Received: 8 … | Accepted: 9 January 2023

DOI: 10.1111/1365-2656.13887

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

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

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Funding information
Cornell University; N… and Space Administrat… Award Number: 80NSSC2… National Science Foun… Award Number: … Seaver College of Sci… Continuing Faculty Gr…

Handling Editor: Annette Fayet…

Abstract

1. The timing of avian migration has evolved … yet plasticity within phenological-respons… nual resource phenology. The diversity of … derlying resources in response to climate … these relationships.
2. We use bird banding records during spring … America to examine macroscale pheno-logica… tions in temperature and long-term trends in phenolo…
3. In total, we examine 19 species of North … Parulidae), summarizing migration timing f… to 2018 across 46 sites during spring and …
4. During spring, warmer spring temperatures … earlier median passage dates for 16 of 19 … vancement in median passage for every 1°C … 0.25 to 1.26 days °C^{-1}. During the fall, relationships … with only 3 of 19 species showing a relati… cases, later departure dates were associat… these trends forward under climate-scenar… cast continued spring advancements under s… 2041 to 2060 and 2081 to 2100 and more mut…
5. These results demonstrate the capacity of … interannual fluctuations in temperatures, … the potential of North American bird band… trends across a wide diversity of avian sp…

KEYWORDS
bird migration, climate change, forecast, pheno[illegible]

1 | INTRODUCTION

As climates change, so do the [illegible] of organisms ([illegible] 2018; [illegible] 2017; Young[illegible] et al., 2021). While climate change can [illegible] organisms, organismal phenology [illegible] ing spring phenophases, including [illegible] which often translate into shift[illegible] organisms, or changes in reprodu[illegible] secondary con[illegible] 2016; [illegible] 2003; [illegible] & Pri[illegible] 2011),

The study of phenological ch[illegible] ing because most datasets prov[illegible] erage or are limited to a f[illegible] 2005; [illegible] Mayor [illegible] 2017; Van Bus[illegible] 2009; [illegible] 2021), especially when changes are sma[illegible] tiple dimensions including tempe[illegible] tion (Ha[illegible] 2019) and land use/land co[illegible] et al., 2022). A more complete underst[illegible] is affecting organisms, now and [illegible] studies to include a multitude o[illegible] temporal scales to address patte[illegible]

Migratory species are particula[illegible] tal impacts of climate change be[illegible] variation in environmental condi[illegible] et al., 2017). One documented vulnerab[illegible] species is the possibility of phe[illegible] ing of prey availability differ[illegible] (Clausen & Clausen, 2013; [illegible] 2019; [illegible] 2012). Yet, while directional pheno[illegible] Usui et al., 2017), interannual fluctuati[illegible] subsequent responses [illegible] as migratory [illegible] a mechanism for coping with pot[illegible] et al., 2021). Disentangling plastic [illegible] tionary changes remains cha[illegible] If inherited circannual clocks c[illegible] believed to be the [illegible] et al., 2017; Gwinner, 1996), shifts in phen[illegible] sult of evolutionary pr[illegible] 2012) than annual responses to current [illegible] ticity). Weather conditions e[illegible] tion in timing ([illegible] 2015; [illegible] 1990), and st[illegible] decisions can ultimately drive [illegible] (Schmal[illegible] 2019). Environmental and [illegible] nology likely interact to drive [illegible] large body of evide[illegible] phases within the same species, [illegible]

place, despite endogeno[illegible] 2015; González[illegible] et al., 2020; Studds & Marra, 2011). Recent evidence s[illegible] [illegible] 2019). [illegible] More than half of North American b[illegible] migratory ([illegible] 2019), providing a rich [illegible]

[illegible] primary and [illegible]

(Wilman 2014). Since insectivorous [illegible] are directly driven by climate [illegible] (e.g. emergence da[...] 1981; [illegible] 2006) [illegible] and because temperature broadly [illegible] (Scranton & [illegible] 2017), we make an inf[...] temperature can serve as a pred[...] resource availability. Warblers [illegible] tween climate change and migrati[...] a consistent pattern across a div[...] while phenology is clearly driven [illegible] a relationship is drawn between [illegible] tive forecasts of migration timi[...] scenarios.

To this end, we examine spring [illegible] species of wood warblers frequen[...] To quantify interannual fluctua[...] for long-term changes in phenology, [illegible] annual migration phenology is l[...] From previous studies, we predic[...] spring phenology than [illegible] tures we predict earlier mi[...] 2018; Van Buskirk 2009). Overall, our predic[...] tain; however, previous studies [illegible] shown earlier migration phenolog[...] Buskirk 2009). To extend these in[...] sonal migration 30-year [illegible] -specific climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Bird banding records

We requested bird banding reco[...] Geological Survey (USGS) Bird B[...] North American wood-warblers (family Par[...] quested in April 2020. In total, [illegible] provided, with 44 species regul[...] least 1000 captures from 1961 to [illegible] this span of years to align wit[...] data (see below). Following fil[...] and used by Covino et al. (2020), 19 species [illegible] spring and fall had adequate samp[...] species cases, Palm Warbler *Setophaga palmarum* and Yellow-rumped Warbler *Setophaga coronata*, both species [illegible] their subspecies names in the BBL. For Palm Warbler [illegible] our summaries by the common name [illegible] ing counts of Western Palm Warbler and Yellow Palm Warbler [illegible] Yellow-rumped Warbler, we used the native [illegible] tion in our summaries, Audubon's [illegible] In the case of Yellow-rumped Warbler, this [illegible] of greater differentiation [illegible] tion. However, of these specific [illegible]

[illegible] bird [illegible] records that was inclu[...] [illegible] Myrtle Warbler, [illegible] Yellow-rumped Warbler. To summa[...] [illegible] the spring [illegible] [illegible] Additionally, [illegible] pulse of songbird migration through [illegible] 2020) [illegible] Northeastern [illegible] greater [illegible] June 15 and August 15 [illegible] 15 and March 15 [illegible] age class '4' (Bird Band[...] [illegible] can influ[...] Horton 2020 [illegible] they were not a[...] Table S1 for a breakdown of age-and s[...] cluded in this study.

Because banding records a[...] [illegible] the banding records to [illegible] where possible. While the zeros do [illegible] estimate, it was important to accou[...] we use as a data filter (e.g. a ze[...] banding was conducted). For each [illegible]

that had both spring and fall banding [illegible] interval (in days) between median passage dates. Lastly, for spring and fall, we calculated the time [illegible] cumulative sum of birds to quantify [illegible] season.

Lastly, to insure that phenolog[illegible] of migrant behaviour, rather than [illegible] tion by [illegible] (0.5° pixel) for spring and fall [illegible] ent annual metrics: earliest banding date [illegible] maximum banding date. For each [illegible] changed significantly (α = 0.05) [illegible] those locations with significant [illegible] tent directionality of the trends [illegible] cause for concern. We conducted [illegible] coefficients with the null hypoth[illegible] cess in a Bernoulli experiment [illegible] positive or negative trends). This [illegible] tent changes for earlier or later [illegible] Supporting Information).

2.2 | Historical temperature data

In our analysis, we choose temperature [illegible] 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 [illegible] etative indices from satellite remote sensing are not available for 1960s or 1970s. However, tempera[illegible] broadly correlated in quant[illegible] (2014) [illegible] and for this reason, we use temperature anomalies [illegible]

To relate phenology measures [illegible] loaded historical mean monthly [illegible] from WorldClim (mean of [illegible] https://www.worldclim.org/data/monthlywth). We used the [illegible] version 2.0 gridded monthly tem[illegible] 1961 to December 2018 (WorldClim [illegible] 2020). temperature data are derived from [illegible] gridded Time Series (CRU TS 4.03) (Harris et al., 2020). CRU TS is global in coverage and [illegible] itude by 0.5° longitude grid over [illegible] except Antarctica. Temperature [illegible] polations are derived from [illegible] stations. For our study, we averaged [illegible] align with spring banding effort[illegible] align with fall banding efforts. [illegible] with banding locations (i.e. 0.5° [illegible] grants responded to annual fluctu[illegible] we calculated anomalies for each [illegible] lated by subtracting the annual [illegible] seasonal mean from 1961 to 2018; [illegible] cooler seasons (relative to the [illegible] denoting warmer seasons.

2.3 | Climate forecast data

To examine how warming [illegible] downloaded climate scenario [illegible] https://www.worldclim.org/data/cmip6/cmip6climate [illegible] 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), [illegible] IPSL-CM6A-LR (Boucher et al., 2020), MIROC-ES2L (Hajima et al., 2020), MIROC6 (Tatebe et al., 2019), MRI-ESM2-0 (Yukimoto et al., 2019) [illegible] SSP1-2.6 [illegible] SSP5-8.5 [illegible] mitigation and adaptation [illegible] modest rates of climate change (O'Neill et al., 2017) [illegible] scenario that sees climate interven[illegible] below 2°C by 2100 [illegible] 8.5 represents [illegible] world [illegible]

2.4 | Statistical analyses

[illegible]

2082–2100. We then took the differ[illegible] dates and those predicted for 2018, [illegible] earlier dates and positive values [illegible]

All analyses and figures were generated [illegible] R (R Core Team, 2020). We used the lme4 package to implement mixed models (Bates et al., 2014) and generated confidence [illegible] using MERTOOLS (Knowles & Frederick, 2020) with 1,000 iterations.

3 | RESULTS

3.1 | Bird banding records

In total, 2,826,588 banded warblers [illegible] from 1961 to 2018; 674,089 birds [illegible] during [illegible] (Figure 1; Figure S1). Through this time [illegible] find evidence of systematic shift [illegible] (see Supporting Information). During spring, [illegible] of warblers were sexed as female, 51.8% as [illegible], 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 class, 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%) [illegible]

[illegible] Warbler (14.5%) [illegible] Yellow- [illegible] (14.2%) [illegible] banded species [illegible] during spring, [illegible] Yellow-rumped Warbler (25.2%) [illegible] Common [illegible] mixed migrants and tallied 52. [illegible] During spring, 46 locations were [illegible] (Figure 2a). On average, spring [illegible] 11.8 [illegible] (±SD) years (Figure 2b) with an average of [illegible] ± [illegible] species represented (Figure S2a). During fall, [illegible] tallied an average of 12 ± [illegible] (Figure 2b) with an average of 46 ± [illegible] species represented (Figure S2e). Comparing the 40 locations w[illegible] banding operations were conducted, [illegible] tween spring and fall median passage [illegible] 2018 [illegible] During spring [illegible] average [illegible] the interval between the [illegible] 61.3 days [illegible] (t_{4990} = [illegible], p < 0.001) [illegible] of warblers [illegible]

3.2 | Historical relationship w[illegible]

During spring, [illegible] temperature [illegible] median passage date for most [illegible]

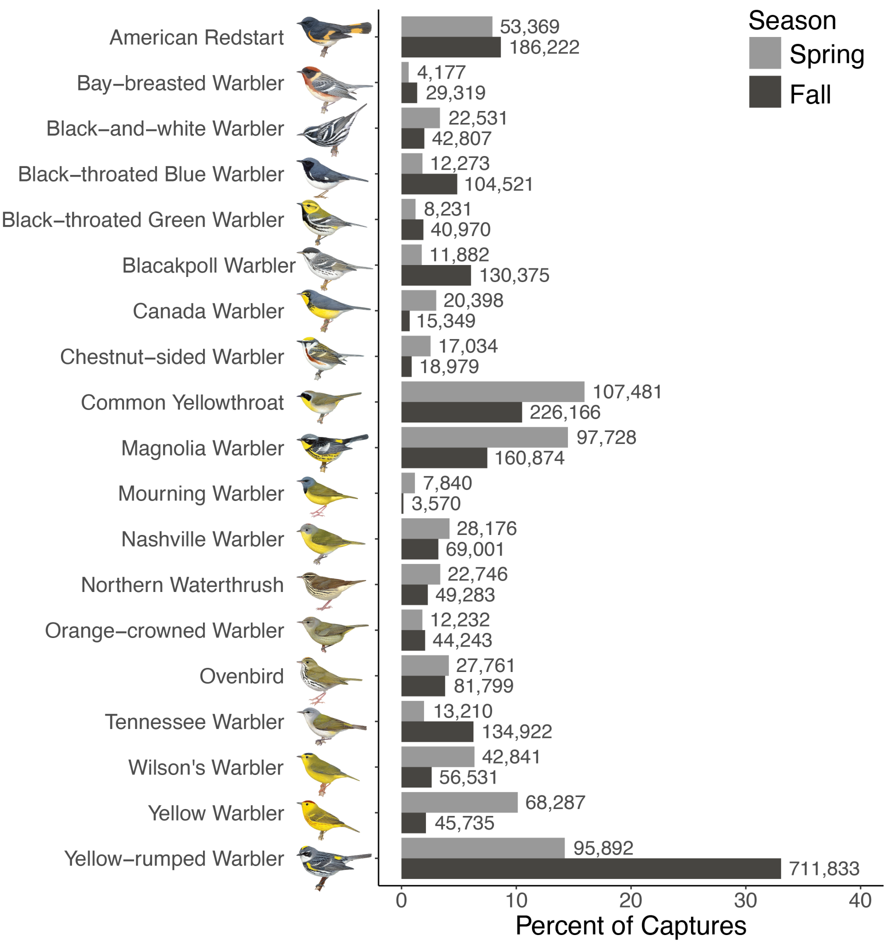


FIGURE 1 Percent of seasonal captures and number of mi[illegible] warblers banded during sp[illegible] 15 to June 15) and fall ([illegible] November 15) from 1961 to [illegible] total, 2,826,588 banded w[illegible] included in phenology an[illegible] illustrations reproduced [illegible] Lynx Edicions.

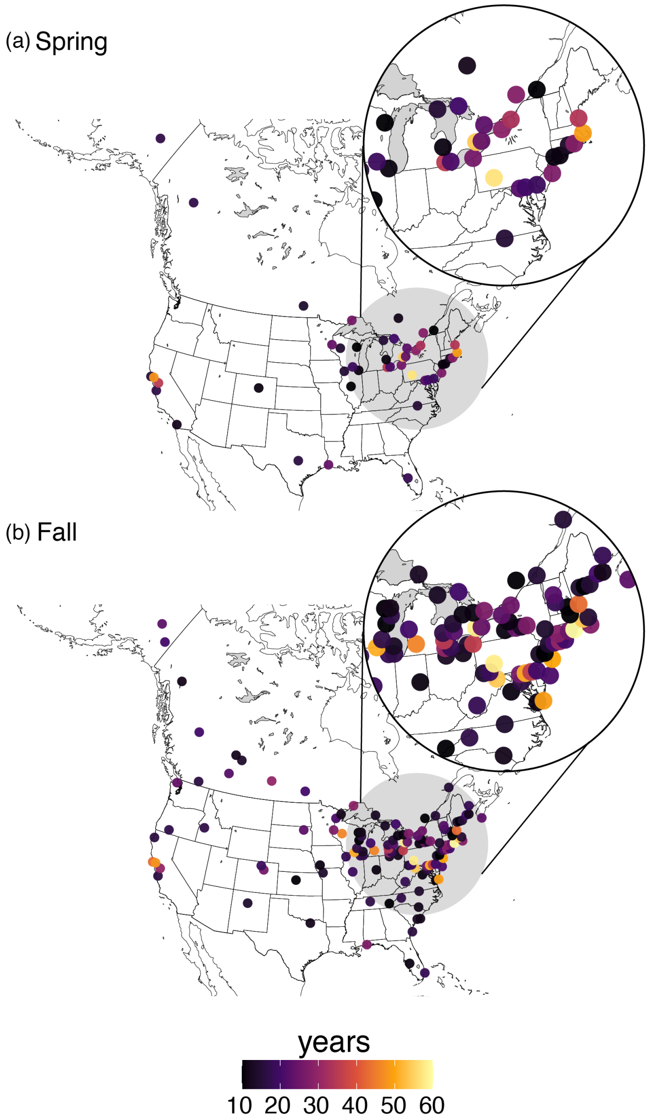


FIGURE 2 Migration banding locations during (a) spring (N = 46) and (b) fall (N = 124) showing the number of years of data included in our analyses. Points represent 0.5° latitude by 0.5° longitude locations. Inset used to highlight higher density banding areas of North America.

showing significantly negative slopes, indicating earlier median passage date during warm anomalies (Figure 4; Table S2). This can be visualized at a single location for the Common Yellowthroat (*Geothlypis trichas*), whereby migrants were earlier during anomalous conditions ($F_{1,30}$ = 6.015, p = 0.020; Figure 3). Year was a significant predictor, with 8 species showing negative slopes ranging from −0.027 to −0.1?0 days year^{-1} (Table S2). Orange-crowned Warbler (β = −1.216 days °C^{-1}, −2.104 to −0.344, 95% CI), ... (β = −0.973 days °C^{-1}, −1.279 to −0.611, 95% CI), ... Warbler (β = −0.906 days °C^{-1}, −1.158 to −0.617, 95% CI) showed the greatest phenological advancement with increasing temperature. Across all species using ...

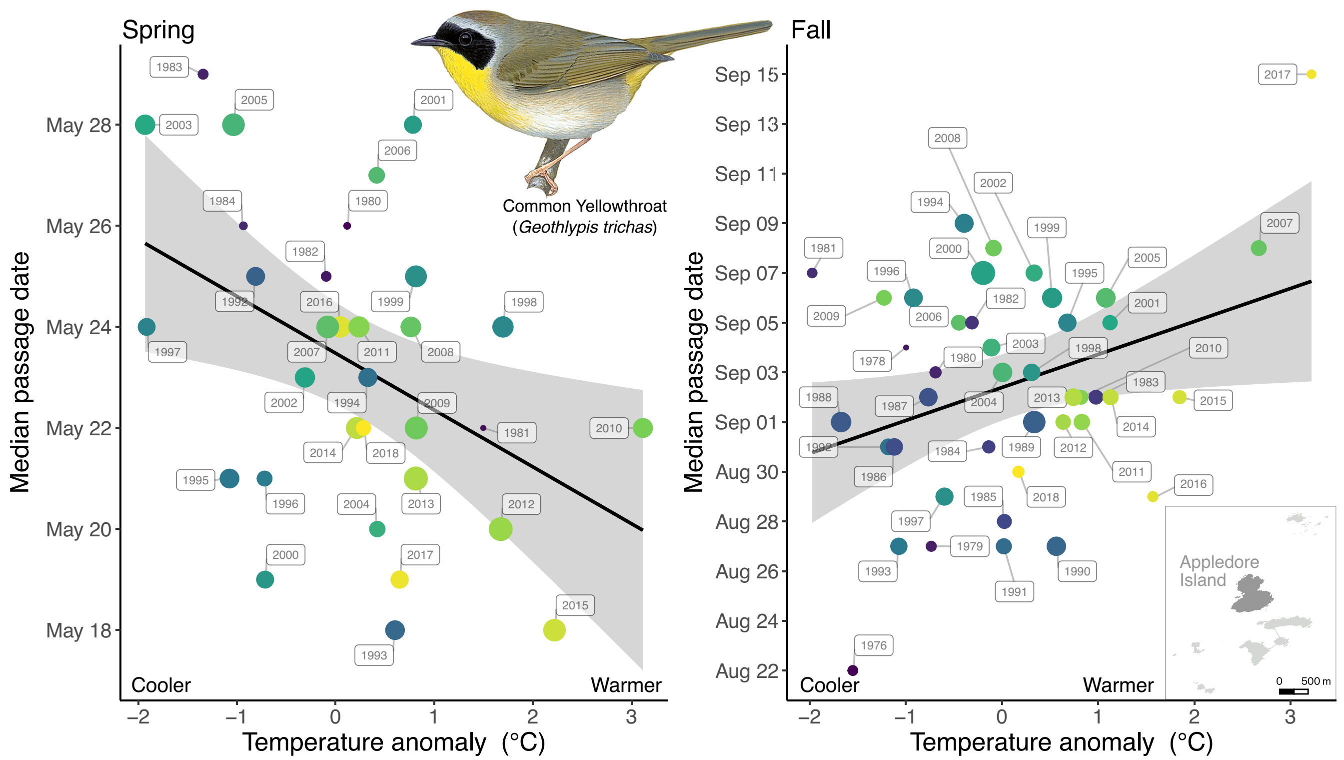
as a random effect, we observed a 0.5? days °C^{-1} (−0.72 to −0.05 ...) advancement in median passage for every ... temperature ... (p < 0.001), and a −0.027 days year^{-1} (−0.036 to −0.017 ...) advancement with each passing year. ... temperatures led to earlier passage ... tory movements also occurring slight...

During fall, temperature anomalies ... of median passage date for only 3 o... species showing a positive slope, i... sage date during warmer periods (Figure 4; Table S3). While ... Common Yellowthroat did not show an ... perature anomalies, it did show a d... long-term banding locations, whereby ... data were later during anomalously ... ($F_{1,40}$ = 4.892, p = 0.032; Figure 3). Year was a significant p... showing a negative slope for 7 spec... species (Table S3). Across all species using a... species as a random effect, we only ... °latitude^{-1}, −1.60 to ... (p < 0.001), 0.27 ... 95% CI), predic... phenology, with temperature anomalies ... icant (p = 0.069 and p = 0.220, respectively).

3.3 | Climate forecast

Examining future spring climate scen... sistently warmer at sampling locati... socioeconomic pathway. Under SSP5-8.5, ... average ... predicted to ... 1.58 ± 0.81 (SD) days earlier unde... predictions from 2041 to 2060 and 3... from 2081 to 2100 (Figure 5). From 2041 to 2060, ... were on average 1.26 ± 0.88°C (SSP1-2.6), 1.09 ± 0.88°C (SSP2-4.5), 1.63 ± 0.73°C (SSP3-7.0) and 2.05 ± 1.12°C (SSP5-8.5) relative to the mean tempera... From 2081 to 2100, temperatures were 1.35 ± 0.85°C (SSP1-2.6), 3.09 ± 1.06°C (SSP2-4.5), 4.58 ± 1.54°C (SSP3-7.0) and 5.80 ± 1.75°C (SSP5-8.5) higher relative to ... perature from 2014 to 2018 (Tables S4 and S5). ... model scenarios.

Like spring, fall future climate models indicated ... median passage ... in all ... although magnitudes were weaker. ... median passage date ... predicted to be 0.58 ± 0.?? (SD) days ... under ... temperature predictions from 2041 to 2060 ... later from 2081 to 2100 (Figure 5). ... temperatures were on average ... 0.8? ± 1.1? (SSP1-2.6), ... 1.49 ± 0.84°C (SSP2-4.5), 1.60 ± 0.7?°C (SSP3-7.0) and 2.04 ± 1.07°C (SSP5-8.5) relative to the mean ... temperatures from 2014 to 2018. From 2... 1.28 ± 1.11°C (SSP1-2.6), 2.25 ± 1.06°C (SSP2-4.5), 3.71 ± 1.04°C (SSP3-7.0) and 5.08 ± 1.47°C (SSP5-8.5) higher relative to the mean temperatures in ... (Tables S4 and S5) ... for all climate model scenarios.



F I G U R E 3 Median passage date for Geothlypis trichas (COYE) relative to temperature anom... to 2018 during spring and 1976 to 2018 for fall for a single locat... Appledore Island, ME. Points are shaded according to year and thei... COYE banded, fall mean 120.8 COYE banded). The sfuiatrteesd llinea rande g9r5e% sci... the slope of the line differs sig $p = 0.011$, $p = 0.013$ ... permission of Lynx Edicions.

4 | DISCUSSION

We amassed six decades of bird banding records from more than 170 species to characterize putative changes in migration phenology, in total summarizing ... from 130 locations in North America. ... phenological responses to inter-annual fluctuations in temperature were largely consistent across ... species, with most species showing earlier median passage dates during warmer ... While many long-distance migrants are thought to time their migration based on cues ... phenology based on cues en (... 1996) ... it is clear that responses to seasonal ... 2020 ... 2020 ... 2009 ... in shaping seasonal migration timing ... ality likely through advancements or delays ... relative to stopover duration or flight ... 2005) ... between spring and fall ... in stopover duration tend to be ... shifts (Schmaljohann, 2017) ... 2020) ... fall delays. These inter... Youngflesh et al. (2021) found that spring phenology showed significant expansions ... ments were more pronounced at northern ... interaction between temperature anomalies ... phenology. This may be, in part, ... pling in this study. The distribution of banding ... shows a strong (Figure 2a) ... resented in the central and western parts ...

that coverage is limited in more re... (e.g. Canada, Alaska), ... banding records from ... America (Dunn ... 2018) ... Gulf of Mexico ... While spring ... in ... fall ...

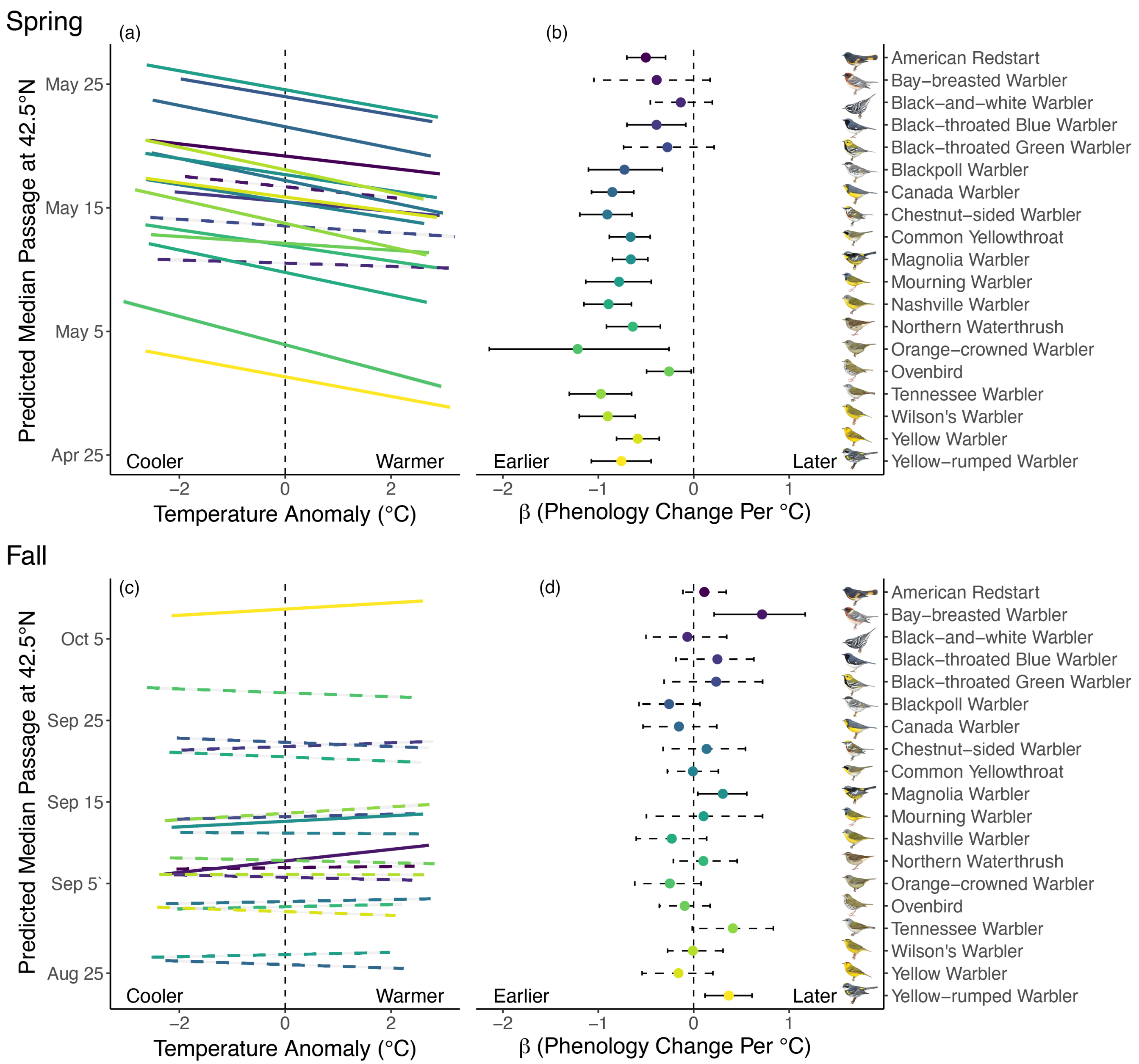


FIGURE 4 Linear regression of spring (a and b) and fall (c and d) media for 19 wwoobdler speciesspe(caiafnid c)ttSpedcilesnes from linear mixed model w random effect and phenolosgpye cpirfeidci cttemdp earcartousrse srpaencgieess -(between the 2. latitude (median of β) cand o95%) .co(nbf ia dle nd)esSpecifiefa(lsiinfeam nspixeedl emnoodelsl change per °C. Regression lines shaped fiin (ca)lourds (ocf) (dor aensdpo(nd) .tiSo trepsd s0.(05, a and c) and solid confidence interval lines represent i significap>nt0 .t0r5e)n dasn d(intervals overlapping zero. Warbler illustratio

rapid spring arrival, and seasoWnaalr bdliefrf,e rTeemncesssiee pWaervbaleirlianngd wNiadsh and suitability for north or southhpbbeunsdcfenlaighlos .oRfegaerdalteesrs ,thwaen d7idd not detect a broadscale signal tpharttifcullcartulayt iaotn smoirne fnaolrlt hienrtleyr asninpueal phenology were driven by the varpiadmioimnein.tsleafsotnoaadl rtemspeurecatsurare.e mo

In a ffuoeslseidl -developmen8t.5s)ce(nKarr(ieogle(eSrSaP 5p-henological mismatch), aard et a2l0.1 7), the models we leveraged sfhaolwle dm iagnr avteiroang pee oriof o2d s1 manydeventual 5.5°C of warming in 2060 and 2100i,t ircemsaple cbtriovoedlsy .o rThbeusfef ecrh aanggaeisnst tne put warblers on pace to shift 1.(5Mø(lyleea r2016e2)t0.6a0l)h.i,alned m3u.c6h (aytetaern t2-i1o0n0)re days earlier in the springc,r owwitnhcda sbmmeisspaetcchlesiisl ikceOlsaedgoen- spring a

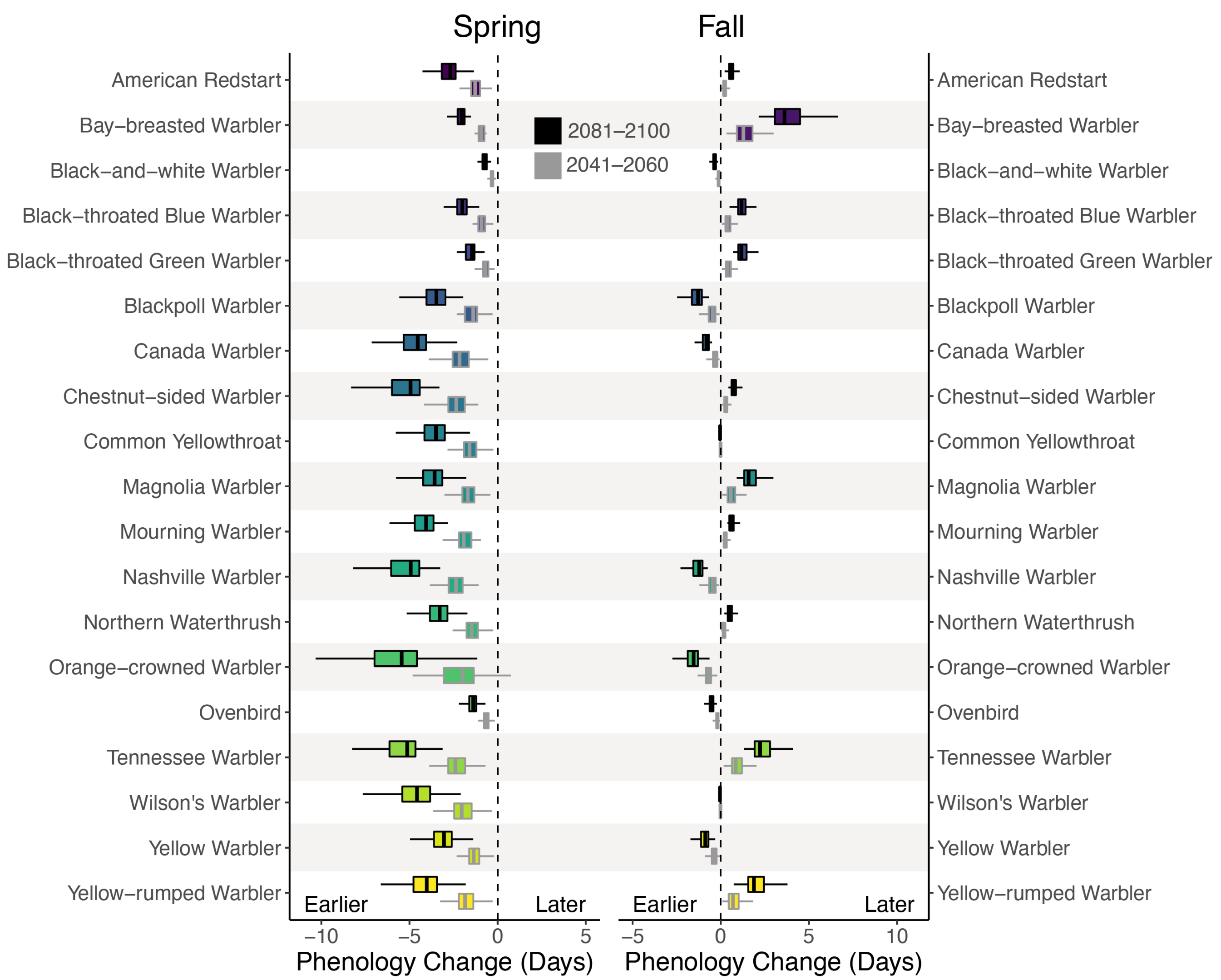


FIGURE 5 Predicted median passage date for spring and fall migration ... climate ... scenarios (2041–2060) ... (2081–2100) ... . Predictions referenced from median ... location-specific mean anomalies from 2014 to 2018 and location latitude. ... separate models across locations (Section 2) ...

unclear how fall changes in temperature and food ... 2017 ... 2019) ... shape migrant fitness (... 2015) ... Our results ... this study ... 2019) ... overwhelming demonstrate changes in ... fall migration ... and by extension, forecast phenologies ... Warming temperatures have already ... 19 species ... overall autumn period, delaying ... 1970 to 2017 ... ditional insect generation ... 2018; ... 2010) ... period. However, some species ... However, fruit ripening may ... 2006) ... Northern Waterthrush and Ma... During fall migration, migrants ... and insects have been shown to ... North Amer... during migration (... 1996) ... temperatures ... fall. Broadly examining ... continue changing in both spring and fall ... migration showing modest shifts ... 2014) ... the potential to be more detrimental ... 2008) ... fall.

With bird migrants facing a multitude of ... (Loss et al., 2015), population declines ... estimates of nearly a net loss of 3 billion breeding birds ... 1970 ...

banding stations collect information [illegible] tions are conducted, for example, [illegible] size of those nets, or more simply, [illegible] ducted. However, these pieces of information are [illegible] the USGS bird banding lab. [illegible] would be a considerable undertak[illegible] sible if records have been lost [illegible] phenology are likely more robust [illegible] abundance or capture rates, but [illegible] assumptions made in this study. [illegible] tional species would surely help [illegible] effort. For instance, the addition [illegible] yond warblers or even migratory [illegible] instances of zeros, and thus a r[illegible] on a particular day. Expanding [illegible] broaden our insights into how mig[illegible] environments.

Through phenotypic plasticity, migrants can respond, to some degree, to changing seasonal temp[illegible] to match the effects of climate change? Unfortunately, our data and results cannot answer this question. While phenotypic plasticity is clearly demonstrated, [illegible] projections predi[illegible] advancements into the future for [illegible] assumes that plasticity is unbounded [illegible] dicators of future climate responses [illegible] true extrapolations. If spring migration [illegible] endogenous cues (Gwinner, 1996), [illegible] there are clearly limits to the amount of change [illegible] for earlier departure [illegible] over time and successive generations [illegible] ation timing (Both, 2006) [illegible] may outpace evolutionary selection [illegible] et al. (2019) suggest change is possible on a relatively short time scale. Quantifying evolutionary change in migration timing is immensely challenging (Charmantier & Gienapp, 2014), [illegible] unstructured datasets like bird banding data. If past plasticity is [illegible] 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.

ACKNOWLEDGEMENTS

The authors are exceedingly grateful to all the banders who have contributed to a growing repository of information on migratory birds throughout North America. [illegible] the hours amassed, likely many hundreds of thousands of hours, [illegible] Island Migration Station, Black Swamp [illegible] Long Point Bird Observatory [illegible] Manomet [illegible] Powdermill [illegible] Geological Survey Bird Banding Laboratory [illegible] Cornell Presidential Postdoctoral Fe[illegible]

CONFLICT OF INTEREST STATEMENT

[illegible]

DATA AVAILABILITY STATEMENT

[illegible] available [illegible] Geological Survey Bird Banding Lab[illegible] replicate these [illegible] https://doi.org/10.6084/m9.figshare.[illegible] (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 ... from 1961 to 2018 during spring (Ma... (August 15 to November 15).

Table S1: Number of migratory ... spring (March 15 to June 15) and fa... from 1961 to 2018.

Figure S2: Migration banding locations ... ($N = 14$) showing the number of spe... location. Points represent 0.5° lat... Inset used to highlight higher den... America.

Table S2: Linear regression of spring ... relationship and mean maximum temper... warbler species. Species-specific slopes generated ... model with location (i.e. 0.5° loca... Confidence intervals (95%) calculate... Coefficients with p-values < 0.05 are shaded in grey.

Table S3: Linear regression of fall media... and mean maximum temperature ... warbler species. Species-specific slopes generated ... model with location (i.e. 0.5° loca... Confidence intervals (95%) calculate... Coefficients with p-values < 0.05 are shaded in grey.

Table S4: Mean (± SD) of predicted median pas... and fall migration periods under fou... pathway climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5) 2041–2060. For each scenario, averag... were taken. Predictions referenced f... from 2018 and mean temperatures from...

Table S5: Mean (± SD) of predicted median pas... and fall migration periods under fou... pathway climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5) 2081–2100. For each scenario, averag... were taken. Predictions referenced f... from 2018 and mean temperatures from...

How to cite this article: Horton, K. G., Morris, S. R., Van Doren, B. M., & Covino, K. M. (2023). ... American bird banding records reve... phenology. *Journal of Animal Ecology*, *92*, 738–750. https://doi.org/10.1111/1365-2656.13887