excavators (Martin 1995, Wiebe et al. 2006). Species with both types of cavity nests are included in our study (chickadees vs. woodpeckers; Supplementary Material Table S1), but in sample sizes too small to determine the effects of the cavity type on our outcome variables.

Thus, the suite of traits that produce the demographic outcomes observed in the nonmigratory species in our study is more complex than simply an absence of migratory behavior. Nevertheless, our results suggest that life in a boreal environment year-round (i.e. without migrating) selects for a balance of survival and reproduction that is more similar to that exhibited by long-distance migrants than species that migrate only short distances away from the boreal region in winter. Aside from cavity nesting, all 6 nonmigratory species have specialized adaptations for surviving harsh boreal winters such as food-caching (Sherry 1989, Waite and Reeve 1993), social cooperation, or the ability to excavate grubs from trees. Our results therefore offer a compelling possibility wherein the most specialized, extreme adaptations—required either to survive the harshest winters *in situ* or perform the longest migrations—exert strong selection pressures (Sol et al. 2010, 2016) that optimize annual adult survival at the cost of annual fecundity. More detailed field studies comparing overwinter survival rates of temperate nonmigratory and short-distance migratory species will shed further light on this dynamic.

Life History Trade-offs and the Evolution of Migration

The evolution of seasonal migration in birds has often been explained as an out-of-the-tropics process wherein species improve reproductive success by escaping the competition in the crowded tropics (Cox 1968, 1985, Rappole and Jones 2002). Support for the out-of-the-tropics models has come in part from studies showing higher fecundity in temperate migrants vs. tropical residents, which has been interpreted to mean that the evolution of migration facilitates greater reproductive success (reviewed in Salewski and Bruderer 2007, Winger et al. 2019a). Winger et al. (2019a) and Salewski and Bruderer (2007) argued that even in lineages of tropical origin, migration does not evolve out of the tropics as a consequence of long-distance dispersal to improve reproductive success. Rather, migration evolves when species expanding their ranges through normal dispersal processes encounter higher seasonality in a breeding location, often at a higher latitude, or when

breeding populations face increases in seasonality through time *in situ*. The adaptive benefits of philopatry (returning to breed in similar locations as one was reared; [Davis and Stamps 2004](#)) select for individuals that return to their breeding grounds in spring ([Winger et al. 2019a](#)). From this perspective, migration is an adaptive survival strategy that facilitates persistence in seasonal areas, regardless of the biogeographic origin of a lineage.

Our study lends support to this survival hypothesis by demonstrating the relationship between migration, reproduction, and survival among a community of species that experience high seasonality in the breeding range. Overall, the annual fecundity of the migratory species in our study is likely greater than that of close tropical-breeding relatives, since it varies along a strong latitudinal gradient in clutch size ([Ricklefs 2000a](#), [Clark and Martin 2007](#)). However, relative to tropical species, annual fecundity is also relatively high among the nonmigratory species that occupy temperate latitudes. Thus, the evolution of migration promotes fecundity only insofar as it promotes survival and persistence of populations in highly seasonal environmental conditions where annual fecundity—and mortality ([Robinson et al. 2010](#), [Scholer et al. 2020](#))—is generally higher than in the tropics. In other words, the colonization of temperate, seasonal environments moves populations toward a “faster” life history compared to tropical species, where high fecundity trades off with high mortality. The evolution of long-distance migration mitigates this high annual mortality by bolstering winter survival, but at a necessary cost to annual fecundity, thereby “slowing down” life history. The longer the migration, the slower the life history. We suggest that the evolution of seasonal migration should be regarded as a fundamental life history trade-off intimately connected to environmentally driven patterns of survival and fecundity, as opposed to a unique strategy with a deterministic benefit for reproductive output.

Opportunities for Further Research

Reliable data on longevity across our study species will be important to understand lifetime reproductive success as opposed to annual patterns. Additionally, although annual survival is thought to be age-independent in adult birds ([Ricklefs 1997](#)), age-specific life tables of survival and fecundity will improve our understanding of how migratory behavior influences the slow-fast continuum. In this context, data on juvenile survival rates, while much more difficult to study due to the likelihood of conflating mortality with natal dispersal, will help illuminate the differences in selection pressures facing species across the migratory spectrum ([Conklin et al. 2017](#)). Such data will be particularly useful for population demographic “life history models” ([Saether and Bakke 2000](#), [Clark and Martin 2007](#), [Rushing et al. 2017](#)), which, if examined comparatively across species, could be instrumental in revealing how

survival and fecundity regulate population growth of species across the migratory distance spectrum.

Our study also highlights the need for information on developmental growth rates to better understand how migration distance influences the pace of life. Recent global studies have suggested that migratory birds undergo faster development than nonmigrants ([Minias and Włodarczyk 2020](#), [Soriano-Redondo et al. 2020](#)), but it remains unclear how migration distance influences developmental durations among co-distributed species such as those in our study. Do long-distance migrants compensate for their short breeding windows with faster development, or do they exhibit slower development consistent with their overall slower pace of life? Studies of growth rate should also extend to the dynamics of pre-basic molt, a critical life cycle event, to better understand how migration distance influences the rate of feather growth and the degree of overlap between breeding, molt, and migration ([De La Hera et al. 2009, 2012](#), [Benson and Winker 2016](#), [Tonra and Reudink 2018](#), [Pageau et al. 2020](#)).

Another important mystery highlighted by our study concerns the post-breeding, premigratory periods, which in general is the most poorly understood period of the avian annual cycle ([Clark and Martin 2007](#)). Even if developmental and molt durations are longer in shorter-distance migrants, short-distance migrants still spend substantially greater time post-development on or near their breeding sites before fall migration than do long-distance migrants. What do hatch-year birds in short-distance migratory and resident species—which will not breed nor molt their flight feathers until the following spring—do with their “extra” time on the breeding grounds?

One possibility is that shorter-distance migratory species and residents invest more time in the prospecting phase of dispersal ([Reed et al. 1999](#)), wherein they use the post-development, premigratory period to search nearby locations for future breeding sites ([Cormier and Taylor 2019](#), [Cooper and Marra 2020](#)). In contrast, long-distance migratory species, with constrained time for prospecting prior to migration, may be under greater selection to return to familiar breeding locations ([Winger et al. 2019a](#)). Counterintuitively, this selection could constrain natal and adult dispersal distances in longer-distance migrants. This possibility is important to investigate because the annual survival estimates we used in this study—which reflect a combination of survival and emigration—could be biased if adult dispersal rates differ systematically across species with different migration distances.

Finally, our study focuses on interspecific differences in survival and fecundity and trade-offs at the species level. Importantly, the relationship between seasonal migration and the balance of survival and reproduction has also received attention in studies of intraspecific variation in

migratory behavior. Indeed, understanding the trade-offs associated with variation in migratory behavior is a primary motivation of research on partial and facultative migration (Ketterson and Nolan 1982, Taylor and Norris 2007, Alves et al. 2013, Ely and Meixell 2015, Hegemann et al. 2015, Lok et al. 2017, Zúñiga et al. 2017, Buchan et al. 2019, Carneiro et al. 2021). Yet, among studies of partially migratory species in which some individuals are more migratory than others, a consensus for the impact of migration on reproductive and survival dynamics remains elusive (Buchan et al. 2019). Further research is required to understand how insights from studies of intraspecific variation relate to the evolution of interspecific differences in migratory behavior and the position of species along the slow-fast continuum.

Implications for Conservation

Our study shows that at its core, migration is a survival strategy that evolves when the benefits of escaping the breeding region during the resource-poor season outweigh the risks of long-distance journeys. It is obvious that the pace at which anthropogenic habitat destruction has occurred on the wintering grounds and at stopover sites for the long-distance migrants in our study far exceeds the ability of these species to adjust their delicately balanced life history strategies. Other major disruptions to migration, such as from artificial light (Loss et al. 2015, Winger et al. 2019b), may further tip the scales against long-distance migration as an effective strategy. Our study, by highlighting that lowered fecundity is a cost of the heightened survival afforded to long-distance migrants in an ecologically intact world, provides an evolutionary context for understanding severe anthropogenically driven population declines observed in long-distance migratory birds (Faaborg et al. 2010b, Rosenberg et al. 2019). Simply put, long-distance migrants require high rates of annual adult survival to persist (Dokter et al. 2018). This highlights the importance of habitat conservation and safe passage for migratory birds throughout their journeys.

SUPPLEMENTARY MATERIAL

Supplemental material is available at *Ornithology* online.

ACKNOWLEDGMENTS

We thank James Saracco and David DeSante for helpful guidance regarding *Vital Rates* parameters and for making these data available. We thank Jacob Berv, Eric Gulson-Castillo, Theunis Piersma, Nathan Senner, Chris Tonra, Kristen Wacker, and Marketa Zimova for constructive feedback on earlier versions of the manuscript and Craig Benkman, Ethan Gyllenhaal, Andy Jones, David Tan, Benjamin Van Doren, Jessie Williamson, Chris Witt, and Scott Yanco for helpful discussion.

Funding statement: This study was funded by the University of Michigan and a National Science Foundation Graduate Research Fellowship to T.M.P.

Ethics statement: All data used in the study were compiled from published, publicly available sources. No permits or protocols were necessary for the research.

Author contributions: B.M.W. conceived the idea; B.M.W. and T.M.P. compiled the data; T.M.P. analyzed the data; B.M.W. wrote the paper with input from T.M.P.

Data availability: Analyses reported in this article can be reproduced using the data provided by Winger and Pegan (2021).

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