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RESEARCH ARTICLE

Six decades of North American bird banding records reveal plasticity in migration phenology

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Abstract

1. The timing of avian migration has evolved to exploit critical seasonal resources, yet plasticity within phenological responses may allow adjustments to interannual resource phenology. The diversity of migratory species and changes in underlying resources in response to climate change make it challenging to generalize these relationships.
2. We use bird banding records during spring and fall migration from across North America to examine macroscale phenological responses to interannual fluctuations in temperature and long-term annual trends in phenology.
3. In total, we examine 19 species of North American wood warblers (family Parulidae), summarizing migration timing from 2,826,588 banded birds from 1961 to 2018 across 46 sites during spring and 124 sites during fall.
4. During spring, warmer spring temperatures at banding locations translated to earlier median passage dates for 16 of 19 species, with an average 0.65-day advancement in median passage for every 1°C increase in temperature, ranging from 0.25 to 1.26 days $°C^{-1}$. During the fall, relationships were considerably weaker, with only 3 of 19 species showing a relationship with temperature. In those three cases, later departure dates were associated with warmer fall periods. Projecting these trends forward under climate scenarios of temperature change, we forecast continued spring advancements under shared socioeconomic pathways from 2041 to 2060 and 2081 to 2100 and more muted and variable shifts for fall.
5. These results demonstrate the capacity of long-distance migrants to respond to interannual fluctuations in temperatures, at least during the spring, and showcase the potential of North American bird banding data understanding phenological trends across a wide diversity of avian species.

KEYWORDS
bird migration, climate change, forecast, phenology, plasticity, warbler

1 | INTRODUCTION

As climates change, so do the phenology, distribution, and fitness of organisms (Potvin et al., 2016; Socolar et al., 2017; Youngflesh et al., 2021). While climate change can have differential impacts on organisms, organismal phenology is often affected through advancing spring phenophases, including leaf out and insect emergence, which often translate into shifting arrival and departure of migratory organisms, or changes in reproductive timing of many primary and secondary consumers (Boggs, 2016; Parmesan & Yohe, 2003; Polgar & Primack, 2011).

The study of phenological change in North America is challenging because most datasets provide limited temporal and spatial coverage or are limited to a few species (except see Marra et al., 2005; Mayor et al., 2017; Van Buskirk et al., 2009; Youngflesh et al., 2021), especially when changes are small, variable and dependent on multiple dimensions including temperature, wind conditions, precipitation (Haest et al., 2019) and land use/land cover change (Saunders et al., 2022). A more complete understanding of how climate change is affecting organisms, now and forecast into the future, requires studies to include a multitude of species across broad spatial and temporal scales to address patterns throughout the annual cycle.

Migratory species are particularly vulnerable to the environmental impacts of climate change because they experience substantial variation in environmental conditions through time and space (Culp et al., 2017). One documented vulnerability for several migratory species is the possibility of phenological mismatch, where the timing of prey availability differs from the timing of consumer needs (Clausen & Clausen, 2013; Saalfeld et al., 2019; Visser et al., 2012). Yet, while directional phenological shifts abound (Cohen et al., 2018; Usui et al., 2017), interannual fluctuations in resources and the subsequent responses to such fluctuations—a measure known as migratory sensitivity—points towards phenotypic plasticity as a mechanism for coping with potential mismatches (Youngflesh et al., 2021). Disentangling plastic annual changes or adaptive evolutionary changes remains challenging (Charmantier & Gienapp, 2014). If inherited circannual clocks control migration phenology, which is believed to be the case for many long-distance migrants (Åkesson et al., 2017; Gwinner, 1996), shifts in phenology are likely the result of evolutionary processes (Van Buskirk et al., 2012), rather than annual responses to current conditions (e.g. phenotypic plasticity). Weather conditions en route are likely to generate variation in timing (Deppe et al., 2015; Richardson, 1990), and stopover decisions can ultimately drive large changes in migration duration (Schmaljohann, 2019). Environmental and genetic drivers of phenology likely interact to drive phenotypic change, and there is a large body of evidence documenting multi-week variation in phenophases within the same species, showing that variation is common place, despite endogenous control (Cooper et al., 2015; González et al., 2020; Studds & Marra, 2011). Recent evidence suggests that adaptation through evolution can occur over short decadal scales for long-distance migrants (Helm et al., 2019). The importance of evolutionary responses in adaptation to global change, especially in long-distance migrants, is of great importance, particularly for making predictions about how birds might respond in the future, but also to understand if such evolutionary adaptations are broadly shown by migratory species.

More than half of North American breeding species of birds are migratory (Horton et al., 2019), providing a rich and diverse assemblage of breeding species for studying phenology in animal populations. Regular and systematic marking and monitoring of birds began in a variety of locations across North America in the middle of the 20th century, allowing a robust and long-term study of phenological patterns relative to a changing climate. Data on both spring and fall migratory seasons are available across large geographical and temporal scales, spanning more than 40° of latitude, 50° of longitude, and in some locations, nearly 60 years of observations. While a number of studies have documented advancement of spring migration in avian species (Covino, Morris, et al., 2020; Marra et al., 2005; Møller et al., 2008; Sparks et al., 2005; Van Buskirk et al., 2009), there are fewer examinations and more mixed patterns of how changing climates may impact fall migration phenology (but see Haest et al., 2019; Jenni & Kéry, 2003; La Sorte et al., 2015; Miles et al., 2017). Advancements of spring timing are relatively consistent and easily understood in the context of the fitness consequences, with birds arriving earlier to their breeding grounds showing greater reproductive success (Cooper et al., 2015; McKellar et al., 2013; Morrison et al., 2019). Predictions of how the timing of fall migration influences fitness are less clear. Existing work on fall phenological changes are more varied, with some recent studies finding earlier fall timing and others finding later timing (Covino, Horton, et al., 2020; Horton et al., 2020). However, because the fall migration system is largely composed of juvenile migrants making their first migration, fall timing may have strong implications for survival and could affect species' abilities to have multiple broods and ultimately influence reproductive output (Both et al., 2019; Jenni & Kéry, 2003).

Wood warblers, family Parulidae, comprise a geographically, behaviorally, and ecologically diverse taxonomic group found throughout the Americas. Approximately 50 wood warbler species regularly breed within the United States and Canada (Chesser et al., 2020). These species vary widely in their breeding range, non-breeding range, and migratory behaviours, including migratory distance, route and residency patterns. While some species have relatively narrow breeding ranges, the ranges of other species span from coast-to-coast. Although this group of birds is almost exclusively insectivorous, their foraging behaviours and food preferences vary

(Wilman et al., 2014). Since insectivorous birds use food sources that are directly driven by climate and seasonal variation in temperature (e.g. emergence date; Nordlie & Arthur, 1981; Visser et al., 2006), and because temperature broadly drives ectothermic phenology (Scranton & Amarasekare, 2017), we make an inferential leap that temperature can serve as a predictor of warbler phenology and resource availability. Warblers can provide insight into the link between climate change and migration phenology and whether there is a consistent pattern across a diverse taxonomic group. Additionally, while phenology is clearly driven by multiple factors (see above), if a relationship is drawn between temperature and phenology, tentative forecasts of migration timing can be drawn from future climate scenarios.

To this end, we examine spring and fall migration phenology of 19 species of wood warblers frequently banded across North America. To quantify interannual fluctuation in timing and the possibility for long-term changes in phenology, we test the hypothesis that annual migration phenology is linked with seasonal temperature. From previous studies, we predict a positive relationship between spring phenology and temperature—that is, with warmer temperatures we predict earlier migration phenologies (Cohen et al., 2018; Van Buskirk et al., 2009). In fall, our predictions were more uncertain; however, previous studies on North American passerines have shown earlier migration phenologies during warmer seasons (Van Buskirk et al., 2009). To extend these inferences, we forecast seasonal migration timing under ~30- and 70-year site-specific future climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Bird banding records

We requested bird banding records from the United States Geological Survey (USGS) Bird Banding Laboratory (BBL) for all North American wood-warblers (family Parulidae). Data were requested in April 2020. In total, 6,741,565 banding records were provided, with 44 species regularly banded as evidenced by at least 1000 captures from 1961 to 2018 (58 years). We choose this span of years to align with available historical temperature data (see below). Following filtering protocols described below, and used by Covino, Horton, et al. (2020), 19 species during both spring and fall had adequate sample sizes for our analyses. In two species cases, Palm Warbler *Setophaga palmarum* and Yellow-rumped Warbler *Setophaga coronata*, both species were coded by their subspecies names in the BBL. For Palm Warbler, we pooled our summaries by the common name, whereby we lumped banding counts of Western Palm Warbler and Yellow Palm Warbler. For Yellow-rumped Warbler, we used the native BBL naming convention in our summaries, Aububon's Warbler and Myrtle Warbler. In the case of Yellow-rumped Warbler, this was done because of greater differentiation in subspecies geographic distribution. However, of these specific cases, only Myrtle Warbler met our sampling criteria and was included in our analyses. To align with accepted species common names, we labelled summaries of Myrtle Warbler as Yellow-rumped Warbler. To summarize warbler ages, 'young' refers to hatch-year birds during the fall and second-year birds during the spring, and 'adult' refers to after-hatch-year birds during the fall and after-second-year birds during the spring. We used the term 'unknown' for birds of unknown age during the fall and the imprecise age category of after-hatch year during the spring.

We defined spring migration from March 15 to June 15 and fall migration from August 15 to November 15, 3-month periods. These dates were selected because they broadly capture the dominant pulse of songbird migration through North America in both spring and fall, respectively (Horton et al., 2020). We excluded all records outside these two seasons. We excluded data from sites that banded extensively during the breeding and non-breeding periods, removing any data from sites where greater than 50% of the captures occurred between June 15 and August 15 (breeding) and between November 15 and March 1 (non-breeding). Additionally, we removed any birds banded with age class '4' (Bird Banding Laboratory Age Codes), indicating a locally hatched bird incapable of sustained flight. We acknowledge that age or sex can influence seasonal timing (Covino, Horton, et al., 2020), however these traits could not be reliably determined for all species and for particular species in specific seasons, and for this reason they were not assessed in this study. However, see Table S1 for a breakdown of age and sex for each species included in this study.

Because banding records are presence only, we zero-filled the banding records to discern true detection/non-detections where possible. While the zeros do not influence our phenology estimate, it was important to account for banding effort, which we use as a data filter (e.g. a zero would at least indicate that banding was conducted). For each species, data were zero-filled using banding records across all warblers for a given site as an indication of banding effort. For example, if *species X* was banded on *day 1* at *site A*, but *species Y* was not banded on *day 1* at *site A*, we assumed zero of *species Y* were banded for *day 1* at *site A*. Banding observations were then pooled into 0.5° latitudinal and longitudinal locational bins for each species (hereafter termed 'location'), equating to about 55 km × 55 km or 3025 km^2. For each season, these 0.5° × 0.5° locations were only included if at least 10 years of observations were present and an overall mean of 10 birds were banded across all years (Marra et al., 2005). Next, of the locations that remained, we only included specific season-year replicates if at least 25 days of banding occurred, and 15 individuals of a specific species were banded. These protocols helped ensure adequate seasonal effort and ensure phenology measures were representative of species passage.

To estimate species phenology, we calculated the date at which 50% of the cumulative sum of birds were captured at each seasonal 0.5° × 0.5°. We termed this median passage date. For our analyses, we only included species that had at least five unique locations represented per season. Additionally, at 40 stations that had both spring and fall banding records, we calculated the interval (in days) between median passage dates. Lastly, for spring and fall, we calculated the time interval between 25% and 75% of cumulative sum of birds to quantify the length of the migratory season.

Lastly, to insure that phenological patterns were representative of migrant behaviour, rather than sampling behaviour, at each location (0.5° by 0.5° pixel) for spring and fall, we examined three different annual metrics: earliest banding date, median banding data and maximum banding date. For each date, we assessed if these dates changed significantly (alpha = 0.05) with year. We further examined those locations with significant trends to see if there was a consistent directionality of the trends, as any directional trends would be cause for concern. We conducted binomial tests on these directional coefficients with the null hypothesis about the probability of success in a Bernoulli experiment being 50:50 (i.e. equal probability of positive or negative trends). This investigation did not reveal consistent changes for earlier or later banding across the time series (see Supporting Information).

2.2 | Historical temperature data

In our analysis, we choose temperature as opposed to normalized difference vegetation index (NDVI) or enhanced vegetation index (EVI) to serve as a proximate cue of phenology, rather than an ultimate factor shaping phenology. We made this decision because vegetative indices from satellite remote sensing are not available for the 1960s or 1970s. However, temperature and vegetative indices are broadly correlated in quantifying phenology (Clinton et al., 2014), and for this reason, we use temperature.

To relate phenology measures with temperature, we downloaded historical mean monthly maximum temperature measures from WorldClim (mean of daily maximum values) (https://www.worldclim.org/data/monthlywth.html). We used the WorldClim version 2.0 gridded monthly temperature data from January 1961 to December 2018 (Harris et al., 2020). WorldClim monthly temperature data are derived from the Climatic Research Unit gridded Time Series (CRU TS, version 4.03) (Harris et al., 2020). CRU TS is global in coverage and disseminated along a 0.5° latitude by 0.5° longitude grid over all land domains of the world, except Antarctica. Temperature measures and subsequent interpolations are derived from a network of ground-based weather stations. For our study, we averaged April and May measures to align with spring banding efforts and September and October to align with fall banding efforts. Temperature data were associated with banding locations (i.e. 0.5° pixels). To understand how migrants responded to annual fluctuations in seasonal temperature, we calculated anomalies for each location. Anomalies were calculated by subtracting the annual seasonal mean from the long-term seasonal mean from 1961 to 2018; hence, negative values denote cooler seasons (relative to the long-term mean) and positive values denoting warmer seasons.

2.3 | Climate forecast data

To examine how warbler phenology could respond to future climate scenarios (i.e. predictions of mean maximum temperature), we downloaded climate scenarios from WorldClim (https://www.worldclim.org/data/cmip6/cmip6climate.html). Specially, we used 10-min resolution (~0.16°) projections from eight global climate models, including BCC-CSM2-MR (Wu et al., 2019), CNRM-CM6-1 (Voldoire et al., 2019), CNRM-ESM2-1 (Séférian et al., 2019), CanESM5 (Swart et al., 2019), IPSL-CM6A-LR (Boucher et al., 2020), MIROC-ES2L (Hajima et al., 2020), MIROC6 (Tatebe et al., 2019) and MRI-ESM2-0 (Yukimoto et al., 2019). We examined four shared socioeconomic pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, ordered by decreasing climate intervention) for projections of temperatures in 2041–2060 and 2081–2100. Shared socioeconomic pathways represent a set of alternative futures of societal development, ranging in challenges towards mitigating and adapting to climate change (e.g. SSP1-2.6 predicts lower societal challenges towards climate change mitigation and adaptation as compared to SSP5-8.5, and thus more modest rates of climate change) (O'Neill et al., 2017). SSP1-2.6 is a scenario that sees climate intervention and aims to keep warming below 2°C by 2100 (between 1880–1900 and 2090–2100). SSP5-8.5 represents a fossil-fuel development world through the 21st century and is viewed as a worst-case scenario.

2.4 | Statistical analyses

We generated season-specific models for each warbler species to quantify the relationship of migrant phenology with seasonal temperature anomalies, year and latitude. We tested for the interaction of temperature anomalies and latitude: however, in both spring and fall it was not an important contributor to the models. For each season and species combination, we fit a linear mixed model with fixed effects of temperature anomaly, year, latitude, and a random intercept of location (i.e. 0.5° location bins). Year was included to detrend phenological time series to reveal the influence of seasonal plasticity (Iler et al., 2017) and latitude used to account for spatial dependencies of phenological timing. The random effect of location accounted for the fact that observations from the same location are not independent. The latitude fixed effect tests for a latitudinal trend in timing. In addition to species-specific models, we also generated two global seasonal models (one for spring and one for fall) with species added as a random effect.

For phenology predictions using future climate scenarios, we set year (a fixed effect) to 2018, rather than extrapolate to the respective years represented by the climate scenarios (e.g. 2041–2060, 2081–2100, ~30- and 70-year horizons). Thus, our future predictions are based on species' measured plasticity to temperature effects. We referenced phenologies under climate scenarios relative to recent phenology patterns predicted using mean anomaly temperatures from 2014 to 2018. Thus, for each location (i.e. 0.5° location bins), we made a prediction of median passage date under location-specific temperature anomaly forecasts for 2041–2060 and

2081–2100. We then took the difference between those forecast dates and those predicted for 2018, with negative values denoting earlier dates and positive values denoting later dates.

All analyses and figures were generated using R version 4.0.2 (R Core Team, 2020). We used the lme4 package to implement mixed models (Bates et al., 2014) and generated confidence intervals using merTools (Knowles & Frederick, 2020) with 1000 bootstrap iterations.

3 | RESULTS

3.1 | Bird banding records

In total, 2,826,588 banded warblers were included in our analyses from 1961 to 2018; 674,089 birds banded during spring and 2,152,499 during fall (Figure 1; Figure S1). Through this time series, we did not find evidence of systematic shifts in spring or fall banding effort (see Supporting Information). During spring, 36.6% of warblers were sexed as female, 51.8% as male, and 11.6% as unknown (Table S1). During fall, 27.2% of warblers were sexed as female, 32.8% as male, and 40.0% as unknown (Table S1). Examining age classes, spring migrants were 40.0% young, 19.6% adult and 40.4% unknown age class and fall migrants were 75.7% young, 16.3% adult, and 8.1% unknown age class (Table S1). Common Yellowthroat (15.9%), Magnolia Warbler (14.5%) and Yellow-rumped Warbler (14.2%) were the three most banded species during spring, accounting for 44.6% of individuals banded during spring. Yellow-rumped Warbler (33.1%), Common Yellowthroat (10.5%) and American Redstart (8.7%) were the most common fall migrants and tallied 52.2% of individuals banded during fall. During spring, 46 locations were represented and 124 locations during fall (Figure 2). On average, spring locations tallied 22.2 ± 11.8 (±SD) years of data (Figure 2), with an average of 7.2 ± 5.3 (±SD) species represented at each location (Figure S2). During fall, locations tallied an average of 21.6 ± 12.2 (±SD) years of data (Figure 2), with an average of 6.4 ± 4.8 (±SD) species represented at each location (Figure S2). Comparing the 40 locations where both spring and fall banding operations were conducted, we found that the interval between spring and fall median passage dates lengthened significantly (0.06 days year^{-1}, 0.04 to 0.08 95% CI, 3.4 days longer from 1961 to 2018). Overall, the duration of fall migration was considerably longer, on average the interval between the dates of 25% and 75% cumulative captures were 6.3 days longer during fall than spring (paired *t*-test, $t_{4790} = -53.8$, $p < 0.001$, 40 locations).

3.2 | Historical relationship with temperature

During spring, temperature anomalies were a significant predictor of median passage date for most species, with 16 of 19 species

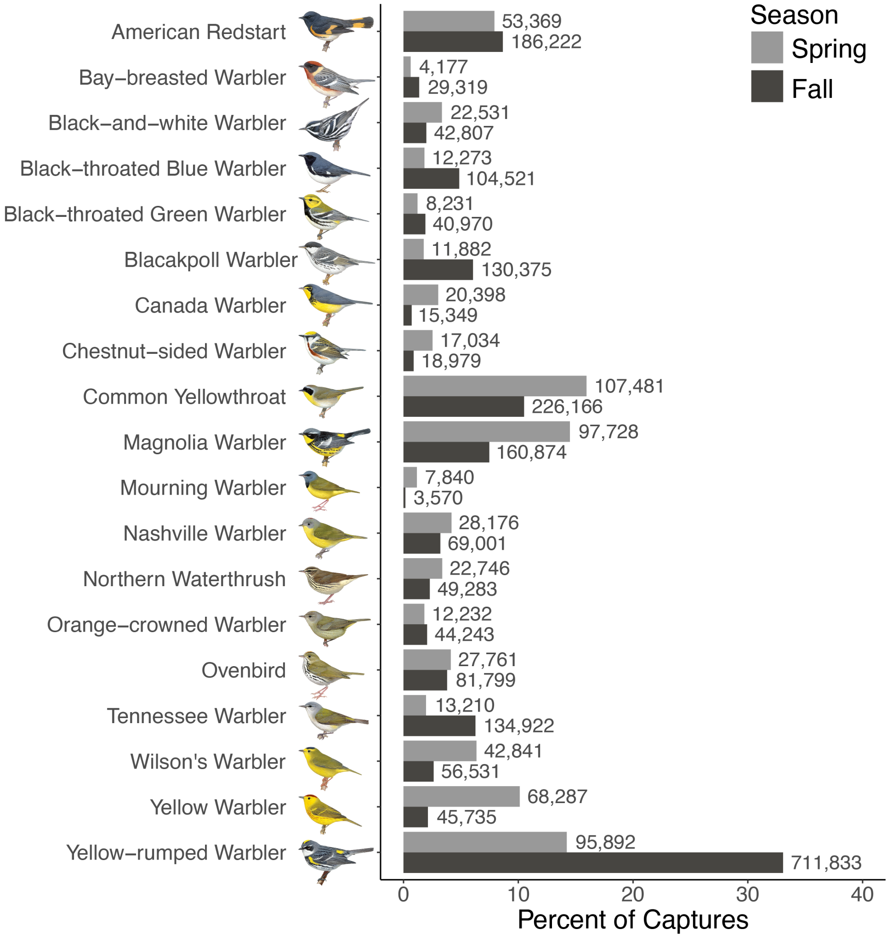

FIGURE 1 Percent of seasonal captures and number of migratory warblers banded during spring (March 15 to June 15) and fall (August 15 to November 15) from 1961 to 2018. In total, 2,826,588 banded warblers were included in phenology analyses. Warbler illustrations reproduced by permission of Lynx Edicions.

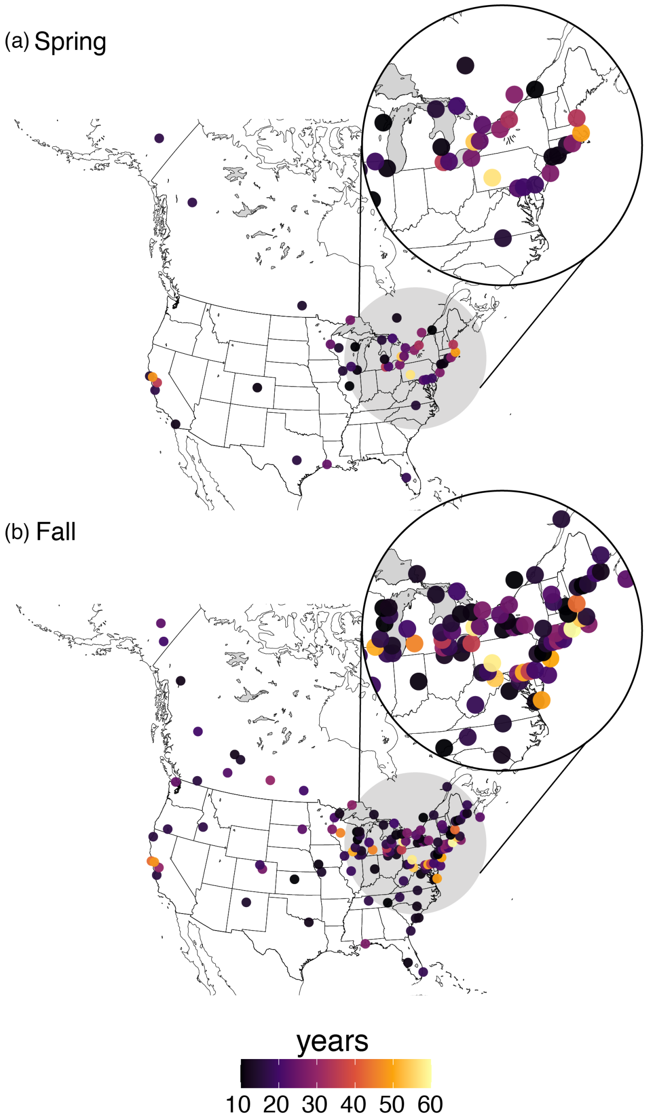

FIGURE 2 Migration banding locations during (a) spring ($N = 46$) and (b) fall ($N = 124$) showing the number of years of data included in our analyses. Points represent 0.5° latitude by 0.5° longitude locations. Inset used to highlight higher density banding areas of North America.

showing significantly negative slopes, indicating earlier median passage date during warmer spring periods (Figure 4a,b; Table S2). This can be visualized at a single location (Appledore Island) for Common Yellowthroat *Geothlypis trichas*, whereby migrants arrive earlier during anomalously warm seasons ($F_{1,30} = 6.66$, $p = 0.015$, Figure 3). Year was a significant predictor in 8 species, with 7 of 8 species showing negative slopes in those cases, ranging from −0.027 to −0.069 days year^{-1} (Table S2). Orange-crowned Warbler ($\beta = -1.216$ days °C^{-1}, −2.104 to −0.344, 95% CI), Tennessee Warbler ($\beta = -0.973$ days °C^{-1}, −1.279 to −0.611, 95% CI), and Chestnut-sided Warbler ($\beta = -0.906$ days °C^{-1}, −1.158 to −0.617, 95% CI) showed the greatest phenological advancements for every 1°C increase in temperature. Across all species using a single mixed model with species as a random effect, we observed a 0.65-day (−0.72 to −0.56, 95% CI) advancement in median passage for every 1°C increase in temperature ($p < 0.001$), and a 0.027-days year^{-1} (−0.036 to −0.017, 95% CI) advancement with each passing year. In other words, warmer spring temperatures led to earlier passage dates, with more recent migratory movements also occurring slightly earlier.

During fall, temperature anomalies were a significant predictor of median passage date for only 3 of 19 species, with those three species showing a positive slope, indicating a delay in median passage date during warmer fall periods (Figure 4c,d; Table S3). While Common Yellowthroat did not show an overall response to temperature anomalies, it did show a directional trend at one of our longest-term banding locations, whereby migrants median passage data were later during anomalously warm seasons ($F_{1,40} = 4.892$, $p = 0.0327$, Figure 3). Year was a significant predictor in 12 species, showing a negative slope for 7 species and a positive slope for 5 species (Table S3). Across all species using a single mixed model with species as a random effect, we only found that latitude (−1.43-days °latitude^{-1}, −1.60 to −1.27, 95% CI, $p < 0.001$) was predictive of fall phenology, with temperature anomalies and year having a nonsignificant influence ($p = 0.069$ and $p = 0.220$, respectively).

3.3 | Climate forecast

Examining future spring climate scenarios, temperatures were consistently warmer at sampling locations, regardless of the shared socioeconomic pathway. Under SSP-585, median passage date was predicted to shift 1.58 ± 0.81 (±SD) days earlier under temperature predictions from 2041 to 2060 and 3.60 ± 1.59 (±SD) days earlier from 2081 to 2100 (Figure 5). From 2041 to 2060, temperatures were on average 1.62 ± 0.85°C (SSP-126, ±SD), 1.98 ± 0.88°C (SSP-245, ±SD), 2.06 ± 1.03 °C (SSP-370, ±SD) and 2.52 ± 1.01°C (SSP-585, ±SD) relative to the mean temperature from 2014 to 2018. From 2081 to 2100, temperatures were 1.66 ± 0.85°C (SSP-126), 3.09 ± 1.06°C (SSP-245, ±SD), 4.54 ± 1.58°C (SSP-370, ±SD) and 5.80 ± 1.75 °C (SSP-585, ±SD) higher relative to the mean temperature from 2014 to 2018. See Tables S4 and S5 for all modelled scenarios.

Like spring, fall future climate scenarios showed consistent warming—although magnitudes were weaker. Under SSP-585, median passage dates are predicted to delay 0.17 ± 0.58 (±SD) days under temperature predictions from 2041 to 2060 and 0.48 ± 1.45 (±SD) days later from 2081 to 2100 (Figure 5). From 2041 to 2060, temperatures were on average 1.11 ± 0.86°C (SSP-126, ±SD), 1.49 ± 0.89°C (SSP-245, ±SD), 1.60 ± 1.07 °C (SSP-370, ±SD), and 2.07 ± 1.04°C (SSP-585, ±SD) relative to the mean temperature anomalies from 2014 to 2018. From 2081 to 2100, temperatures were 1.12 ± 1.85°C (SSP-126, ±SD), 2.62 ± 1.05°C (SSP-245, ±SD), 4.17 ± 1.61°C (SSP-370, ±SD), and 5.47 ± 1.80 °C (SSP-585, ±SD) higher relative to the mean temperature from 2014 to 2018. See Tables S4 and S5 for all modelled scenarios.

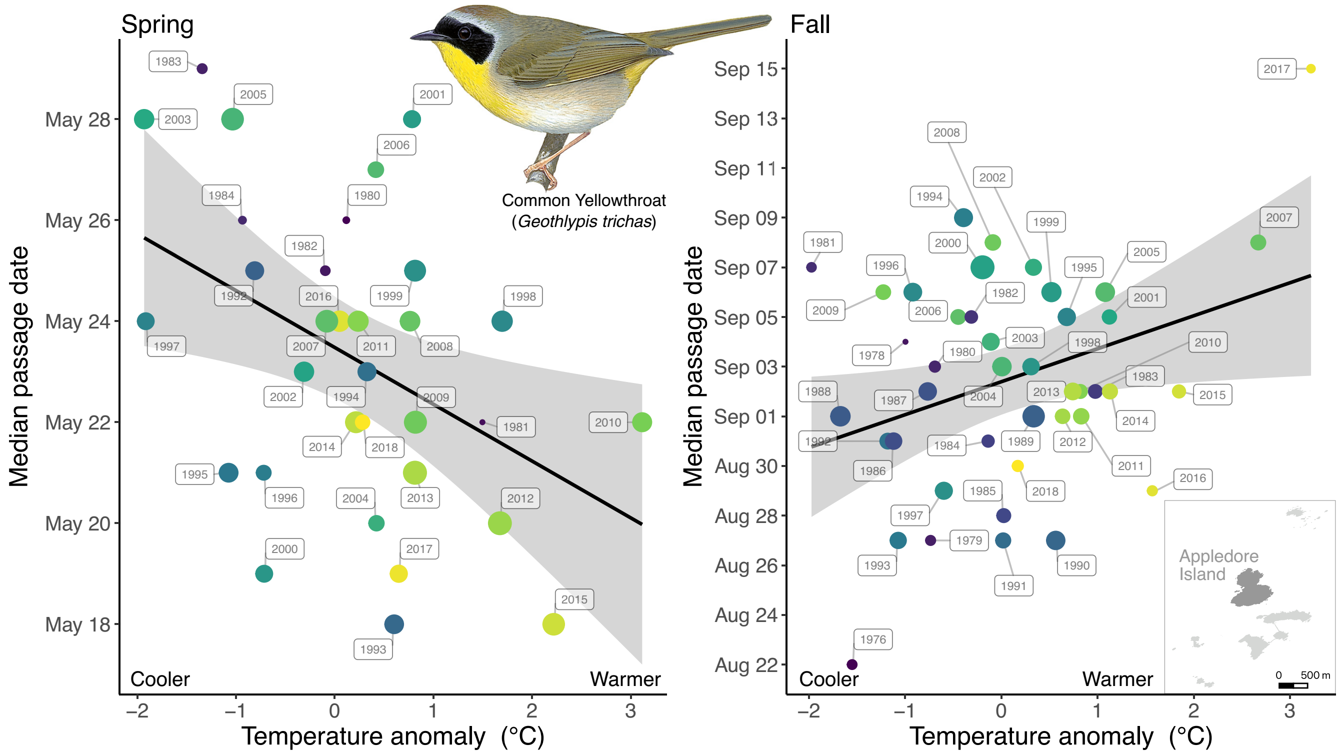

FIGURE 3 Median passage date for Common Yellowthroat (*Geothlypis trichas*, *COYE*) relative to temperature anomalies (°C) from 1980 to 2018 during spring and 1976 to 2018 for fall for a single location. This location (43°N, −70.5°W), refers to a single banding station, Appledore Island, ME. Points are shaded according to year and their size scaled to the number of seasonal captures (spring mean 599.8 COYE banded, fall mean 120.8 COYE banded). The fitted line and 95% confidence band are from least-squares linear regression. Here, the slope of the line differs significantly from zero for both seasons (spring $p = 0.011$, fall $p = 0.033$). Warbler illustration reproduced by permission of Lynx Edicions.

4 | DISCUSSION

We amassed six decades of bird banding records from 19 warbler species to characterize putative changes in spring and fall migration phenology, in total summarizing records from 2.8 million migrants from 130 locations in North America. During spring, the direction of phenological responses to interannual fluctuations in mean temperature were largely consistent across all warbler species, with most species showing earlier median passage dates during warmer seasons. While many long-distance migrants are thought to initiate migration phenology based on cues entrained by day length (Gwinner, 1996), it is clear that responses to seasonal conditions plays an important role in shaping seasonal migration timing. Annual adjustments to seasonality likely occur *en route* through advancements or delays in stopover duration or flight speed (Marra et al., 2005), although changes in stopover duration tend to be the greatest contributor to seasonal shifts (Schmaljohann & Both, 2017). While Horton et al. (2020) and Youngflesh et al. (2021) found that spring phenological advancements were more pronounced at northerly sites, we found no interaction between temperature anomalies and latitude in influencing phenology. This may be, in part, due to more limited latitudinal sampling in this study. The distribution of banding locations in this study shows a strong eastern bias (Figure 2), with relatively few sites represented in the central and western flyways. While it is unsurprising that coverage is limited in more remote regions of North America (e.g. Canada, Alaska), is it particularly notable that long-term records are lacking from some of the most import migrant corridors in North America (Dokter et al., 2018), including broad regions surrounding the Gulf of Mexico, lower mid-west, and southeast.

While spring migrants showed clear phenological variation in response to seasonal conditions, fall migrants showed mixed and nonsignificant trends, with only latitude serving as an important broadscale driver of the timing of migratory passage (i.e. earlier at northern sites, later at southern sites). Our results are largely in line with others that have examined fall migration (Covino, Horton, et al., 2020; Horton et al., 2020; Van Buskirk et al., 2009), where comparatively, fall migration timing patterns are more variable and trends are more muted relative to spring phenological change. The interval between spring and fall median passage dates lengthened significantly, largely driven by spring advancement, but in some instances, fall delays. These intervals varied by species, with 9 species showing significant expansions in the spring to fall passage interval, ranging from 0.5 to 2.9 days decade^{-1}, with Tennessee Warbler showing the greatest change. We also observed significantly wider intervals between the dates of 25% and 75% cumulative captures during fall than spring (~6 days longer). Differences in seasonal migration length are likely a reflection of differential departure by age classes in the fall, general fitness advantages of

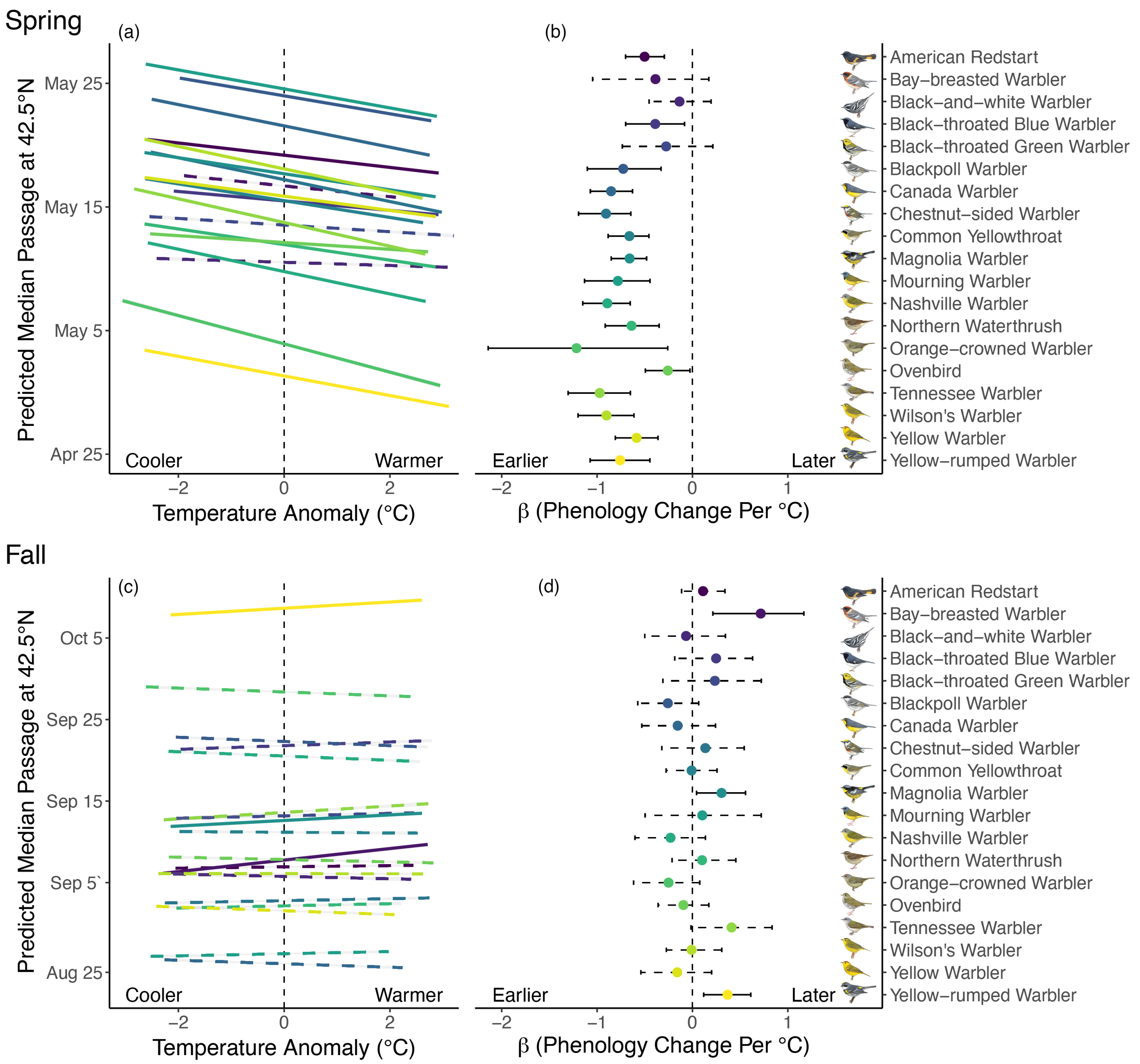

FIGURE 4 Linear regression of spring (a and b) and fall (c and d) median passage date relationship relative to mean maximum temperature for 19 wood-warbler species. (a and c) Species-specific fitted lines from linear mixed model with locations (i.e. 0.5° locational bins) as a random effect and phenology predicted across species-specific temperature ranges (between the 2.5% and 97.5% quantiles) and at 42.5°N latitude (median of locations). (b and d) Slope (β) and 95% confidence intervals from species-specific linear mixed models showing phenology change per °C. Regression lines shaded in (a) and (c) correspond to species-specific colours of (b) and (d). Solid lines represent significant trends ($p < 0.05$, a and c) and solid confidence interval lines represent intervals not overlapping zero (b and d). Dashed lines show non-significant trends ($p > 0.05$) and intervals overlapping zero. Warbler illustrations reproduced by permission of Lynx Edicions.

rapid spring arrival, and seasonal differences in prevailing winds and suitability for north or southbound flights. Regardless, we did not detect a broadscale signal that fluctuations in fall interannual phenology were driven by the variation in seasonal temperature.

In a fossil-fueled development scenario (SSP5-8.5) (Kriegler et al., 2017), the models we leveraged showed an average of 2.1 and 5.5°C of warming in 2060 and 2100, respectively. These changes put warblers on pace to shift 1.5 (year 2060) and 3.6 (year 2100) days earlier in the spring, with some species like Orange-crowned Warbler, Tennessee Warbler and Nashville Warbler showing multiple scenarios of greater than 7 days of advancement by 2100, particularly at more northerly sites where warning trends are most prominent. If food resources are not ultimately a limiting resource (i.e. a phenological mismatch), additional time between spring and fall migration periods may eventually afford opportunities for additional broods or buffer against nest failure if renesting is possible (Møller et al., 2010). While much attention regarding phenological mismatch is focused on spring and summer phenophases, it is

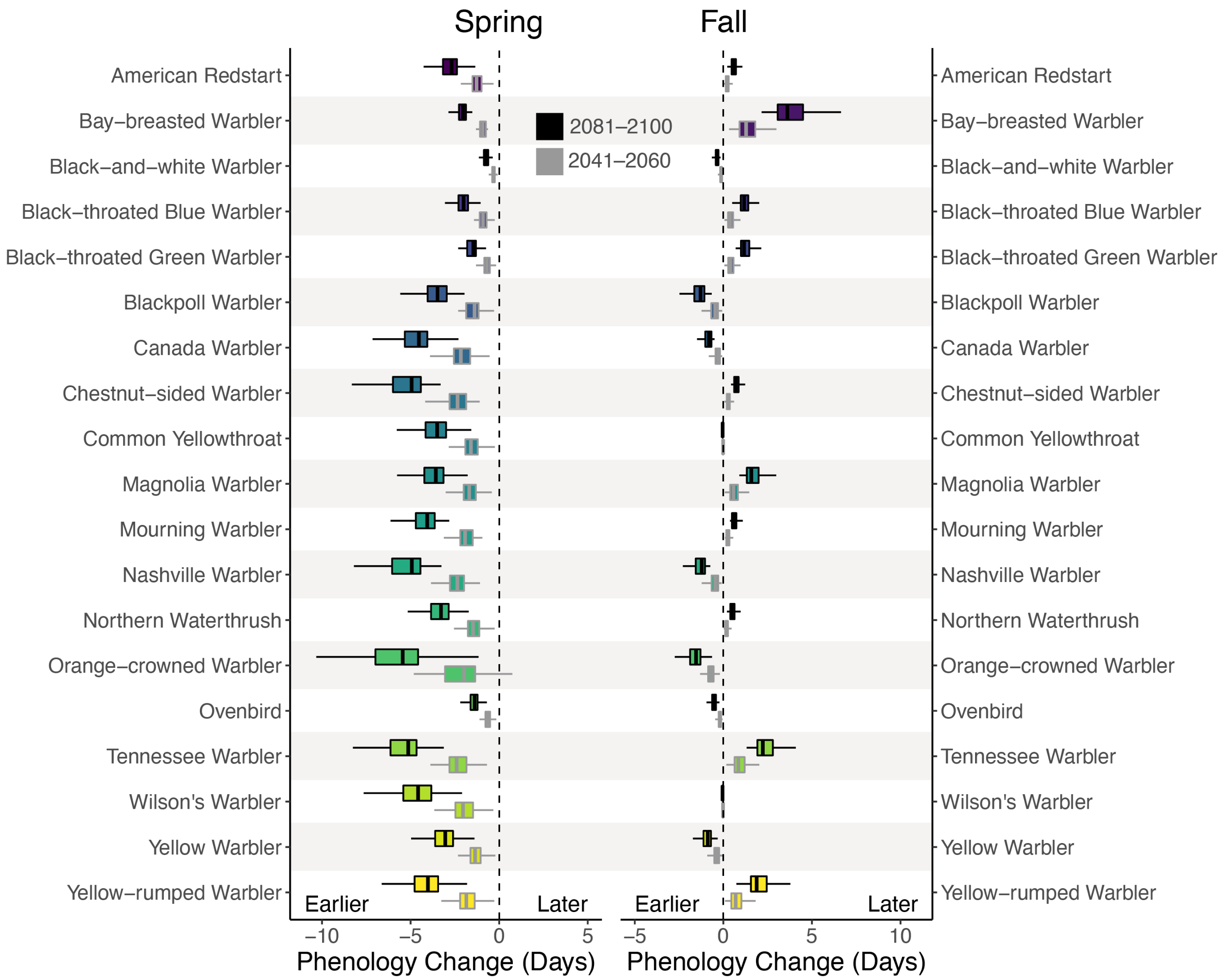

FIGURE 5 Predicted median passage date for spring and fall migration periods using shared socioeconomic pathway (SSP-585) climate scenarios for 2041–2060 (grey) and 2081–2100 (black). Predictions referenced from median passage predictions from year 2018 and location-specific mean anomalies from 2014 to 2018 and location latitude. Box plots show the distribution of predictions from eight separate models (see Section 2) across all locations.

unclear how fall changes in temperature and food resources will shape migrant fitness (Gallinat et al., 2015). Our results did not overwhelming demonstrate changes in the timing of fall migration, and by extension, forecast phenologies were similarly equivocal. Warming temperatures have already been shown to extend the overall autumn period, delaying leaf senescence and affording additional insect generations (Fu et al., 2018; Ibáñez et al., 2010). However, fruit ripening may be advancing (Menzel et al., 2006). During fall migration, migrants with diets composed of both fruit and insects have been shown to gain significantly more mass during migration (Parrish, 1996). With temperatures forecast to continue changing in both spring and fall, and the timing of fall migration showing modest shifts, phenological mismatches have the potential to be more detrimental in the fall.

With bird migrants facing a multitude of environmental threats (Loss et al., 2015), population declines are hardly a surprise. Recent estimates of nearly a net loss of 3 billion breeding birds from 1970 to 2017 are sobering (Rosenberg et al., 2019). Of the 19 warbler species examined in this study, Rosenberg et al. (2019) found 13 to be in decline, with Blackpoll Warbler showing the greatest magnitude (307 million) and proportional decline (88%). In total, a net of 599 million breeding warblers of these 19 species were estimated to have disappeared over from 1970 to 2017, a period largely overlapping with our study period. However, some species including Black-throated Blue Warbler, Northern Waterthrush and Magnolia Warbler have shown population increases, yet our estimated changes in phenology do not appear to covary with North American population trends, either in spring or fall. Broadly examining these patterns, across a diverse suite of species is necessary to understand the potential for interactions of population changes and phenology (Dunn & Møller, 2014; Møller et al., 2008).

One of the key challenges faced in using bird banding records is the inability to verify seasonal or daily effort—key figures that aid in zero filling and standardization of station effort. While nearly all banding stations collect information pertaining to how daily operations are conducted, for example, how many nets were opened, the size of those nets, or more simply, if banding activities were conducted. However, these pieces of information are not archived by the USGS bird banding lab. Amassing this information, site-by-site, would be a considerable undertaking, and at times, may not be possible if records have been lost through time. Estimates of seasonal phenology are likely more robust than other banding metrics, like abundance or capture rates, but effort data can alleviate some the assumptions made in this study. Acquiring information from additional species would surely help to support efforts to account for effort. For instance, the addition of commonly banded species, beyond warblers or even migratory birds, would help resolve additional instances of zeros, and thus a reference point for if a station banded on a particular day. Expanding this taxonomic lens also serves to broaden our insights into how migrants are responding to changing environments.

Through phenotypic plasticity, migrants can respond, to some degree, to changing seasonal temperatures, but will this be enough to match the effects of climate change? Unfortunately, our data and results cannot answer this question. While phenotypic plasticity is clearly demonstrated, and future climate projections predict advancements into the future for spring migrants, our approach assumes that plasticity is unbounded and past behaviours are indicators of future climate response—our future projections are true extrapolations. If spring migration initiation is constrained by endogenous cues (Gwinner, 1996), then there are clearly limits to the amount of change that can occur *en route*. However, selection for earlier departures—evolution—is an alternative mechanism that over time and successive generations, can reshape migration initiation timing (Jonzén et al., 2006). The pace of changing resources may outpace evolutionary selection, although results from Helm et al. (2019) suggest change is possible on a relatively short time scale. Quantifying evolutionary changes in migration timing is immensely challenging (Charmantier & Gienapp, 2014), especially in unstructured datasets like bird banding data. If past plasticity is an indication of future phenological patterns, we predict continued advancements, with the magnitude largely dependent on humanity's ability to mitigate climate impacts.

AUTHOR CONTRIBUTIONS

Kyle G. Horton, Sara R. Morris and Kristen M. Covino conceived the idea for this paper. Sara R. Morris and Kristen M. Covino organized the data request and obtained data permissions where needed. Kyle G. Horton and Benjamin M. Van Doren processed data, led statistical analyses and generated figures. All authors worked to draft and edit the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Original banding data are available through the United States Geological Survey Bird Banding Laboratory. Processed projects needed to replicate these products are made available here: https://doi.org/10.6084/m9.figshare.21803880.v1 (Horton et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Annual totals of 19 focal wood-warbler species banded from 1961 to 2018 during spring (March 15 to June 15) and fall (August 15 to November 15).

Table S1: Number and percent of migratory warblers banded during spring (March 15 to June 15) and fall (August 15 to November 15) from 1961 to 2018.

Figure S2: Migration banding locations during (A) spring ($N = 46$) and (B) fall ($N = 124$) showing the number of species recorded at each location. Points represent 0.5° latitude by 0.5° longitude locations. Inset used to highlight higher density banding areas of North America.

Table S2: Linear regression of spring median passage date relationship and mean maximum temperature and year for 19 wood-warbler species. Species-specific slopes generated from linear mixed model with location (i.e. 0.5° location bins) as a random intercept. Confidence intervals (95%) calculated from 1000 bootstrap samples. Coefficients with *p*-values <0.05 are shaded in grey.

Table S3: Linear regression of fall median passage date relationship and mean maximum temperature and year for 19 wood-warbler species. Species-specific slopes generated from linear mixed model with location (i.e. 0.5° location bins) as a random intercept. Confidence intervals (95%) calculated from 1000 bootstrap samples. Coefficients with *p*-values <0.05 are shaded in grey.

Table S4: Means (±SD) of predicted median passage date for spring and fall migration periods under four different shared socioeconomic pathway climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) for *2041–2060*. For each scenario, averages from eight model were taken. Predictions referenced from median passage predictions from 2018 and mean temperatures from 2014 to 2018.

Table S5: Means (±SD) of predicted median passage date for spring and fall migration periods under four different shared socioeconomic pathway climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) for *2081–2100*. For each scenario, averages from eight model were taken. Predictions referenced from median passage predictions from 2018 and mean temperatures from 2014 to 2018.

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