Received: 29 July 2022 | Revised: 7 October 2022 | Accepted: 17 October 2022

DOI: 10.1111/gcb.16492

Global Change Biology WILEY

RESEARCH ARTICLE

Adult male birds advance spring migratory phenology faster than females and juveniles across North America

Montague H. C. Neate-Clegg | **Morgan W. Tingley**

Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

Correspondence
Montague H. C. Neate-Clegg, Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA.
Email: monteneateclegg@gmail.com

Funding information
National Science Foundation, Grant/Award Number: EF 1703048 and EF 2033263

Abstract

Advances in spring migratory phenology comprise some of the most well-documented evidence for the impacts of climate change on birds. Nevertheless, surprisingly little research has investigated whether birds are shifting their migratory phenology equally across sex and age classes—a question critical to understanding the potential for trophic mismatch. We used 60 years of bird banding data across North America—comprising over 4 million captures in total—to investigate both spring and fall migratory phenology for a total of 98 bird species across sex and age classes, with the exact numbers of species for each analysis depending on season-specific data availability. Consistent with protandry, in spring ($n = 89$ species), adult males were the first to arrive and immature females were the last to arrive. In fall ($n = 98$), there was little difference between sexes, but adults tended to depart earlier than juveniles. Over 60 years, adult males advanced their phenology the fastest (−0.84 days per decade, 95 CrI = −1.22 to −0.47, $n = 36$), while adult and immature females advanced at a slower pace, causing the gap in male and female arrival times to widen over time. In the fall, there was no overall trend in phenology by age or sex ($n = 57$), driven in part by high interspecific variation related to breeding and molt strategies. Our results indicate consistent and predictable age- and sex-based differences in the rates at which species' springtime phenology is shifting. The growing gap between male and female migratory arrival indicates sex-based plasticity in adaptation to climate change that has strong potential to negatively impact current and future population trends.

KEYWORDS
age, arrival date, breeding latitude, climate change, fall migration, molt strategy, protandry, sex

1 | INTRODUCTION

Every year, billions of birds migrate to temperate latitudes in the Northern Hemisphere to breed (Horton et al., 2019). This annual migration has captured the imagination of people for millennia (Mynott, 2018), and the timing—or phenology—of bird migration has been studied for well over two centuries (Margary, 1926). Due to these long historical records, changes in spring bird arrival times formed the backbone of the earliest arguments for a pervasive ecological response to global warming (Bradley et al., 1999; Root et al., 2003; Sparks, 1999; Walther et al., 2002). Over the ensuing decades, consistent advances in spring migratory phenology (Bitterlin & Van Buskirk, 2014; Lehikoinen et al., 2019; Usui et al., 2017) have been found across Europe (Cotton, 2003; Newson et al., 2016; Saino et al., 2011; Sparks et al., 2005) and North America (Horton et al., 2020; Mayor et al., 2017; Zimova et al., 2021), and these advances are invariably linked to increases in global temperatures (Cotton, 2003; Horton et al., 2020; Hurlbert & Liang, 2012; Lehikoinen et al., 2019; Marra et al., 2005; Sparks et al., 2005). Variation exists within migratory birds, however, with greater phenological advances and tighter ties to vegetation phenology for short-distance migrants compared to Neotropical, trans-Saharan, or Southeast Asian migrants (Bitterlin & Van Buskirk, 2014; Horton et al., 2019; Hurlbert & Liang, 2012; Lehikoinen et al., 2019; Nakata et al., 2011; Tøttrup et al., 2012; Usui et al., 2017; Youngflesh et al., 2021; Zimova et al., 2021).

Our knowledge of phenological trends in fall is far less certain (Gallinat et al., 2015), at least partly due to overall fewer numbers of published studies and available data on fall phenology. In birds, fall migration trends are more variable (Bitterlin & Van Buskirk, 2014; Haest et al., 2019; Morris et al., 2016; Newson et al., 2016), with many studies showing no trends in departure dates (Covino, Horton, et al., 2020; Van Buskirk et al., 2009; Zimova et al., 2021), and high interspecific variability driven in part by migration distance (Ellegren, 1993; Jenni & Kéry, 2003; Van Buskirk et al., 2009), breeding strategy (Jenni & Kéry, 2003), and exogenous cues (Haest et al., 2019). Birds are also harder to study in the fall, as many species have more cryptic plumage and inconspicuous behaviors to avoid predation, making them harder to observe (e.g., through citizen science programs).

Despite the preponderance of studies on migratory phenology, few have examined how temporal trends in migratory phenology might vary among different demographic groups (Cadahía et al., 2017; Covino, Horton, et al., 2020; Møller, 2004; Tøttrup & Thorup, 2008). Age and sex, in particular, could affect both general migratory phenology, as well as phenological trends. In spring, males are expected to arrive earlier than females (protandry) to compete for territories and secure more mating opportunities (Canal et al., 2012; Coppack et al., 2006; Kokko et al., 2006; Morbey & Ydenberg, 2001; Rubolini et al., 2004; Saino et al., 2010), and protandry has been widely documented in Europe (Spina et al., 1994; Tøttrup & Thorup, 2008), Asia (Nam et al., 2011; Wobker et al., 2021), and North America (Covino, Horton, et al., 2020; Covino, Morris, et al., 2020; Francis & Cooke, 1986; McKinnon et al., 2016; Morris & Glasgow, 2001; Swanson et al., 1999). Although there has been no wide-scale appraisal of sex-specific phenology during fall migration (Stegman et al., 2017), single-species studies have documented protogyny (females depart first; Mills, 2005), protandry (McKinnon et al., 2016), and no discernable sex-specific differences (Covino, Horton, et al., 2020; Mills, 2005; Morris & Glasgow, 2001). Sex-specific differences in fall migratory phenology could result from differences in territoriality or parental roles (McKinnon et al., 2016; Mills, 2005; Newton, 2008, 2011), for example if males seek to defend their territory until after the females have left, or if females invest more in post-fledging provisioning—requiring more time post-breeding to recuperate lost energy.

Among different age groups, a distinction is drawn between immatures/juveniles (i.e., birds <1 year old) and adults. In spring, adults tend to arrive earlier than immatures (Covino, Horton, et al., 2020; Francis & Cooke, 1986; Spina et al., 1994; Stewart et al., 2002; Wobker et al., 2021), perhaps due to competitive interactions between these two age categories (Marra et al., 1993; Sherry & Holmes, 1989), or due to adults being more experienced leading to higher migratory efficiency (Ellegren, 1993). In fall, young have been demonstrated to migrate earlier in at least two species (Covino, Horton, et al., 2020; McKinnon et al., 2016), explained by the logic that immatures post-fledging tend to be well-fed and fully feathered—and so ready to migrate—while their parents may still need to molt and regain fat and muscle before migrating (Newton, 2008; Pyle et al., 2018). Given the myriad potential differences in migratory phenology between spring and fall migration, between males and females, and between adults and immatures, it is important to assess migratory phenology at larger geographic and taxonomic scales.

The consequences of changes in phenology (or a lack thereof) could be severe for fitness. During spring, it is critical that migratory birds time their breeding to coincide with green-up and peak food abundance (Both et al., 2006; Mayor et al., 2017). Advances in phenology are therefore advantageous for species tracking temperature-sensitive resources, such as insects. Failure to track resources may lead to trophic mismatches, which, in turn, can cause population declines (Both et al., 2006, 2010; Jones & Cresswell, 2010; Møller et al., 2008; Saino et al., 2011). If males and females or adults and immatures differ in their phenological trends, this could produce mismatch differentials, with more negative consequences for certain demographic groups. A recent study in North America (Covino, Horton, et al., 2020) found that male and female Black-throated Blue Warblers (*Setophaga caerulescens*) showed similar levels of phenological shifts in both spring and fall, but we do not know how this pattern varies across a wider ecological and phylogenetic spectrum of migratory birds. Assessing sex- and age-specific differences in migratory phenology and trends across many bird species requires large quantities of data with suitable geographic and taxonomic coverage. Large databases, such as eBird, have proved fruitful for estimating phenological trends in avian arrival (Horton et al., 2019; Hurlbert & Liang, 2012; Youngflesh et al., 2021), but such datasets tend to lack systematic information on sex and age. Since 1920, the U.S. Geological Survey has run the Bird Banding Laboratory (BBL), a continental-scale program that distributes bird bands and collates banding data. BBL has amassed a dataset of millions of bird banding records for hundreds of species from across North America and, importantly, most of these records contain data on age and/or sex.

Here, we use the BBL dataset to assess the phenology and phenological trends of a suite of North American migratory birds. Dividing the data into spring and fall migration, we use sampling-corrected phenological estimates and Bayesian hierarchical random effects models to quantify sex- and age-dependent differences in overall migratory phenology for 98 species, and to quantify sex- and age-dependent trends in phenology for 54 species. Following published literature, we predicted that males migrate earlier in spring than females and adults migrate earlier than immatures. As previous studies have not found consistent differences in phenological trends between demographic groups (Covino, Horton, etal., 2020; Tøttrup & Thorup, 2008), we predicted that spring arrival would advance at an equal rate across groups. In the fall, we predicted high interspecific variability in departure dates as consistent patterns have rarely been found across studies (Bitterlin & Van Buskirk, 2014; Zimova et al., 2021). For this reason, we also predicted that there would be no overall trends in fall phenology, as the varied phenological trends of different species would cancel each other out. Ultimately, upon finding species-specific variation in phenological trends, we explored several trait-based hypotheses that sought to explain this variation post hoc.

2 | METHODS

2.1 | Data filtering

All data filtering and analyses were conducted in R v. 4.1.1 (R Core Team, 2021). From the USGS BBL, we requested spring and fall bird banding records for all migratory land bird species present in North America, which comprised nearly 27 million band records of 234 species for the years 1960–2019. Records for 122 eastern species were received on 16 July 2020 and the remainder were received on 26 August 2020. We chose to focus on long-distance Neotropical migrants to investigate a group of well-studied species with similar migratory ecologies that have a definitive entry into and exodus from the United States and/or Canada each year. We therefore removed species that overwinter in the United States or Canada (e.g., chickadees, *Poecile*; most wrens, Troglodytidae; many sparrows, Passerellidae; Northern Cardinal, *Cardinalis cardinalis*; and American Robin, *Turdus migratorius*). We also removed swallows (Hirundinidae), as they seldom fly into mist nets unless targeted, and when they do, they often do so as a flock. We then applied a series of stringent filters for analysis inclusion, building off previous methods studying phenology with banding data (Covino, Horton, et al., 2020). To focus on bird phenology in the portions of North America, where BBL sampling has been densest, we removed data below 24° latitude and west of −140° longitude and removed any sites located outside of the United States or Canada. After this initial restriction, the data contained records from over 37,000 localities, but many of these sites focused banding efforts on periods outside of migration, did not operate for many years, or focused only on certain species. We therefore defined the migratory seasons as March 1–June 15 (spring) and July 15–November 15 (fall) and removed localities where >50% of records occurred outside of these migration seasons (Covino, Horton, et al., 2020). We then separated the data by season into spring and fall datasets and applied subsequent filters to each dataset separately. Next, we removed locality-year combinations which began banding well after migration had begun (date of first capture >30 April for spring, >30 August for fall) or ended banding well before migration had ended (last bird captured <30 May for spring, <30 September for fall). We also removed locality-years that ran <10 banding days, spanned a period <30 days, or banded at a rate <1 day per week. We then removed all species with <100 total records across each dataset (spring or fall). The resulting spring dataset (hereafter "spring phenology dataset") contained 1,158,497 records of 89 species (Table S1) and the fall dataset (hereafter "fall phenology dataset") contained 3,539,157 records of 98 species (Table S1).

To assess differences in phenological trends in migration over time, we applied some additional filters based on data coverage over the study duration to create a "spring trends dataset" and a "fall trends dataset." For each species, we removed localities where that particular species was banded in <20 unique years or where there were <10 records per year on average. We also removed species with <300 records across the whole dataset (i.e., minimum 5 records per year over 60 years). The spring trends dataset contained 495,284 records of 36 species over 97 sites and the fall trends dataset contained 1,816,531 records of 53 species over 271 sites.

As we wanted to analyze the effects of both age and sex on phenology, we needed to filter the data to known ages and to categorize the sexes. When filtering based on age, we removed "local" birds (i.e., immediately post-fledging) and records with missing age data. For spring, we also removed hatch-year birds and categorized the remaining records with known ages as immature (second year) or adult (after second year) birds. For fall, we categorized all records as either juvenile (hatch-year) or adult (after hatch-year). For sex, species were considered dichromatic if they could be reliably sexed in the hand based on plumage (Pyle, 1997) or otherwise monochromatic (Table S1). Most dichromatic species were sexed when banded, but some individual records remained "unknown." Of the monochromatic species, a small proportion of individuals were sexed when banded, however these were usually based on breeding characteristics (e.g., brood patches and cloacal protuberance). These breeding characteristics have their own phenologies which tend to occur later than arrival dates and could confound migratory phenology. We did not want to determine arrival dates based on breeding phenology and therefore re-categorized all monochromatic species as sex "unknown."

For each season, we aggregated data into 10-minute hexagonal grid cells (provided in the BBL dataset). Subsequently, in the spring and fall phenology datasets, we filtered out data where a particular species/sex/age combination was caught <10 times in a given cell, and in the spring and fall trends datasets we filtered out data where a species/sex/age combination was caught <10 times over <5 days in a given year and cell. After applying these filters, the spring phenology dataset contained 1,009,620 records, the fall phenology dataset contained 3,030,611 records, the spring trends dataset contained 385,448 records, and the fall trends dataset contained 1,399,798 records (Table 1). The fall phenology dataset (i.e., the dataset with the most species) contained 60 dichromatic species and 38 monochromatic species spread over 13 avian families.

2.2 | Phenology estimation

Estimating phenological events, such as the arrival times of birds, can involve a variety of metrics (hereafter "phenometrics"). At

TABLE 1 Sample sizes for migratory phenology estimates for 98 North American bird species over 60 years. Records of birds from the Bird Banding Lab (a) were aggregated into grid cells and categorized based on age and sex. From these data, Weibull-corrected phenometrics (b) were calculated for every species, cell, sex, and age. Spring and fall phenology datasets were used to estimate general phenology across the study period; spring and fall trends datasets were used to estimate changes in migratory phenology during the study period and resulted from more stringent filters. In spring, ages were categorized as adult (after second year) or immature (second year); in fall, ages were categorized as adult (after hatch-year) or juvenile (hatch-year). Sexes were categorized as female (F), male (M), or unknown (U)

A	Total	No. species	No. cells	Adult-F	Adult-M	Adult-U	Imm-F	Imm-M	Imm-U
Spring phenology	1,009,620	89	1015	198,047	275,090	256,028	81,897	145,974	52,584
Spring trends	385,448	36	59	65,965	88,788	88,545	40,668	75,299	26,283
	Total			**Adult-F**	**Adult-M**	**Adult-U**	**Juv-F**	**Juv-M**	**Juv-U**
Fall phenology	3,030,611	98	1391	203,798	223,436	233,930	483,262	595,768	1,290,427
Fall trends	1,399,798	53	134	53,785	73,563	88,931	222,937	268,151	692,431

B	Total	Adult-F	Adult-M	Adult-U	Imm-F	Imm-M	Imm-U
Spring phenology	12,179	2712	3496	3329	792	1299	551
Spring trends	11,797	2316	2747	2457	1334	2064	879
	Total	**Adult-F**	**Adult-M**	**Adult-U**	**Juv-F**	**Juv-M**	**Juv-U**
Fall phenology	24,863	2708	2860	3294	3621	4108	8272
Fall Trends	32,949	1787	2162	2830	5665	6583	13,922

the simplest level, phenometrics such as the first (Miller-Rushing et al., 2008) or median dates provide a rough approximation of phenology (Covino, Horton, et al., 2020). More complex phenometrics, such as estimating the day when migration reaches half of its maximum value, provide a more robust estimation of migratory phenology (Youngflesh et al., 2021); however, such methods are data hungry, requiring sufficient data per species and site to produce annual phenology curves. Based on these trade-offs, we opted to use Weibull-parameterized estimators of phenology from the R package *phenesse* (Belitz et al., 2020). These phenometrics use Weibull distributions to correct for bias and calculate accurate estimates of phenology for any percentile of a distribution—therefore representing a compromise between simple phenometrics, where biases are not accounted for (Miller-Rushing et al., 2008), and more complex phenometrics based on large quantities of presence/absence data (Youngflesh et al., 2021). The estimates are also accompanied by bootstrapped confidence intervals to provide a measure of error.

For the spring datasets, we chose the 1st quartile (Q1) of ordinal day to represent the onset of spring migration (hereafter "arrival dates"). For the fall datasets, we chose the 3rd quartile (Q3) to represent the offset of fall migration (hereafter "departure dates") and to avoid high capture rates during the tail end of the breeding season. For the spring and fall phenology datasets, we calculated the Weibull-corrected arrival/departure dates for every species, cell, sex, and age. For the spring and fall trends datasets, we calculated the Weibull-corrected dates for every species, cell, year, sex, and age. Estimates were based on 100 iterations and confidence intervals were calculated over 100 bootstraps. The spring phenology dataset contained 12,179 estimates (Appendix S1), the fall phenology dataset contained 24,863 estimates (Appendix S2), the spring trends dataset contained 11,797 estimates (Appendix S3), and the fall trends dataset contained 32,949 estimates (Appendix S4; Table 1).

2.3 | Modeling

Migratory phenology was modeled in a Bayesian hierarchical random effects framework (see Appendix S5 for code) using Markov Chain Monte Carlo simulation from the program JAGS (Plummer, 2003) via the R package *R2jags* (Su & Yajima, 2021). Our general modeling strategy was to hierarchically model all species at once, using species-specific random slopes and species- and location-specific random intercepts. For each model, this provided inference on a 'general effect' across all included species, while still allowing individualized phenological responses for species over time and space. We ultimately ran four different statistical models to answer our questions: how migratory (1) spring arrival and (2) fall departure differ by age and sex and how the rate of phenological advancement or delay differs by age and sex in (3) spring and (4) fall.

To model the effects of age and sex on migratory phenology, we used an identical model structure for both spring and fall, as follows:

$$y_{ij} \sim \text{Normal}\left(z_{ij}, \sigma_{ij}\right)$$

$$z_{ij} \sim \text{Normal}\left(\mu_{ij}, \sigma_{z}\right)$$

$$\mu_{ij} = \alpha_{ij} + \alpha_{imm,i} \bullet age + \alpha_{F,i} \bullet sexF + \alpha_{intF,i} \bullet age \bullet sexF + \alpha_{M,i} \bullet sexM + \alpha_{intM,i} \bullet age \bullet sexM,$$

where the Weibull-estimated migratory phenometric (i.e., arrival or departure date), y_{ij}, for species i in cell j was modeled as a normally distributed random variable with mean z_{ij} and standard deviation σ_{ij}. In this parameterization, z_{ij} is the true and unknown phenometric, while σ_{ij} is observed data, calculated as the width of the 95% confidence interval of the Weibull-estimated phenometric divided by 3.92 (to approximate a standard deviation). This parameterization allowed the uncertainty in the Weibull-corrected phenometrics to be propagated throughout the Bayesian hierarchical models. To place phenometrics within a linear-modeling framework, z_{ij} was then modeled as a normally distributed random variable with mean μ_{ij} and standard deviation σ_z, where mean μ_{ij} was a linear combination of an intercept, α_{ij}, for adults of unknown sex and five offsets: $\alpha_{imm,i}$ measures the effect of *age* (binary, 0 for adults and 1 for immature/juvenile birds), $\alpha_{F,i}$ measures the relative effect of being female (*sexF*; 0 for unknown or male and 1 for females), $\alpha_{M,i}$ measures the relative effect of being male (*sexM*; 0 for unknown or female and 1 for males), $\alpha_{intF,i}$ measures the interaction between *age* and *sexF*, and $\alpha_{intM,i}$ measures the interaction between *age* and *sexM*. To account for species-specific variation in migration date and phenological trends, we used a random effects approach, where all of the species-specific parameters (α_{ij}, $\alpha_{imm,i}$, $\alpha_{F,i}$, $\alpha_{intF,i}$, $\alpha_{M,i}$, $\alpha_{intM,i}$) were drawn from hierarchical normal distributions with associated means and standard deviations. In addition, we accounted for the fact that phenology varied as a function of latitude by drawing the following global intercept term,

$$\alpha_{ij} \sim \text{Normal}\left(\mu_{\alpha j}, \sigma_{\alpha}\right)$$

from a linear equation where

$$\mu_{\alpha j} = \gamma + \theta \bullet lat_j,$$

such that σ_α represents random noise and the expected cell-specific intercepts across all species, $\mu_{\alpha j}$, were estimated as a linear function of latitude with intercept γ and slope θ. For both spring and fall models, we used vague priors (i.e., normal with mean of 0 and standard deviation of 100).

Similar to our year-independent models of phenology, to model the effects of age and sex on phenological trends, we used an identical model structure for both spring and fall:

$$y_{ijk} \sim \text{Normal}\left(z_{ijk}, \sigma_{ijk}\right)$$

$$z_{ijk} \sim \text{Normal}\left(\mu_{ijk}, \sigma_z\right)$$

$$\begin{aligned} \mu_{ijk} = {} & \alpha_{ij} + \alpha_{imm,i} \bullet age + \alpha_{F,i} \bullet sexF + \alpha_{intF,i} \bullet age \bullet sexF \\ & + \alpha_{M,i} \bullet sexM + \alpha_{intM,i} \bullet age \bullet sexM + \beta_{ij} \bullet year \\ & + \beta_{imm,i} \bullet age \bullet year + \beta_{F,i} \bullet sexF \bullet year + \beta_{intF,i} \bullet age \bullet sexF \bullet year \\ & + \beta_{M,i} \bullet sexM \bullet year + \beta_{intM,i} \bullet age \bullet sexM \bullet year, \end{aligned}$$

where the Weibull-estimated migratory phenometric, y_{ijk}, for species *i* in cell *j* during year *k* was modeled as a normally distributed random variable and z_{ijk} is the true unknown phenometric with mean μ_{ijk}. In turn, μ_{ijk} was a linear combination of an intercept, α_{ij} (for adults of unknown sex) and a slope, β_{ij}, for the effect of *year* on phenology, plus five intercept offsets (as above) and five slope offsets: $\beta_{imm,i}$ measures the year-specific effect of *age*, $\beta_{F,i}$ measures the relative year-specific effect of being female, $\beta_{M,i}$ measures the relative year-specific effect of being male, $\beta_{intF,i}$ measures the interaction between *age* and *sexF* on the year-slope, and $\beta_{intM,i}$ measures the interaction between *age* and *sexM* on the year-slope. In this model, the slope parameters (β_{ij}, $\beta_{imm,i}$, $\beta_{F,i}$, $\beta_{intF,i}$, $\beta_{M,i}$, $\beta_{intM,i}$) were drawn from hierarchical normal distributions with associated means and standard deviations. In addition, we allowed the global slope to vary as a function of latitude,

$$\beta_{ij} \sim \text{Normal}\left(\mu_{\beta j}, \sigma_{\beta}\right),$$

where

$$\mu_{\beta j} = \omega + \varphi \bullet lat_j,$$

such that the expected cell-specific slopes across all species, $\mu_{\beta j}$, were estimated as a linear function of latitude with intercept ω and slope φ. For these models, we used informed priors for the six α terms, where the parameters were drawn from a normal distribution with a mean and standard deviation equal to the mean and standard deviations of the posteriors from the first set of models:

$$\alpha_{model2} \sim \text{Normal}\left(\alpha_{model1}, \sigma_{\alpha\, model1}\right).$$

All other priors were vague, as in the first model set.

We ran each of the four Bayesian hierarchical models with three chains of 3000 iterations each and a burn-in of 1000 and thinned half of the posteriors. From the posterior draws of the phenology models, we calculated the mean and 95% credible intervals of the phenometrics of each demographic group overall, as well as for each species. For the trend models, we calculated the mean and 95% credible intervals of the intercepts and slopes of each demographic group overall, as well as for each species. Certainty of effect was based on whether or not a 95% credible interval included 0. We also report, where applicable, probabilities of effects based on the proportion of posterior samples relative to key indices. Even though the models will estimate them, we do not present species-specific phenology estimates or trends for demographic groups with no data. For example, there are no data on male and female trends for monochromatic species so we do not present them. This affects the number of species with estimates in each demographic group.

2.4 | Phylogeny

We conducted a check for phylogenetic signal in our results, as models assumed that all species were randomly drawn from a normal distribution. From birdtree.org (Jetz et al., 2012), we downloaded 500 phylogenetic trees with the Hackett backbone for the full complement of species. We then created a consensus tree using the function "ls.consensus" from the R package *phytools* (Revell, 2012). For each demographic group (i.e., age and sex groupings), we assessed the phylogenetic signal in the spring and fall phenometrics. For each group, we pruned the consensus tree to include only species with representative data in the dataset.

For example, monochromatic species were removed from the trees for males and females, and so forth. We used the mean estimates from the posteriors of the first set of Bayesian models to represent the mean phenology of each species and demographic group. We then calculated Pagel's λ (Pagel, 1999) as a measure of phylogenetic signal and tested for significance. We repeated this exercise for the species-specific slopes from the models of phenological trend. We also tested for phylogenetic signal in age and sex-based differences in the phenometrics and the phenological trends. To test for age-based differences in phenometrics, we subtracted mean estimates for adults from immatures/juveniles. For sex-based differences, we subtracted adult male estimates from adult female estimates. We repeated this process for differences in phenological trends.

2.5 | Post hoc tests across species

In light of our results (see below), we conducted additional analyses seeking to explain some of the species-specific variation in modeled outcomes. These tests were necessarily simple due to the relatively low number of species available for comparison (e.g., only dichromatic species produce estimates for males and females). In addition, there are multiple ways to compare groups (e.g., adult males/adult females, immature males/immature females) and so we avoided complications arising from multiple comparisons. Thus, these post hoc results may indicate interesting patterns that warrant further investigation, but we caution that post hoc analyses do not provide strong scientific inference.

We used a one-way ANOVA to test whether age-based differences in fall departure dates across species varied as a function of molt strategy. We categorized the molt strategy (Pyle et al., 2018; Pyle, pers. comm.) of all species (Table S1) as: breeding (occurring mostly on breeding grounds), fall (occurring either during fall migration or on both breeding and wintering grounds), or winter (occurring mostly on wintering grounds). Additionally, we used a simple linear model to test whether sex-based differences in spring arrival trends across species (female trend minus male trend) varied as a function of breeding latitude and hand–wing index (HWI). To calculate breeding latitude for each species, we downloaded breeding range polygons from eBird Status and Trends (Fink et al., 2020), sampled 10,000 points from each range, and calculated the mean latitude of the sampled points. HWI, a proxy for dispersal ability (Sheard et al., 2020), was extracted from AVONET (Tobias et al., 2022). We removed Ruby-throated Hummingbird (*Archilochus colubris*) from this test as it has dramatically higher HWI than all other species in our sample.

Finally, we examined correlations among trend differentials in common species across our analyses. We tested whether age- or sex-based differences in spring arrival trends across species were correlated (Pearson's correlation) with the corresponding differences in fall departure trends. For example, is the difference between adult female and adult male arrival trends in spring correlated with the difference between adult female and adult male departure trends in fall? To explain the high variation in fall phenological trends, we also tested whether age- and sex-based differences in fall departure dates across species were correlated with differences in fall departure trends. For example, for species where the adults leave before the juveniles, are adults also advancing their fall phenology relative to juveniles?

3 | RESULTS

During spring migration at the mean latitude (Figure 1a), the earliest demographic group to arrive was adult males (posterior mean across all species = day 127.5, 95% credible interval [95 CrI] = 125.8–129.3), followed by immature males (129.5, 95 CrI = 127.6–131.5), adult females (132.3, 95 CrI = 130.8–133.9), and finally immature females (133.5, 95 CrI = 131.9–135.1). Model posterior distributions indicated complete certainty (Pr = 1.0) that adult males arrived earlier than all other demographic groups. Birds of unknown sex had spring arrival dates intermediate to known sexes within the respective age group (adults = 130.4, 95 CrI = 128.8–131.9; immatures = 132.6, 95 CrI = 130.9–134.3).

During fall migration (Figure 1b), adult birds tended to depart earlier (female = 248.0, 95 CrI = 245.0–251.1; male = 247.6, 95 CrI = 244.5–250.7; unknown = 247.0, 95 CrI = 244.0–249.9) than juvenile birds (female = 252.6, 95 CrI = 249.3–255.9; male = 253.6, 95 CrI = 250.2–257.2; unknown = 250.5, 95 CrI = 247.2–253.7). However, differences in departure date between the sexes depended on age, with high probability (Pr = 0.798) that adult males departed before adult females, but no evidence (Pr = 0.064) that juvenile males departed before juvenile females.

The spring migratory phenology of all demographic groups advanced over time (Figure 2a,c) with high certainty ($\Pr[\text{slope} < 0] = 0.999$). Adult males advanced the fastest (−0.84 days per decade, 95 CrI = −1.22 to −0.47, Pr = 1.0) followed by adult females (−0.64, 95 CrI = −1.02 to −0.27, Pr = 1.0) and immature males (−0.63, 95 CrI = −1.03 to −0.24, Pr = 1.0), with the slowest being immature females (−0.59, 95 CrI = −1.00 to −0.17, Pr = 0.996). Of unknown sex species—largely comprising monochromatic species—adults (−0.61, 95 CrI = −1.01 to −0.23, Pr = 1.0) and immatures (−0.66, 95 CrI = −1.09 to −0.25, Pr = 1.0) advanced with intermediate speed. Models showed high certainty that adult males advanced their spring arrival faster than other demographic groups (Pr = 0.951). Focusing on species-specific estimates (Figure S1a), of the 24 dichromatic species, no species significantly delayed their spring phenology, but adult males of 17 species, adult females of 14 species, immature males of 12 species, and immature females of 12 species advanced their spring phenology with high confidence ($\Pr > 0.95$). Of these species, the fastest advancing species and group was adult male Black-throated Green Warblers (*Setophaga virens*), which advanced their arrival by an average of −1.57 days per decade (95 CrI = −2.16 to −1.00). Of the 12 monochromatic species, adults of six species and

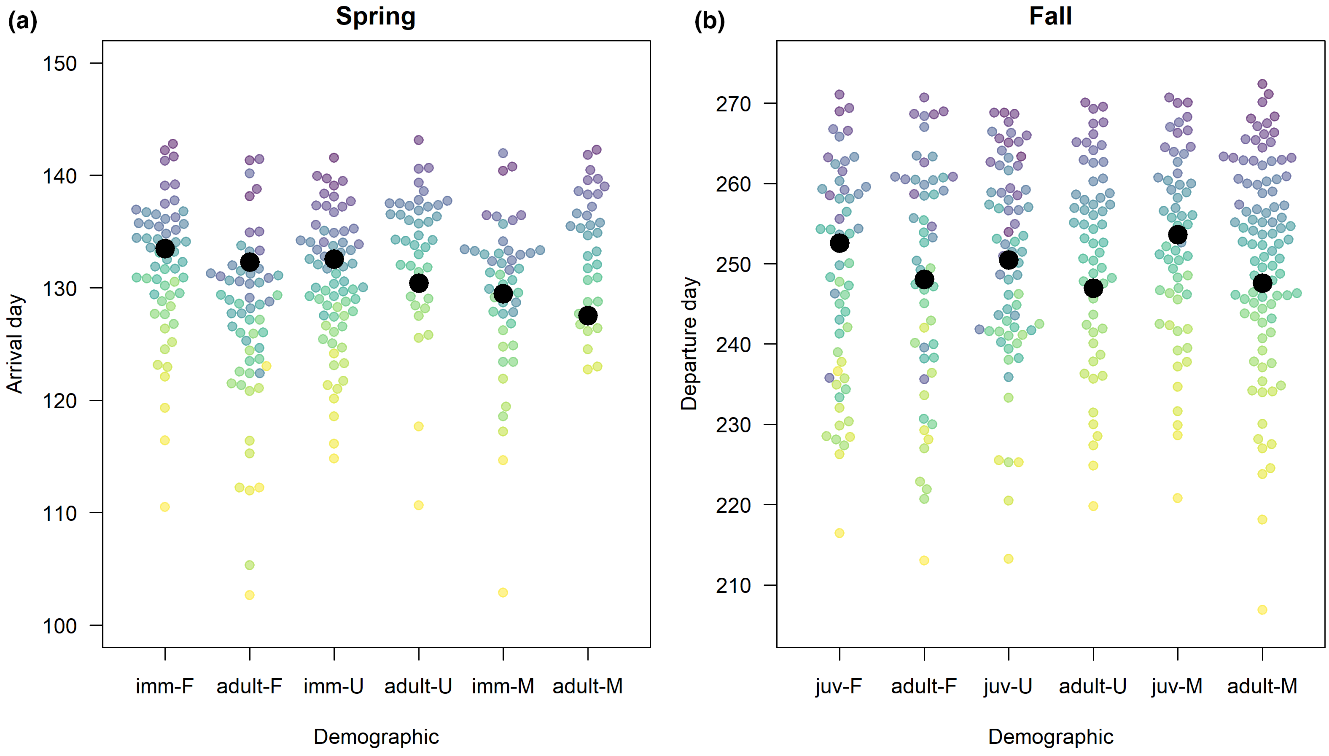

FIGURE 1 Variation in migratory phenology as a function of age and sex for 98 North American bird species. Phenology estimates were based on the Weibull-corrected 1st and 3rd quartile estimates of capture records for (a) spring ($n = 89$ species) and (b) fall ($n = 98$ species), respectively. Large points represent global means for each demographic group. Each small point represents the species-specific mean phenology estimate from the posterior distribution of a given demographic group. Colors are based on the ranked arrival/departure day of immature females from earliest (yellow) to latest (purple), with each species colored consistently across demographic group within each panel. For sex, F = female, M = male, U = unknown; for age, imm = immature (second year), juv = juvenile (hatch-year).

immatures of five species advanced their spring phenology with high certainty (Figure S1a), the fastest being immature Warbling Vireo (*Vireo gilvus*; −1.83, 95 CrI = −2.57 to −1.15). One species, the Gray-cheeked Thrush (*Catharus minimus*), delayed its spring migratory phenology (adults: 0.85, 95 CrI = 0.37–1.32).

There was no clear trend in fall migratory phenology overall (Pr[slope < 0] = 0.59) or across demographic groups (Figure 2b,d; adult females: Pr[slope < 0] = 0.58; juvenile females: Pr = 0.50; adult males: Pr = 0.21; juvenile males: Pr = 0.42). Most groups showed little overall change in phenology (max change = 0.24 days per decade for adult males), although adults (−0.43, 95 CrI = −0.99–0.17, Pr = 0.92) and juveniles (−0.39, 95 CrI = −1.01 to 0.22, Pr = 0.89) of unknown sex tended to advance their departure. However, there was a large amount of variation in trends between species, with both phenological advances and delays in the timing of fall departure. Of 33 dichromatic species (Figure S1b), adult females of one species, juvenile females of eight species, and adult males of six species advanced their fall phenology, while adult females of two species, juvenile females of four species, adult males of three species, and juvenile males of four species delayed their fall phenology. Of the 20 monochromatic species, adults of two species and juveniles of three species advanced their fall phenology (Figure S1b). Juvenile female Prairie Warbler (*Setophaga discolor*) was the fastest group to advance its fall phenology (−2.89, 95 CrI = −4.54 to −1.20). Juvenile male Black-headed Grosbeak (*Pheucticus melanocephalus*) was the fastest group to delay its fall phenology was (4.95, 95 CrI = 2.97–7.16).

In the species-specific spring phenology estimates (Figure S2), adult females ($\lambda = 0.51$, $p = 0.021$) and adult males ($\lambda = 0.59$, $p = 0.002$) showed significant phylogenetic signal, but no other groups did ($\lambda < 0.4$, $p > 0.05$; Figure S2). The difference between adult male and female arrival (Figure 3a) also showed significant phylogenetic signal ($\lambda = 0.59$, $p = 0.002$), unlike the difference between immature and adult arrival (Figure 3b). In the fall, there was high phylogenetic signal across all demographic groups (Figure S3), as well as between males and females (Figure 3c), and between juveniles and adults (Figure 3d; $\lambda = 0.58–0.78$, $p \leq 0.011$). There was little phylogenetic signal in either the species-specific spring and fall phenology trends ($\lambda \leq 0.1$, $p > 0.05$) or the age and sex-based differences in phenology trends ($\lambda \leq 0.1$, $p > 0.05$).

Exploring species-specific variation post hoc, we found that molt strategy had a significant effect on age-based differences in departure date (one-way ANOVA: $F_{2,90} = 25.88$, $p < 0.001$), with adults more likely to leave first in species that molt during migration or on the wintering grounds compared to species that molt on the breeding grounds (Figure 4a). We also found that the rate of increase in protandry—that is, the number of days per decade by which males were advancing faster than females—was positively associated with

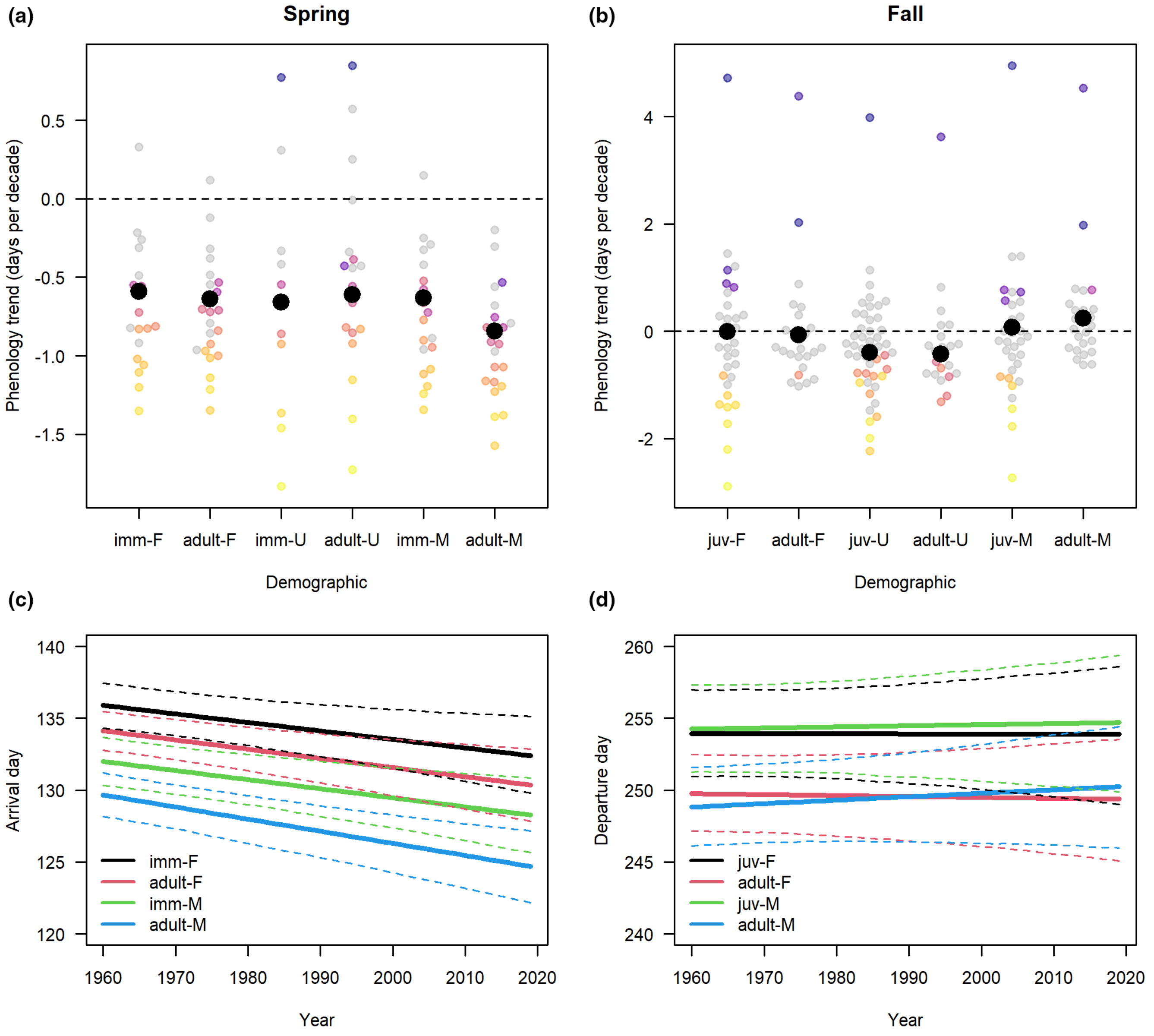

FIGURE 2 Trends in migratory phenology over 60 years as a function of age and sex for 54 North American bird species. Phenology estimates were based on the Weibull-corrected 1st and 3rd quartile estimates of capture records for spring and fall, respectively. Species-specific rates of phenological shift (days per decade) are shown for (a) spring ($n = 36$ species) and (b) fall ($n = 53$ species), along with global means (black points), for each demographic group. Species points (a, b) are colored based on the ranked phenological trend of immature females, from fastest advance (yellow) to slowest delay (purple), with each species colored consistently across demographic group within each panel (a, b). Points are colored gray when the trend was not certain, that is, where the 95% credible interval overlapped 0. Trends over time are also shown collectively for each demographic group in (c) spring and (d) fall. Thick lines represent global mean trends for each group and dashed lines represent the 95% credible intervals. Trend lines for unknown sex are not shown for simplicity. For sex, F = female, U = unknown, and M = male; for age, imm = immature (second year), juv = juvenile (hatch-year).

breeding latitude (Figure 4b; 0.022 ± 0.010 SE, $n = 21$, $t = 2.17$, $p = 0.044$) but not with HWI (0.004 ± 0.010 SE, $t = 0.39$, $p = 0.698$).

When comparing sex-based differences in spring arrival trends with corresponding differences in fall departure trends, we found little correlation between spring and fall for sex-based differences in adult trends ($n = 20$, Pearson's $r = 0.03$) or sex-based differences in immature trends ($n = 18$, $r = -0.33$). There was also little correlation (Figure S4) between spring and fall for age-based differences in males ($n = 17$, $r = -0.21$) but moderate inverse correlation for females ($n = 16$, $r = -0.46$) and unknown sex ($n = 9$, $r = -0.55$). Thus, overall, there was little evidence to suggest that differences in trends among demographic groups carried over from spring to fall, except perhaps between females or unknown sex individuals where spring trends were anticorrelated with fall trends. When comparing age-based differences in departure dates with age-based differences in departure trends (Figure S5a), we found positive correlation between the two (females: $n = 24$, $r = 0.51$; males: $n = 25$, $r = 0.61$; unknown: $n = 22$, $r = 0.55$). Similarly, we found a positive correlation ($n = 22$, $r = 0.45$)

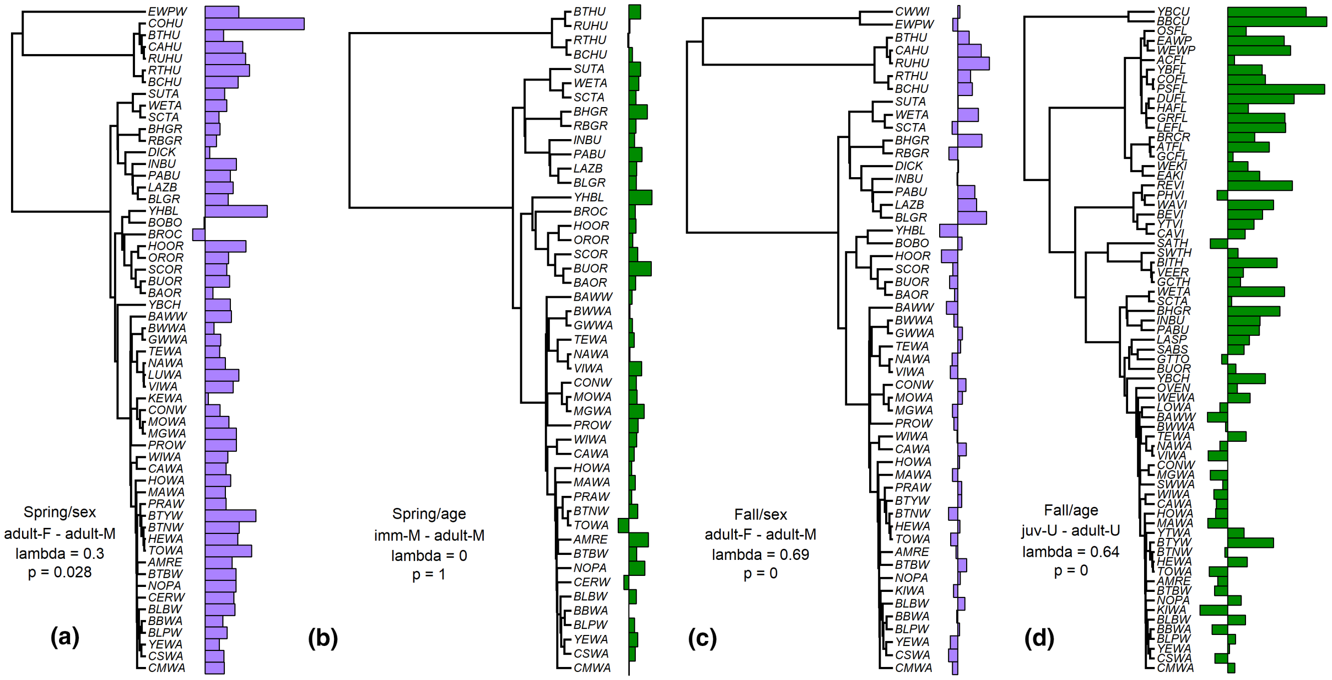

FIGURE 3 Phylogenetic signal of sex- and age-based differences in bird migratory phenology over 60 years in North America. In spring, phylogenies are shown for (a) the difference between adult female and adult male arrival (Weibull-corrected 1st quartile of capture records), and (b) the difference between immature male and adult male arrival. In fall, phylogenies are shown for (c) the difference between adult female and adult male departure (Weibull-corrected 3rd quartile of capture records), and (d) the difference between immature unknown and adult unknown arrival. Comparisons were only made when data were available for each pair of demographic groups. The phylogenies shown represent those demographic groups with the most pairwise-species comparisons. Inset text denotes the demographic groups compared as well as Pagel's λ, a measure of phylogenetic signal, and its associated *p*-value. For sex, F = female, M = male, U = unknown; for age, imm = immature (second year), juv = juvenile (hatch-year). Full species names corresponding to the four-letter codes can be found in Table S1.

between sex-based differences in departure dates and sex-based differences in departure trends for adults (Figure S5b). Thus, the demographic group that departs first in fall was more likely to advance in phenology relative to the group that departs second.

4 | DISCUSSION

The advancing pace of bird migration in spring is one of the most well-documented responses to recent global climate change, yet little research has assessed whether these advances are consistent across sexes and age groups, while phenological trends in fall migration are often neglected (Gallinat et al., 2015). In this study, we found that adult male birds are advancing their spring arrival times (by an average of −0.84 days per decade) substantially faster than other demographic groups (between −0.64 and −0.59 days per decade). This imbalance in shift rates is the average result across 24 dichromatic species over 60 years in North America (Figure 2a,c), a result that has not been demonstrated before at this geographic and taxonomic scale. In Europe, spring phenological trends have been found to be similar between males and females for eight species over 22 years (Tøttrup & Thorup, 2008), but male Barn Swallows (*Hirundo rustica*) showed an advance in phenology while females did not (Møller, 2004). In North America, trends in spring migratory phenology have been documented for both male and female Black-throated Blue Warblers, but an interaction between sex and year has not been tested (Covino, Horton, et al., 2020). The trends that we estimated for male (adults: −0.72; immatures: −0.37) and female (adults: −0.57; immatures: −0.46) Black-throated Blue Warblers corroborate those estimated by Covino et al. (5th percentile: −1.16, median: −0.45), but suggest that this species additionally shows sex and age-based differences in phenological trends.

Our general finding of advancing spring migratory phenology supports the substantial literature on phenological trends (e.g., Bitterlin & Van Buskirk, 2014; Lehikoinen et al., 2019; Usui et al., 2017). Estimates of phenological advance show high variation between studies, ranging from −0.6 days per decade (Horton et al., 2020) to −2.67 days per decade (Cotton, 2003). Many factors can affect the estimation of phenological trends, so any individual estimate should be considered in context. For example, studies examining the first or early (5th percentile) arrival date may find stronger trends than those examining the median or mean arrival date (Bitterlin & Van Buskirk, 2014; Covino, Horton, et al., 2020; Lehikoinen et al., 2019; Van Buskirk et al., 2009). While earlier arrival dates are more sensitive to outliers, median arrival dates may be slower to shift, and so our use of 1st quartile arrival date is a compromise that better represents the onset of migration (Belitz et al., 2020), similar to (but less computationally intensive than) the half-max of arrival (Youngflesh et al., 2021). Moreover, the use of Weibull-corrected estimates minimizes potential bias

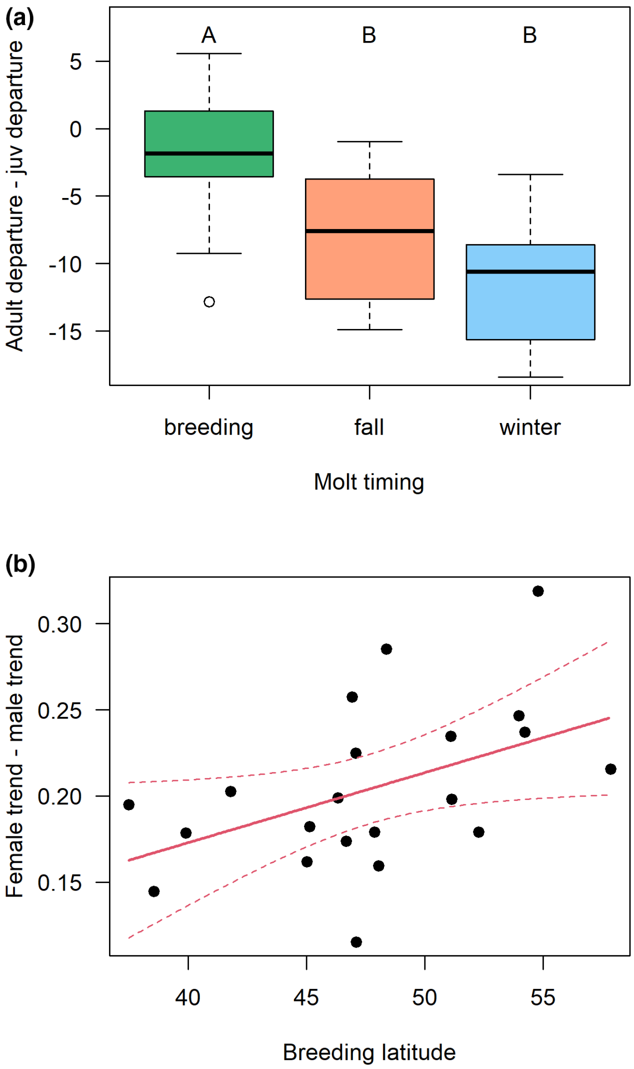

FIGURE 4 Phenological patterns in relation to species attributes for North American migratory bird species. Age-based differences in fall departure dates (a) varied among molt strategies. Molt strategies were classified as: breeding (occurring mostly on breeding grounds), fall (occurring either during fall migration on both breeding and wintering grounds), or winter (occurring mostly on wintering grounds). Capital letters denote significant ($p < 0.05$) differences between groups based on a Tukey's HSD test. Sex-based differences in spring arrival trends (b) varied positively as a function of breeding latitude (mean latitude of breeding range), with males advancing faster than females faster at higher latitudes. A trend line is shown with 95% confidence intervals.

in the data (Belitz et al., 2020). Another important aspect that can affect trend estimation is the temporal scale of the study (Kolářová et al., 2017). Whereas our study spans 60 years of phenological variation, other studies covering shorter time spans may find stronger signals of advance due to more recent acceleration in climate warming (Mayor et al., 2017). Despite variation in the magnitude of individual trend estimates, our results are definitive on the direction of trends in spring migratory phenology with high confidence (Pr ≈ 1) of advancing trends across demographic groups and for ~90% of species.

In support of other studies (Francis & Cooke, 1986; Spina et al., 1994; Tøttrup & Thorup, 2008), we found a general pattern of protandry (Figure 1a), with adult males arriving 4.8 days earlier than adult females across 58 dichromatic species. We also found high phylogenetic signal in the degree of protandry (Figure 3a). Males are expected to arrive earlier than females to establish territories and gain more mating opportunities once females arrive (Kokko et al., 2006; Morbey & Ydenberg, 2001; Rubolini et al., 2004; Saino et al., 2010), including extra-pair paternity (Canal et al., 2012; Coppack et al., 2006). This selection on protandry may be facilitated by latitudinal segregation on and earlier departure from wintering grounds (Briedis et al., 2019; Coppack & Pulido, 2009), and shorter duration at stopover sites (Seewagen et al., 2013). We also found across 89 species that adults tended to arrive earlier than immatures (males by 2.1 days, females by 1.2 days, on average), corroborating other studies (Francis & Cooke, 1986; Spina et al., 1994; Stewart et al., 2002). Adults are known to migrate faster than immature birds (Ellegren, 1993) and tend to outcompete young birds in the wintering grounds, enabling adults to feed more efficiently than immatures prior to migration (Marra et al., 1993).

Understanding the mechanisms and drivers of earlier male and adult arrival helps to both explain the sex and age-based trends in phenology and interpret their consequences. For example, as males often winter farther north than females (Coppack & Pulido, 2009; Komar et al., 2005), they could be exposed to different migratory cues. Temperatures in more northerly wintering grounds may correlate better with temperatures on breeding grounds, allowing males to more accurately track increasing temperatures (Bauer et al., 2020). Alternatively, because they depart the wintering grounds earlier (Briedis et al., 2019; Coppack & Pulido, 2009), males may have more time to adjust their migration speed en route. Future studies should attempt to quantify age and sex-based trends in wintering latitude and spring departure times to see whether they correlate with our observed phenological trends. Interactions on the wintering grounds could also be responsible for the faster advancement of males. If climate change causes conditions to worsen on the wintering grounds, increased competition between adults and immature birds could result in larger differentials in body condition, which, in turn, affects migration timing (Marra et al., 1993).

While protandry is probably adaptive, the degree of protandry is likely under balancing selection between the costs of arriving too early and the benefits of arriving before other males and/or females (Morbey et al., 2012; Saino et al., 2010). Climate change could be reducing the cost of arriving earlier and, given that sexual selection is an important driver of protandry, increasing the degree of protandry (Møller, 2004). However, if increasing protandry reflects a greater inability of females to track climate change, this could have important consequences for reproduction. Despite shifts in phenology, migratory birds are not currently keeping track with increasing temperatures (Saino et al., 2011) or earlier green-up (Mayor et al., 2017), and this is thought to result in trophic mismatches, whereby the timing of hatching does not coincide with the timing of peak food abundance (Both et al., 2006, 2010). Copulation, laying, and rearing can obviously not occur until females have arrived, and the growing gap between male and female arrival could be causing us to underestimate the degree of trophic mismatch. Population declines associated with lags in phenological change (Møller et al., 2008) may be driven more by lags in female arrival than male arrival, and future studies could test this relationship. In addition, our post hoc test indicated that the growing degree of protandry is greater for species that breed farther north. Perhaps the mechanisms that drive these phenological trend differentials occur during migration itself, and are exacerbated for species that need to migrate farther. Or perhaps the mechanisms occur on the breeding grounds and are more pronounced in the colder north. These are important avenues for future research.

During the fall, we did not find strong overall trends in phenology (Figure 2b,d). In particular, females showed almost no change in departure date. Males, however, did show a slight trend toward earlier departure. A lack of overall trend is consistent with other studies (Van Buskirk et al., 2009; Zimova et al., 2021), as is a lack of difference in departure times (Figure 1b) between males and females (Covino, Horton, et al., 2020; Morris & Glasgow, 2001). The earlier departure of adults in our study, however, contradicts the hypothesis that juveniles should leave earlier given that they molt before their parents (Covino, Horton, et al., 2020; Newton, 2008; Pyle et al., 2018)—although species-specific results do support earlier juvenile departure in Black-throated Blue Warblers (Covino, Horton, et al., 2020). The reason why our finding of earlier adult departure differs from previous studies could be the choice of phenometric. While juveniles are expected to depart earlier, they are also expected to have a more protracted migratory period than adults (Morris et al., 2016). By choosing the 3rd quartile of departure dates—that is, the offset of migration—we are capturing a different part of the curve than most previous studies, where the wider distribution of juvenile departure could lead to apparently later departure dates. Another explanation could be the existence of breeding adults at banding stations. We deliberately chose the 3rd quartile of departure dates to distance ourselves from the breeding season but, inevitably, breeding adults are captured at the start of the migration season, and they could be biasing the phenology estimates to earlier in the season. Ultimately, capture dates provide only a single glimpse into the migration of individual birds; with the continued miniaturization of bird-mounted tracking technology, future work will be able to provide greater understanding of the complex dynamics of fall migration.

Despite a lack of overall trends during the fall, we found high interspecific variation in both departure dates and departure trends (Figures 1 and 2; Figure S1), with strong phylogenetic signal in departure dates (Figure S3). This variation could be driven by species-specific differences in territoriality or molt strategy. For example, many of the species in our dataset with adults departing first are hummingbirds (Trochilidae) and flycatchers (Tyrannidae), while warblers (Parulidae) dominate the species whose juveniles depart first—a trend supported by high phylogenetic signal in age-based differences in departure dates (Figure 3d). Adult hummingbirds tend to molt on their wintering grounds, while many flycatchers undergo a protracted prebasic molt, mostly occurring on the wintering grounds (Pyle, 1997). By contrast, the adult prebasic molt of warblers occurs over a short period on the breeding grounds. Thus, while adult warblers must molt prior to migration—departing after juveniles—hummingbirds and flycatcher adults can leave immediately post breeding—before their offspring. Indeed, we found that adults were statistically more likely to leave first in species that molt during migration or on the wintering grounds (Figure 4a).

What does this mean for fall phenological trends? In species where adults leave earlier, adults may be able to advance their departure, while in species where adults need to molt before leaving, juveniles may advance their departure relative to adults. Indeed, we found a positive correlation between age-based differences in departure dates and age-based differences in departure trends (Figure S5a). Similarly, in species where females depart first, females were also more likely to advance their departure dates (Figure S5b). Sex-based differences in departure dates could result from a number of factors. For example, male hummingbirds do not provision for their offspring, so can depart before females. Conversely, the males of some species may continue to defend territories even after the females have left (Mills, 2005). The important take-away is that age and sex-based gaps in departure phenology have increased over time, and these shifts are likely driven by the selective forces that shaped those gaps over evolutionary time. However, there was little evidence that differences in departure trends were correlated with differences in spring arrival trends, suggesting that the forces driving variation in phenological trends vary from spring to fall. Better understanding of these mechanisms will substantially improve predictive models of phenological change.

In summary, we demonstrate consistent sex- and age-based differences in spring migratory phenology for bird species over 60 years across North America. Adult males are advancing their arrival times faster than other demographic groups and this has important implications for conservation, as the gap between male and female arrival widens. In the fall, a lack of overall trend in phenology hides important interspecific variation driven by differences in breeding and molt strategies. Understanding the implications of these autumnal changes will require a more nuanced, species-specific approach that integrates climate change with life history.

AUTHOR CONTRIBUTIONS

Montague H. C. Neate-Clegg led formal analysis and writing of the original draft. Both Montague H. C. Neate-Clegg and Morgan W. Tingley shared conceptualization, planning the analysis, and editing drafts.

ACKNOWLEDGMENTS

This study was funded by National Science Foundation grants EF 1703048 and EF 2033263. We are grateful to the thousands of bird banders who have contributed data to the Bird Banding Lab, and to D. Bystrak for access to the dataset. The manuscript and analyses benefitted from the perspectives of B. Tonelli, C. Youngflesh, and P. Pyle.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw banding data are available via a direct download from ScienceBase at https://www.usgs.gov/labs/bird-banding-laboratory/data. Processed data and code are available on Dryad at https://doi.org/10.5061/dryad.m905qfv4v.

ORCID

Montague H. C. Neate-Clegg https://orcid.org/0000-0001-9753-6765
Morgan W. Tingley https://orcid.org/0000-0002-1477-2218

REFERENCES

Bauer, S., McNamara, J. M., & Barta, Z. (2020). Environmental variability, reliability of information and the timing of migration. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20200622.

Belitz, M. W., Larsen, E. A., Ries, L., & Guralnick, R. P. (2020). The accuracy of phenology estimators for use with sparsely sampled presence-only observations. *Methods in Ecology and Evolution*, *11*, 1273–1285.

Bitterlin, L. R., & Van Buskirk, J. (2014). Ecological and life history correlates of changes in avian migration timing in response to climate change. *Climate Research*, *61*, 109–121.

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, *441*, 81–83.

Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J., & Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1259–1266.

Bradley, N. L., Leopold, A. C., Ross, J., & Huffaker, W. (1999). Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 9701–9704.

Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Liechti, F., Meier, C. M., Procházka, P., & Hahn, S. (2019). A full annual perspective on sex-biased migration timing in long-distance migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20182821.

Cadahía, L., Labra, A., Knudsen, E., Nilsson, A., Lampe, H. M., Slagsvold, T., & Stenseth, N. C. (2017). Advancement of spring arrival in a long-term study of a passerine bird: Sex, age and environmental effects. *Oecologia*, *184*, 917–929.

Canal, D., Jovani, R., & Potti, J. (2012). Multiple mating opportunities boost protandry in a pied flycatcher population. *Behavioral Ecology and Sociobiology*, *66*, 67–76.

Coppack, T., & Pulido, F. (2009). Proximate control and adaptive potential of protandrous migration in birds. *Integrative and Comparative Biology*, *49*, 493–506.

Coppack, T., Tøttrup, A. P., & Spottiswoode, C. (2006). Degree of protandry reflects level of extrapair paternity in migratory songbirds. *Journal für Ornithologie*, *147*, 260–265.

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 12219–12222.

Covino, K. M., Horton, K. G., & Morris, S. R. (2020). Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler. *Auk*, *137*, 1–11.

Covino, K. M., Morris, S. R., Shieldcastle, M., & Taylor, P. D. (2020). Spring migration of blackpoll warblers across North America. *Avian Conservation and Ecology*, *15*, 1.

Ellegren, H. (1993). Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scandinavica*, *24*, 220–228.

Fink, D., Auer, T., Johnston, A., Ruiz-Gutierrez, V., Hochachka, W. M., & Kelling, S. (2020). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*, *30*, 1–16.

Francis, C. M., & Cooke, F. (1986). Differential timing of spring migration in wood warblers (Parulinae). *Auk*, *103*, 548–556.

Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, *30*, 169–176.

Haest, B., Hüppop, O., van de Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. *Global Change Biology*, *25*, 4064–4080.

Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T. Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change*, *10*, 1–6.

Horton, K. G., Van Doren, B. M., La Sorte, F. A., Cohen, E. B., Clipp, H. L., Buler, J. J., Fink, D., Kelly, J. F., & Farnsworth, A. (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Global Change Biology*, *25*, 1106–1118.

Hurlbert, A. H., & Liang, Z. (2012). Spatiotemporal variation in avian migration phenology: Citizen science reveals effects of climate change. *PLoS ONE*, *7*, 31662.

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 1467–1471.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448.

Jones, T., & Cresswell, W. (2010). The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? *The Journal of Animal Ecology*, *79*, 98–108.

Kokko, H., Gunnarsson, T. G., Morrell, L. J., & Gill, J. A. (2006). Why do female migratory birds arrive later than males? *The Journal of Animal Ecology*, *75*, 1293–1303.

Kolářová, E., Matiu, M., Menzel, A., Nekovář, J., Lumpe, P., & Adamík, P. (2017). Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries. *International Journal of Biometeorology*, *61*, 1279–1289.

Komar, O., O'Shea, B. J., Townsend Peterson, A., & Navarro-Sigüenza, A. G. (2005). Evidence of latitudinal sexual segregation among migratory birds wintering in Mexico. *Auk*, *122*, 938–948.

Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I. S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, *101*, 985–991.

Margary, I. D. (1926). The marsham phenological record in Norfolk, 1736–1925, and some others. *Quarterly Journal of the Royal Meteorological Society*, *52*, 27–54.

Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia*, *142*, 307–315.

Marra, P. P., Sherry, T. W., & Holmes, R. T. (1993). Territorial exclusion by a long-distance migrant Warbler in Jamaica: A removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk*, *110*, 565–572.

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *7*, 1–10.

McKinnon, E. A., Macdonald, C. M., Gilchrist, H. G., & Love, O. P. (2016). Spring and fall migration phenology of an Arctic-breeding passerine. *Journal für Ornithologie*, *157*, 681–693.

Miller-Rushing, A. J., Inouye, D. W., & Primack, R. B. (2008). How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology*, *96*, 1289–1296.

Mills, A. M. (2005). Protogyny in autumn migration: Do male birds "play chicken"? *Auk*, *122*, 71–81.

Møller, A. P. (2004). Protandry, sexual selection and climate change. *Global Change Biology*, *10*, 2028–2035.

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 16195–16200.

Morbey, Y. E., Coppack, T., & Pulido, F. (2012). Adaptive hypotheses for protandry in arrival to breeding areas: A review of models and empirical tests. *Journal für Ornithologie*, *153*, 207–215.

Morbey, Y. E., & Ydenberg, R. C. (2001). Protandrous arrival timing to breeding areas: A review. *Ecology Letters*, *4*(6), 663–673.

Morris, S. R., Covino, K. M., Jacobs, J. D., & Taylor, P. D. (2016). Fall migratory patterns of the Blackpoll Warbler at a continental scale. *Auk*, *133*, 41–51.

Morris, S. R., & Glasgow, J. L. (2001). Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. *The Wilson Bulletin*, *113*, 202–210.

Mynott, J. (2018). *Birds in the ancient world: Winged words*. Oxford University Press.

Nakata, M., Chino, N., Chiba, A., Komatsu, Y., Itoh, Y., Akahara, K., Ichimura, Y., Okino, M., Satoh, H., Tachikawa, K., & Fujisawa, M. (2011). Chronological trends in the timing of spring bird migration and its relationship with temperature in a coastal forest near the city of Niigata. *Japanese Journal of Ornithology*, *60*, 63–72.

Nam, H. Y., Choi, C. Y., Park, J. G., Hong, G. P., Won, I. J., Kim, S. J., Bing, G. C., & Chae, H. Y. (2011). Protandrous migration and variation in morphological characters in Emberiza buntings at an East Asian stopover site. *Ibis*, *153*, 494–501.

Newson, S. E., Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P. W., Miller, R., Grantham, M. J., & Baillie, S. R. (2016). Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. *Ibis*, *158*, 481–495.

Newton, I. (2008). *The migration ecology of birds*. Academic Press.

Newton, I. (2011). Migration within the annual cycle: Species, sex and age differences. *Journal für Ornithologie*, *152*, 169–185.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* (DSC 2003), March 20–22, Vienna, Austria.

Pyle, P. (1997). *Identification guide to North American birds: A compendium of information on identifying, ageing, and sexing "near-passerines" and passerines in the hand*. Slate Creek Press.

Pyle, P., Saracco, J. F., & Desante, D. F. (2018). Evidence of widespread movements from breeding to molting grounds by North American landbirds. *Auk*, *135*, 506–520.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*, 57–60.

Rubolini, D., Spina, F., & Saino, N. (2004). Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology*, *15*, 592–601.

Saino, N., Ambrosini, R., Rubolini, D., Von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., & Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 835–842.

Saino, N., Rubolini, D., Serra, L., Caprioli, M., Morganti, M., Ambrosini, R., & Spina, F. (2010). Sex-related variation in migration phenology in relation to sexual dimorphism: A test of competing hypotheses for the evolution of protandry. *Journal of Evolutionary Biology*, *23*, 2054–2065.

Seewagen, C. L., Guglielmo, C. G., & Morbey, Y. E. (2013). Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. *Behavioral Ecology*, *24*, 634–642.

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., Macgregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*, 2463.

Sherry, T. W., & Holmes, R. T. (1989). Age-specific social dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): A removal experiment. *Behavioral Ecology and Sociobiology*, *25*, 327–333.

Sparks, T. H. (1999). Phenology and the changing pattern of bird migration in Britain. *International Journal of Biometeorology*, *42*, 134–138.

Sparks, T. H., Bairlein, F., Bojarinova, J. G., Hüppop, O., Lehikoinen, E. A., Rainio, K., Sokolov, L. V., & Walker, D. (2005). Examining the total arrival distribution of migratory birds. *Global Change Biology*, *11*, 22–30.

Spina, F., Massi, A., & Montemaggiori, A. (1994). Back from Africa: Who's running ahead? Aspects of differential migration of sex and age classes in palearctic-African spring migrants. *Ostrich*, *65*, 137–150.

Stegman, L. S., Primack, R. B., Gallinat, A. S., Lloyd-Evans, T. L., & Ellwood, E. R. (2017). Reduced sampling frequency can still detect changes in abundance and phenology of migratory landbirds. *Biological Conservation*, *210*, 107–115.

Stewart, R. L. M., Francis, C. M., & Massey, C. (2002). Age-related differential timing of spring migration within sexes in passerines. *The Wilson Bulletin*, *114*, 264–271.

Su, Y.-S. & Yajima, M. (2021). *R2jags: Using R to run "JAGS"*. R package version 0.7-1.

Swanson, D. L., Liknes, E. T., & Dean, K. L. (1999). Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. *The Wilson Bulletin*, *111*, 61–69.

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F., Leandro-Silva, V., Claramunt, S., Darski, B., … Schleunning, M. (2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*, 581–597.

Tøttrup, A. P., Klaassen, R. H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jorgensen, P. S., Fox, J., Afanasyev, V., Rahbek, C., & Alerstam, T. (2012). The annual cycle of a trans-equatorial Eurasian-African passerine migrant: Different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1008–1016.

Tøttrup, A. P., & Thorup, K. (2008). Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *Journal für Ornithologie*, *149*, 161–167.

Usui, T., Butchart, S. H. M., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: A phylogenetic meta-analysis. *The Journal of Animal Ecology*, *86*, 250–261.

Van Buskirk, J., Mulvihill, R. S., & Leberman, R. C. (2009). Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biology*, *15*, 760–771.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T. J. C., Fromentin, J. I. O. H., & Bairlein, F. (2002). Ecological response to recent climate change. *Nature*, *416*, 389–395.

Wobker, J., Heim, W., & Schmaljohann, H. (2021). Sex, age, molt strategy, and migration distance explain the phenology of songbirds at a stopover along the East Asian flyway. *Behavioral Ecology and Sociobiology*, *75*, 25.

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*, 987–994.

Zimova, M., Willard, D. E., Winger, B. M., & Weeks, B. C. (2021). Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. *The Journal of Animal Ecology*, *90*, 2348–2361.

SUPPORTING INFORMATION

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

How to cite this article: Neate-Clegg, M. H. C., & Tingley, M. W. (2022). Adult male birds advance spring migratory phenology faster than females and juveniles across North America. *Global Change Biology*, *00*, 1–14. https://doi.org/10.1111/gcb.16492