



*Avian Behavior, Ecology, and Evolution*

# Multi-year change and annual variation in fall migratory timing of songbirds captured across a 19-year time span in northeastern Pennsylvania, USA

## Cambio multianual y variación anual en el momento de la migración otoñal de aves canoras capturadas a lo largo de un periodo de 19 años en el noreste de Pensilvania, EE.UU.

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**ABSTRACT.** Although there is abundant evidence that timing of spring migration in landbirds is influenced by annual variation in temperature and longer-term warming due to climate change, much less is known about how these factors influence fall migration, especially in North America. Similarly, less is known about the influence of annual variation in temperature and precipitation and the combination of intrinsic factors (age, sex, wintering location, diet, number of broods produced in a breeding season) on the timing of fall migration. We used 13 years of capture data, spanning a 19-year period (2006–2024) to look for species-specific evidence of multi-year change in fall migratory timing while also looking to see if precipitation amount or temperature experienced by birds using our site changed. Finally, we looked for evidence that the above extrinsic and intrinsic factors influenced annual variation in migratory timing. We found evidence that (1) 46% (6 of 13) of the species exhibited either delays (4 species) or advances (2 species) in migratory timing, (2) average temperature increased by 1.4 °C during the fall migratory period, (3) sex and wintering location influenced timing with females (2.3 days) and species that winter in Central or South America (14.3 days) passing through our site before males and species wintering in North America, and (4) in warmer and/or wetter years birds advanced timing. Our results increase understanding of how intrinsic and extrinsic factors influence annual timing of fall migration. Further, our findings add to the growing evidence that climate change has altered fall migratory timing and that differences exist in how species and populations have responded. More work is necessary to determine whether changes in timing of fall migration are due to developmental plasticity, selection on heritable variation, or some combination.

**RESUMEN.** Aunque existe abundante evidencia de que el momento de la migración primaveral de las aves terrestres está influenciado por la variación anual de la temperatura y el calentamiento a largo plazo debido al cambio climático, se sabe mucho menos sobre cómo influyen estos factores en la migración otoñal, especialmente en Norteamérica. Del mismo modo, se sabe menos sobre la influencia de la variación anual de la temperatura y las precipitaciones y la combinación de factores intrínsecos (edad, sexo, lugar de invernada, dieta, número de nidadas producidas en una temporada de cría) en el momento de la migración otoñal. Utilizamos 13 años de datos de capturas, abarcando un periodo de 19 años (2006-2024), para evaluar evidencia específica por especie de cambios multianuales en el momento de la migración otoñal, así como para examinar si la cantidad de precipitación o la temperatura experimentadas por las aves que utilizaron nuestro sitio han cambiado. Finalmente, buscamos evidencia de que los factores extrínsecos e intrínsecos mencionados influenciaron en la variación anual del momento de la migración. Encontramos evidencia de que (1) el 46 % (6 de 13) de las especies mostraban retrasos (4 especies) o adelantos (2 especies) en el momento de la migración, (2) la temperatura media aumentó 1.4 °C durante el periodo de migración otoñal, (3) el sexo y el lugar de invernada influyeron en el momento de la migración, ya que las hembras (2.3 días) y las especies que invernaban en América Central o del Sur (14.3 días) pasaron por nuestro sitio antes que los machos y las especies que invernaban en América del Norte, y (4) en los años más cálidos y/o húmedos, las aves adelantaron el momento de la migración. Nuestros resultados aumentan la comprensión de cómo los factores intrínsecos y extrínsecos influyen en el momento anual de la migración otoñal. Además, nuestros hallazgos se suman a la creciente evidencia de que el cambio climático ha alterado el momento de la migración otoñal y que existen diferencias en cómo han respondido las especies y las poblaciones. Más trabajo es necesario para determinar si los cambios en el calendario de la migración otoñal se deben a la plasticidad del desarrollo, a la selección sobre la variación hereditaria o a una combinación de ambos factores.

**Key Words:** *climate change; fall migration; migratory timing; songbirds*

### INTRODUCTION

Anthropogenic climate change has been linked to changes in organism distribution, abundance, and morphology as well as timing of critical events throughout an organism's annual cycle (Van Buskirk et al. 2009, Ambrosini et al. 2019, Dunn 2019, Newton 2024). There is abundant evidence that timing of spring

migration in landbirds varies in response to both annual variation in temperature (Balbontin et al. 2009, Haest et al. 2018, Smith et al. 2022) and longer-term warming due to climate change (Lehikoinen and Sparks 2010, Ambrosini et al. 2019, Lehikoinen et al. 2019). Although a few studies have identified similar patterns for fall migrating landbirds, our understanding of their response

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to these changes is relatively poor (Gallinat et al. 2015, Brisson-Curadeau et al. 2019, Haest et al. 2019), especially in North America (Ellwood et al. 2015, Miller et al. 2015).

How a species responds to the effects of climate change may depend upon species-specific traits such as reproductive strategy, diet, and migration distance (Miller et al. 2015). For example, facultatively multi-brooded species that have additional clutches following an early spring could delay fall migration (Møller 2007, Ellwood et al. 2015, Newton 2024) while single-brooded species, which depart the breeding grounds after the first brood has matured, may shift the annual cycle earlier in years with warmer springs (Ellwood et al. 2015). In support of this hypothesis Ellwood et al. (2015) found that the number of broods produced in a breeding season was positively associated with fall passage timing. However, Van Buskirk et al. (2009) found no evidence that the number of clutches produced in a year influenced fall migratory timing.

Further, as climate influences primary productivity and food resources (thought to be the ultimate driver of migratory behavior; Miller et al. 2015, Newton 2024), variation in climate is predicted to influence migratory timing differently depending upon diet as climate should influence availability of food types, such as seeds, arthropods, or fruit differently (Miller et al. 2015, Newton 2024). For example, Miller et al. (2015) found relationships between annual variation in climate, fall migratory timing, and energetic condition and that diet was associated with both the strength and direction of these relationships.

There is also evidence that geographic location, intrinsic factors such as age and sex, and extrinsic factors such as temperature and precipitation influence both annual and long-term trends in migratory timing (Gordo 2007, Bitterlin and Van Buskirk 2014, Smith et al. 2022, Newton 2024). For example, relative locations of breeding or wintering grounds have been associated with timing of migration and the magnitude of long-term change in timing for spring (Sokolov et al. 1999, Jenni and Kéry 2003, Thorup et al. 2007) and to a lesser extent, fall migration (Ellwood et al. 2015, Miller et al. 2015). Additionally, the influence of age and sex on migratory timing is better understood for the spring (e.g., dimorphic males and older birds tend to precede females and younger individuals in many species; Rubolini et al. 2004, Kokko et al. 2006, Newton 2024), than the fall (Lehikoinen et al. 2017, Newton 2024). Age- and sex-related differences in breeding, *en route* or wintering ecology may result in differential timing of these demographic groups. For example, differences in autumn molt strategies (Jenni and Winkler 2020, Newton 2024) or acquisition of food resources (Woodrey 2000) may result in age- or sex-related differences in onset and timing of migration.

Multi-year, multi-species data sets collected from the same location are especially useful in addressing questions about general trends in songbird migration. Of particular interest are changes in migratory timing associated with climate change, about which we know relatively little during fall migration. With this in mind we used multi-year data sets to look for evidence that (1) one or more species have exhibited change in the timing of fall migration over the duration of our study, (2) one or more geographic (wintering location), intrinsic (age, sex, diet, number of broods in a season), or extrinsic (temperature or precipitation)

factors influenced annual migratory timing, (3) precipitation and temperature experienced by fall migrating landbirds using our site during stopover changed, and (4) the proximity of our study site to that of Ellwood et al. (2015, Manomet Center for Conservation Sciences, Manomet Massachusetts ~430 km east of our site) and Van Buskirk et al. (2009, Powdermill Nature Reserve, Rector Pennsylvania, ~340 km west of our site) permitted us to compare multi-year change in fall migratory timing in a suite of species captured at all three sites to investigate regional responses to climate change.

## METHODS

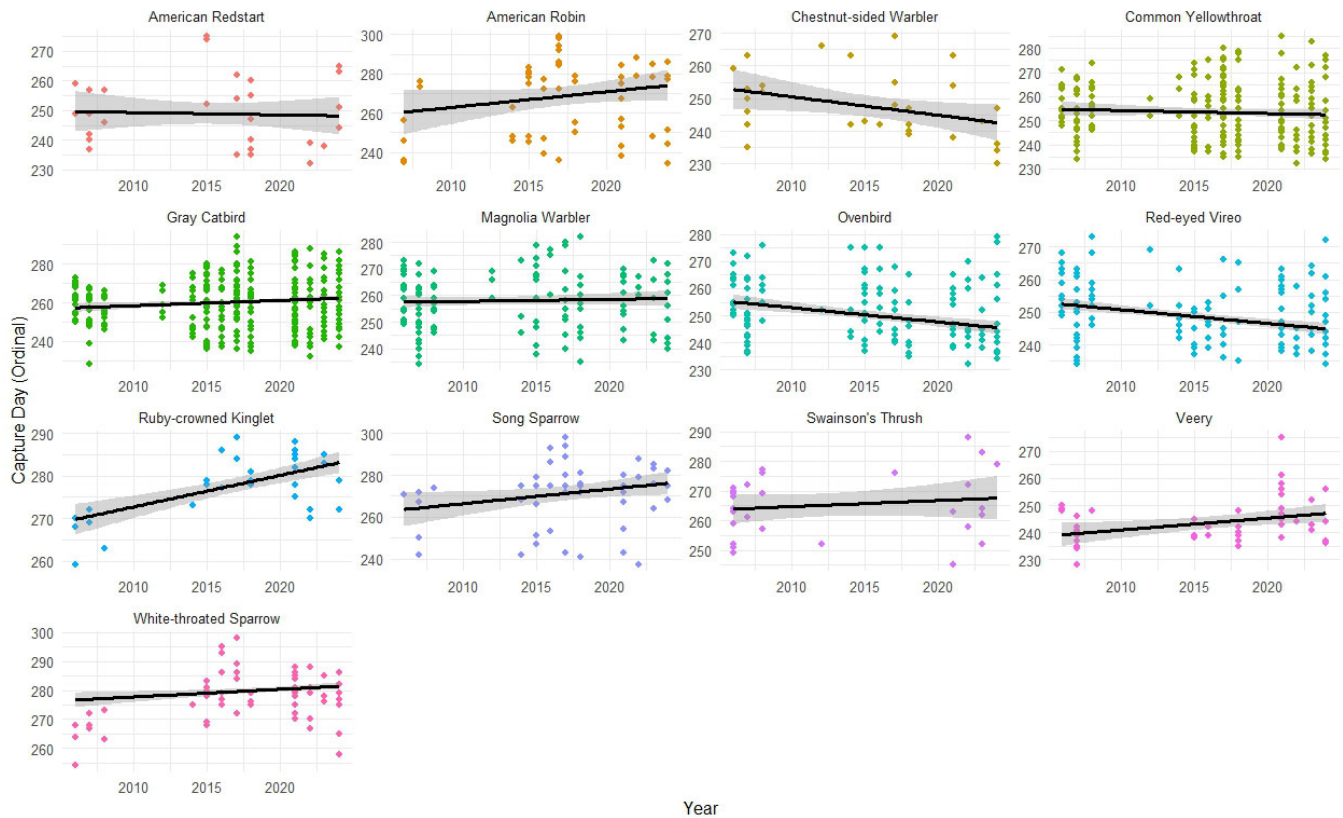
### Study area and field methods

We collected data during 13 fall migratory periods across three netting locations over a period spanning 19 years (2006–2024) from 13 species (Fig. 1, Table A1.1) using our upland shrub-dominated sites both within (2014–2018, 2021–2024) and adjacent (2006–2008, 2012) to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA (41.55° N, 75.71° W). All netting locations were within 1.8 km of each other, consisting of upland shrub habitat resulting from similar anthropogenic history with elevation ranging from 305 to 360 m. These sites were approximately 25–40 years post agriculture, containing a mix of exotic (primarily honeysuckle [*Lonicera* spp.] and native shrubs (primarily dogwood [*Cornus* spp.]). The site also held a small number of saplings and adults of most tree species found in nearby forested habitat.

We captured birds during fall migration (~second week of August through mid-October), operating between 10 and 16 permanently positioned mist-nets, checking nets at 30-minute intervals. We captured birds from sunrise through between 10:00 and 11:00 am though did not capture birds when air temperature was below 3 °C or there was rain. For each individual we recorded species, age as either hatch year (HY: a young individual hatched within the last few months) or after hatch year (AHY: an individual at least one year old; Pyle 2022). We used the 6-point scale of Helms and Drury (1960) to categorize amount of visible subcutaneous fat, scored extent of body molt using the protocol of DeSante et al. (2024), recorded mass, tail length, wing chord, weigh time, and capture date. We recorded weigh time as the time a bird was weighed just prior to release. We banded birds with a U.S. Geological Service aluminum leg band and measured recaptures without reference to previous records. Further, because overlap between the last stages of body molt and the first stages of migration occurs regularly in time-constrained birds (Jenni and Winkler 2020) we included both birds with no or minimal body molt (trace, very few feathers molting anywhere on the body; see DeSante et al. 2024) in our analysis, including body molt score as part of the model.

As part of a separate project, we captured birds during spring migration into the early breeding season. This permitted identification of individuals breeding at our site (e.g., presence of a brood patch for females or obvious cloacal protuberance for males). We excluded these verified breeding individuals as well as any HY captured in August with juvenile plumage, indicative of having hatched in the area (DeSante et al. 2024) to enhance the probability of including only migrants in our data set. In 2015 we

**Fig. 1.** Arrival day by species and year of birds captured at three sites in and around Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, over the study period (2006–2008, 2012, 2014–2018, 2021–2024) using raw capture data. See Table A1.1 for species scientific names.



began using DNA collected from blood sampling to determine sex for some sexually monomorphic species (Table A1.2; see Smith et al. 2023 for methodology). We used Billerman et al. (2022) to define diet, migratory distance, and typical number of broods produced within a season (all variables included in our model, Table A1.1). For all analyses we only use data collected the first time an individual was captured.

### Statistical analysis

#### *Multi-year change, intrinsic and extrinsic effects on migratory timing*

We used a mixed-model to test for evidence of multi-year change in timing of fall migration for 13 species using our site (Fig. 1, Table A1.1). We chose these species after examining species-specific histograms of capture dates. The empirical distribution for each was reasonably symmetric with consistently low values at the tails relative to the means, suggesting that our sampling captured the full range of migration. We modeled capture date (response variable) using the lmer function from package lme4 (Bates et al. 2015). We included year (continuous, transformed to start at zero to facilitate model fitting), sex, age, number of potential broods in a season, diet, body molt score, migration distance (short or long), and temperature and precipitation during the fall migratory period within 200 km north of our study area.

We defined short-distance migrants as those species wintering primarily in the southern United States and long-distance migrants as species in which most or all individuals winter south of the United States (Van Buskirk et al. 2009, Billerman et al. 2022). Thus, we looked for multi-year change in timing of fall migration through our site while also looking for evidence that sex, age, number of broods in a season, diet, and annual fluctuations in temperature and precipitation (anomalies) experienced during the fall migratory period influenced passage timing. We also included a random intercept and slope for year and for each species as well as a random intercept for netting location to control for site. We compared results of a null model to the more complete (biological) model, evaluating fixed effects as the more complete model was better than the null (Table A1.3). We used the performance package (Lüdecke et al. 2021) to evaluate model assumptions, evaluated parameter significance using the Satterthwaite method in the R package lmerTest (Kuznetsova et al. 2017), and used package emmeans (Lenth 2023) to calculate and compare parameter estimates using Tukey post hoc tests for more than two groups. Finally, we used the language of evidence when interpreting our statistical results, as suggested by Muff et al. (2022).

### Temperature and precipitation

We used the package GSODR (Sparks et al. 2017) in R (version 4.3.3; R Core Team 2023) to access daily temperature and precipitation data (Global Surface Summary of the Day, U.S. National Centers for Environmental Information) from 2006 through 2024. For most species, our study location was included within the breeding range. Even so, many individuals likely bred some distance from our site, so in addition to using data collected from the Avoca Airport, ~25 km south of our study site, we downloaded temperature and precipitation data from weather stations at 200 km inclusive increments to 1400 km north of our study site, bounded by 70° W and 80° W. For example, data for the 1400 km increment included average temperature and precipitation for all stations within 1400 km from our site, including data from the Avoca Airport. This resulted in eight separate data sets. We then ran nine models, with one being a null model and the following eight mixed models using the same response variables using average yearly temperature and precipitation data collected from the different distance intervals. We chose the distance that best explained the response variable (capture day) by comparing Akaike information criterion (AIC) values for models of varying distance, with the model including temperature and precipitation data collected within 200 km of our site as best explaining the response variable (Table A1.3). We used this model in subsequent analyses to look for factors influencing the timing of fall migration through our study site.

We used package mgcv (Wood 2006) to run generalized additive models (GAMs) on the same temperature and precipitation data (within 200 km of our site) to look for evidence of multi-year change in average daily temperature, and precipitation amount during the fall migratory period. For these analyses both ordinal day and year were included as smoothing terms using thin plate splines to account for multi-year trends and to address nonlinearity. We evaluated model assumptions using the appraise function in package gratia (Simpson 2024) for the temperature analysis and package DHARMA (Hartig 2022) for the precipitation analysis.

## RESULTS

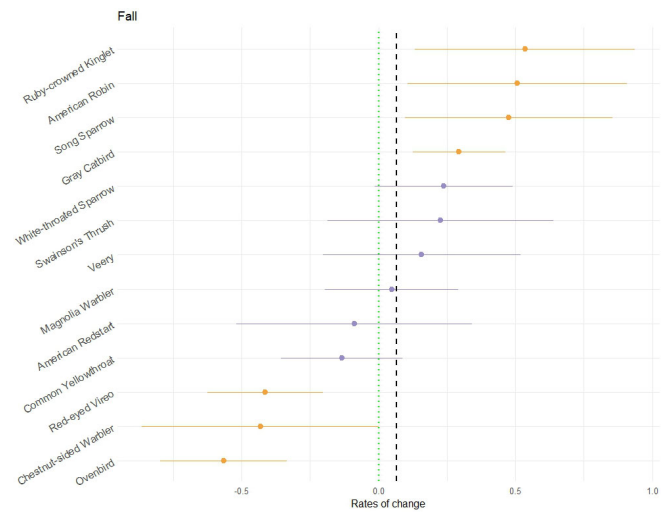
### Multi-year change in migration timing

We used 2181 individuals of 13 species to look for evidence of multi-year change in migratory timing controlling for year, site, and species (see Table A1.5 for summary model output). We found no evidence that, across all species included in our analysis, birds have delayed migratory timing ( $F_{1,15.1} = 0.2$ ,  $P = 0.64$ ,  $\beta = 0.07 \pm \text{SE } 0.14$ ). However, we found evidence of species-specific multi-year change such that Ruby-crowned Kinglet (*Corthylio calendula*; 5.4 days per decade), Gray Catbird (*Dumetella carolinensis*; 3.0 days per decade), American Robin (*Turdus migratorius*; 5.1 days per decade), and Song Sparrow (*Melospiza melodia*; 4.8 days per decade) delayed, whereas both Red-eyed Vireo (*Vireo olivaceus*; 4.1 days per decade) and Ovenbird (*Seiurus aurocapilla*; 5.7 days per decade) have advanced migratory timing through our site (Fig. 2, Table A1.6).

### Intrinsic and extrinsic effects on annual timing

We found no evidence that the number of potential broods ( $F_{1,7.6} = 0.76$ ,  $P = 0.44$ ) or diet ( $F_{2,8.1} = 0.19$ ,  $P = 0.83$ ) influenced timing of passage. We found little evidence that young birds were earlier

**Fig. 2.** Conditional means and corresponding 95% confidence intervals extracted from the linear mixed-effects model for the change in arrival day for birds captured during fall migration at three sites in and around Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA, over the study period (2006–2008, 2012, 2014–2018, 2021–2024). The dashed black vertical line corresponds to the community level average (with each species weighted by sample size), that is, the fixed-effect slope for change over time. The yellow points and bars indicate species in which the rate of change was greater than or less than the average rate of change for all species. See Table A1.1 for species scientific names.



than adults ( $F_{1,2,154.8} = 1.6$ ,  $P = 0.20$ ) and strong evidence that females were 2.3 days earlier than males ( $F_{1,2,153.0} = 4.8$ ,  $P = 0.008$ , Fig. 3a). We also found moderate evidence that short-distance migrants passed through our site 14.3 days later than long-distance species ( $F_{1,9.0} = 6.8$ ,  $P = 0.03$ ; Fig. 3b). Further, we found very strong evidence that birds with no indication of molt were captured 3.9 days later ( $F_{1,2,154.9} = 50.6$ ,  $P < 0.001$ ; Fig. 3c). We also found very strong evidence that both temperature ( $F_{1,1,621.8} = 19.3$ ,  $P < 0.001$ ,  $\beta = -1.07 \pm \text{SE } 0.24$ ), and precipitation ( $F_{1,2,128.2} = 16.3$ ,  $P < 0.001$ ,  $\beta = -1.16 \pm \text{SE } 0.24$ ) experienced during the fall migratory period advanced migratory timing.

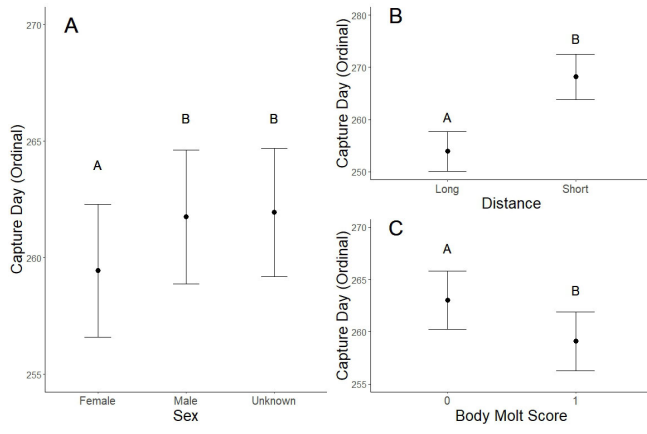
### Multi-year change in temperature and precipitation

We found very strong evidence that temperatures increased by 1.4 °C during the fall migratory period ( $F_{\text{effective df } 2.85} = 2.9$ ,  $P < 0.001$ , Fig. 4, Table A1.4) but no evidence that amount of precipitation changed ( $F_{\text{effective df } 1.99} = 1.0$ ,  $P = 0.45$ , Table A1.4).

## DISCUSSION

Our results add to the growing body of evidence that timing of fall migration is changing potentially in response to anthropogenic climate change and that differences exist in how species and populations respond. For example, we found evidence of species-specific responses in multi-year timing of several species using our site during fall migration. Both Red-eyed Vireo and Ovenbird advanced migratory timing while Ruby-crowned

**Fig. 3.** Comparisons of arrival day by sex (A), migration distance (B), and molt score (C) for birds captured during fall migration, Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA (2006–2008, 2012, 2014–2018, 2021–2024). Whiskers represent  $\pm 1$  SE and different letters represent statistical difference at  $P < 0.05$  within each figure.

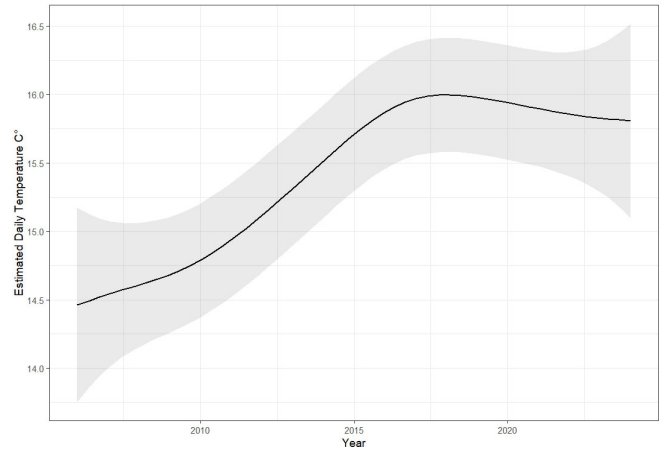


Kinglet, American Robin, Gray Catbird, and Song Sparrow delayed migratory timing through our site. Further, we found evidence of multi-year change in migratory timing in 100% (4 of 4) of the short-distance species and 33% (3 of 9) of the long-distances species included in our analysis, supporting the hypothesis that short distance species are reacting more strongly than long-distance migrants to climate change (Bitterlin and Van Buskirk 2014).

All short-distance species for which we detected multi-year change delayed timing through our site and most are multi-brooded (Billerman et al. 2022). This life-history characteristic could delay departure from the breeding grounds as longer breeding seasons due to increasing temperatures may facilitate more second broods (Mills 2005). Young from later broods typically migrate later and their parents may as well (Mills 2005). Further, optimal migration strategies likely differ between short-distance and long-distance species (Gordo 2007). For example, long-distance species may be less variable in migratory timing because they both move greater distances and have a longer migratory period relative to short-distance species (Brisson-Curadeau et al. 2019). More time spent *en route* increases the possibility of encountering poor migratory conditions (Rappole and Warner 1976, Brisson-Curadeau et al. 2019), which may be magnified if a long-distance migrant departs from northerly latitudes later in the fall. Hence staying longer on the breeding grounds may be too risky for long-distance species, even in good weather (Brisson-Curadeau et al. 2019).

We found evidence that three long-distance species changed migratory timing, and that the two species in which most (Ovenbird, see Porneluzi et al. 2020) or all (Red-eyed Vireo, see Cimprich et al. 2020) individuals winter in the tropics, have advanced passage timing through our site. Some have argued that migration in long-distance migrants is controlled by a rigid

**Fig. 4.** Multi-year change in temperature determined from Avoca Airport, ~25 km south of our study location and weather stations within 200 km north of our study location within and adjacent to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, bounded by 70° W and 80° W, during the fall migratory period, 2006–2024. Shaded area represents  $\pm 95\%$  CI.



endogenous program (Both and Visser 2001, Coppack and Both 2002), and there is strong evidence of endogenous control of migratory timing for at least some species (see, e.g., Knudsen et al. 2011). However, our results demonstrating multi-year change in long-distance species add to the growing body of literature showing that at least some of these species can adjust migratory timing.

Interestingly, we found that Gray Catbirds, typically classified as a long-distance species (e.g., Van Buskirk et al. 2009, Ellwood et al. 2015), have delayed migratory timing through our site. Although we do not know specifically where the catbirds using our site overwinter, there is evidence that a substantial number of individuals winter in southern North America (Smith et al. 2020) and that those breeding in northeastern Pennsylvania winter in southern Florida (Ryder et al. 2011, Somveille et al. 2021). Thus, we hypothesize that the multi-year delay we identified is because we captured individuals wintering in southern Florida, which are more variable in migratory timing, and are accruing advantages from staying longer on the breeding grounds, similar to what has been hypothesized for short-distance species.

Even as we found evidence that temperature has increased within 200 km of our study location during the fall migratory period, our results suggest that multi-year changes in precipitation or temperature during the fall migratory period are not a major cause of the changes in migratory timing we detected, at least in most of the species we examined. First, we found no evidence of multi-year change in precipitation amount during the fall migratory period. Second, our results relating annual temperature to fall migration timing indicate that overall birds advanced timing in warmer years. If the multi-year change in timing was due to long-term increases in temperatures during fall migration, we would expect species to have advanced migratory timing, not delayed.

We found that of the seven species exhibiting multi-year change, five delayed migratory timing. However, we did find that both Red-eyed Vireos and Ovenbirds advanced timing, perhaps partly in response to the multi-year increase in temperature during the fall migratory period.

There are other possible causes for our results which, unfortunately, our data do not permit us to examine. For example, a trend for declining tailwind speeds in northeastern North America could at least partially explain our results for several species with multi-year delay in migratory timing, as decreasing speed of favorable winds would decrease migration speed while increasing energetic expenditure (Horton et al. 2016). Further, increasing frequency of climate extremes, as has happened within Northern Hemisphere mid-latitudes over the past decades (La Sorte and Fink 2017), may cause delays in migratory timing.

#### **Intrinsic effects on annual migratory timing**

On average, short-distance migrants passed through our site 14.8 days later than long-distance species, adding support to the hypothesis that wintering location influences annual migration timing in North America (Bitterlin and Van Buskirk 2014, Miller et al. 2015). However, we found little evidence that age influenced migratory timing through our site. Carlisle et al. (2005), working in the western United States, found substantial support that young-of-the-year, which undergo an incomplete molt (only replacing body feathers) are able to depart the breeding grounds before adults, hence migrate earlier (adults undergo a complete molt, replacing both body and flight feathers; see Jenni and Winkler 2020, Newton 2024). However, support for this hypothesis in eastern North America is mixed, suggesting more species-specific responses. For example, Woodrey and Chandler (1997) examined fall capture dates across three sites finding evidence of consistent age-related differences in migratory timing in only two of five species, and in only one species (*Magnolia Warbler* [*Setophaga magnolia*]) young birds preceded adults. Further, Murray (1966), who looked at more than 40 species in coastal New Jersey, found that migration timing largely overlapped across age groups for most species. Finally, using a smaller data set and different analysis methods we (Smith and Hatch 2020) found no evidence of age differences in fall migratory timing in 100% (7 of 7) of species captured in northeastern Pennsylvania.

Our results suggest that females passed through our site a few days (2.3) earlier than males. Several hypotheses have been proposed to explain why females migrate earlier than males (see Newton 2024 and citations therein) including males may migrate later to prospect for or protect future breeding territories (rank advantage hypothesis) or depart after females to maximize mating probability (mate opportunity hypothesis). Females have also been hypothesized to leave the breeding grounds first to gain advantage in acquiring winter territories (winter territory acquisition hypothesis), or females might precede males to cover longer distance to reach more distant wintering grounds (longer migration hypothesis). Unfortunately, even as we identified sex differences in timing our data do not permit more detailed evaluation of the mechanisms causing these timing differences.

#### **Extrinsic effects on annual migratory timing**

We found evidence of annual flexibility in migratory timing due to precipitation and temperature experienced *en route*. For example, we found evidence that for every 1 mm per day increase in precipitation during the fall migratory period, birds were 1.2 days earlier. Further, for every 1 °C increase during fall migration birds were 1.0 days earlier through our site. Our migratory timing estimates differ from both Van Buskirk et al. (2009) and Ellwood et al. (2015), who found that fall migrants were later in warmer years. Although these differences add support to the hypothesis that within species, different populations experience and consequently respond to climate change differently (Mills 2005, Tøttrup et al. 2008), we cannot rule out discrepancies due to differences in study methodology. For example, we included temperature and precipitation from the fall migratory period (mid-August through mid-October) in our model whereas neither Van Buskirk et al. (2009) nor Ellwood et al. (2015) modeled precipitation. Further, studies covering shorter time spans may identify stronger or otherwise differing signals if those studies sampled birds in recent years, where there has been acceleration in climate warming (Mayor et al. 2017, Neate-Clegg and Tingley 2023); our study spanned 19 yrs (2006–2024) whereas Van Buskirk et al. (2009) used data collected over a 46 year period (1961–2006), and Ellwood et al. (2015) used data spanning 44 yrs (1969–2012).

We can think of at least two reasons that may explain our results indicating that birds advanced timing of fall migration in warmer or wetter years. First, invertebrate activity and abundance (Crossley et al. 2021, Schowalter 2022) is often positively influenced by temperature and precipitation. In warmer, wetter years increased abundance and activity of arthropods along with reduced thermoregulatory costs (Dawson et al. 1983) may reduce the time necessary for foraging to acquire sufficient energy stores to fuel migration, in turn advancing migratory timing.

Alternatively, if food supply was low, birds may have reduced time spent on stopover at a particular site, moving on to a site with more abundant food (Zaifman et al. 2017, Newton 2024). We previously provided evidence that our exotic-dominated study area does not provide high-quality habitat for most species either during spring (Smith and Hatch 2017) or fall (Smith and Hatch 2020) migration. More work is clearly necessary to better understand the negative associations we detected between temperature and precipitation during the fall migratory period and migratory timing.

#### **Species-specific site comparisons of multi-year change in timing**

More than 30% of the species we captured in common with Van Buskirk et al. (2009), working at Powdermill Nature Research ~340 km west of our site and 33% of the species we captured in common with Ellwood et al. (2015), working at the Manomet Center for Conservation Sciences, ~430 km east of our site, differed in response estimates ( $\beta$  values, see Table 1). Similar to Ellwood et al. (2015) we identified differences in multi-year trends among a number of the same species captured at both Manomet (Ellwood et al. 2015) and Powdermill (Van Buskirk et al. 2009) supporting the hypothesis that populations of the same species may respond differently to climate change, even over short geographic distances (Van Buskirk et al. 2009).

**Table 1.** A comparison of timing change estimates ( $\beta$ ) and estimate direction for species in common between this study in northeastern Pennsylvania (NEPA, Lackawanna State Park, Lackawanna County, Benton Township), Van Buskirk et al. (2009; Powdermill Nature Reserve, Stahlstown, Pennsylvania, USA), and Ellwood et al. (2015; Manomet Wildlife Research Center, Manomet, Massachusetts, USA).

Species	NEPA change	Powdermill change 50% passage	Compare to NEPA	Powdermill change 90% passage	Compare to NEPA	Manomet change	Compare to NEPA
Red-eyed Vireo <i>Vireo olivaceus</i>	-0.4139	0.0850	different	0.0720	different	0.14	different
Ruby-crowned Kinglet <i>Corthylio calendula</i>	0.5346	-0.0600	different	-0.0120	different	0.08	same
Gray Catbird <i>Dumetella carolinensis</i>	0.2945	-0.1450	different	0.0030	same	-0.16	different
Veery <i>Catharus fuscescens</i>	0.1572	-1.3810	different	-0.3940	different	0.11	same
Swainson's Thrush <i>Catharus ustulatus</i>	0.2261	0.0050	same	0.0640	same	0.23	same
American Robin <i>Turdus migratorius</i>	0.5064	0.2550	same	0.1850	same	0.17	same
White-throated Sparrow <i>Zonotrichia albicollis</i>	0.2377	0.1370	same	0.1700	same	0.16	same
Song Sparrow <i>Melospiza melodia</i>	0.4763	-0.0002	different	-0.0740	different	0.1	same
Ovenbird <i>Seiurus aurocapilla</i>	-0.5656	-0.4610	same	-0.0730	same	-0.05	same
Common Yellowthroat <i>Geothlypis trichas</i>	-0.1341	-0.1090	same	-0.0130	same	0.21	different
American Redstart <i>Setophaga ruticilla</i>	-0.0889	-0.6990	same	-0.0790	same	0.11	different
Magnolia Warbler <i>Setophaga magnolia</i>	0.0479	-0.0150	different	0.1100	same	0.13	same
Chestnut-sided Warbler <i>Setophaga pensylvanica</i>	-0.4313	-0.1640	same	-0.0360	same	-	-
		Percent different	46			31	33

Even as our results add to the growing evidence that climate change is influencing timing of fall migration, our data are not sufficient to determine the mechanisms involved. In addition to the hypotheses already discussed, changes in migratory timing could be a consequence of developmental plasticity, selection on heritable variation (microevolutionary change; see Gardner et al. 2011, Weeks et al. 2020), or some combination. More work is clearly necessary to determine the origin (plasticity vs evolution) of the measured responses to climate change in birds (Teplitsky and Charmantier 2019).

#### Author Contributions:

RJS conceived this study, RJS and MIH collected all field data, JMG (lead) and RJS analyzed the data. EL-N and AMR (laboratory) determined sex (DNA) for assorted monochromatic species, RJS wrote the manuscript, other authors provided editorial advice.

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#### Data Availability:

The data/code that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.15116258>. Ethical approval for this research study was granted by the University of Scranton Institutional Animal Care and Use Committee (IACUC) protocol #2-20.

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## APPENDIX 1

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## Supplementary Tables

**Table A1.1.** Sample size and life history characteristics for species included in the mixed model analysis looking for evidence of change in fall migratory timing though our study location within and adjacent to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024). Life history information from Billerman et al. (2022).

Species	Scientific Name	<i>n</i>	Winter Location	Migration Distance	Diet	Number of Broods
Red-eyed Vireo	<i>Vireo olivaceus</i>	251	South America	Long	arthropod, fruit	1
Ruby-crowned Kinglet	<i>Corthylio calendula</i>	45	North America	Short	arthropod	1
Gray Catbird	<i>Dumetella carolinensis</i>	626	Central America	Long	arthropod, fruit	2
Veery	<i>Catharus fuscescens</i>	54	South America	Long	arthropod, fruit	1
Swainson's Thrush	<i>Catharus ustulatus</i>	31	South America	Long	arthropod, fruit	1
American Robin	<i>Turdus migratorius</i>	62	North America	Short	arthropod, fruit	2
White-throated Sparrow	<i>Zonotrichia albicollis</i>	282	North America	Short	arthropod, seed, fruit	1
Song Sparrow	<i>Melospiza melodia</i>	67	North America	Short	arthropod, seed, fruit	3
Ovenbird	<i>Seiurus aurocapilla</i>	194	Central America	Long	arthropod	1
Common Yellowthroat	<i>Geothlypis trichas</i>	298	Central America	Long	arthropod	1
American Redstart	<i>Setophaga ruticilla</i>	40	Central America	Long	arthropod	1
Magnolia Warbler	<i>Setophaga magnolia</i>	197	Central America	Long	arthropod	1
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	34	Central America	Long	arthropod	1

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**Table A1.2.** Monochromatic species and sample sizes captured within and adjacent to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA, (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024) for which we determined sex using DNA.

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Common Name	Scientific Name	<i>n</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>	25
Gray Catbird	<i>Dumetella carolinensis</i>	214
Veery	<i>Catharus fuscescens</i>	17
Wood Thrush	<i>Hylocichla mustelina</i>	7
White-throated Sparrow	<i>Zonotrichia albicollis</i>	44

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**Table A1.3.** Comparison of models using daily weather data from weather stations within 200 km cumulative increments, bounded by 70° W and 80° W from our study location within and adjacent to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA, (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024). Data used for the distance 0 category come from the Avoca Airport, ~ 25 km south of our study site and are included in each interval estimate. Also included is the null model. AICc = Akaike information criterion.

Distance	K	AICc	$\Delta$ AICc
200	18	16,460.8	0.0
0	18	16,478.6	17.8
400	18	16,486.9	26.1
600	18	16,495.3	34.5
800	18	16,497.5	36.7
1000	18	16,498.6	37.8
1200	18	16,498.9	38.1
1400	18	16,499.2	38.3
Null	5	16,578.2	117.4

**Table A1.4.** Model output from generalized additive models examining multi-year change in temperature, and separately, precipitation during the fall migratory period (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024). Data used in these analyses were downloaded from all weather stations within 200 km north of our study site located within and adjacent to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, bounded by 70° W and 80° W.

	$r^2$	Parametric variables	$\beta \pm SE$	$t$	$P$
Temperature	0.314	Intercept	15.41 $\pm$ 0.123	125.50	< 0.001
Precipitation	0.00	Intercept	0.23 $\pm$ 0.02	13.37	< 0.001
		Smooth terms	Effective df	$F$	$P$
Temperature		s(Date)	1.01	366.39	< 0.001
		s(Year)	2.85	6.33	< 0.001
Precipitation		s(Date)	1.99	0.99	0.45
		s(Year)	1.60	0.24	0.79

**Table A1.5.** Results of a linear mixed-effects model evaluating change in arrival day (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024) for birds captured during fall migration at three sites in and around Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA.

<i>Predictors</i>	<b>Dependent Variable</b>		
	<i>Estimate</i>	<i>SE</i>	<i>P</i>
Intercept	257.5889	5.1409	<b>&lt;0.001</b>
Year	0.0651	0.1524	0.675
Sex (M)	2.3078	0.8957	<b>0.010</b>
Sex (U)	2.4943	0.9548	<b>0.009</b>
Age (HY)	-0.7403	0.5822	0.204
Number of Broods	-3.0501	4.2175	0.490
Body Molt Score 1	-3.9365	0.5549	<b>&lt;0.001</b>
Winter (North America)	14.2820	6.0325	<b>0.041</b>
Diet (Arthropod and Fruit)	-0.9612	4.7157	0.844
Diet (Arthropod, Seed and Fruit)	3.2749	8.2571	0.701
Fall Migration Temperature	-1.0649	0.2485	<b>&lt;0.001</b>
Fall Migration Precipitation	-1.1552	0.2873	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	110.0410		
$\tau_{00}$ species	36.0214		
$\tau_{00}$ site	1.6250		
$\tau_{11}$ species.year_zero	0.1658		
$\rho_{01}$ species	0.0089		
ICC	0.3942		
$N_{\text{species}}$	13		
$N_{\text{site}}$	3		
Observations	2181		
Marginal $R^2$ / Conditional $R^2$	0.269 / 0.557		

**Table A1.6.** Species estimates of multi-year change in timing of fall migration at three sites in and around Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA, (2006 – 2008, 2012, 2014 – 2018, 2021 - 2024). Rate of Change =  $\beta$  (slope parameter estimates), SE = standard error, CI = 95% confidence intervals.

Species	Rate of Change	SE	Lower 95% CI	Upper 95% CI	Change (Days per Decade)	CI Contains Zero?
Red-eyed Vireo	-0.4139	0.1073	-0.6242	-0.2037	-4.1394	No
Ruby-crowned Kinglet	0.5346	0.2048	0.1333	0.9359	5.3459	No
Gray Catbird	0.2945	0.0863	0.1254	0.4636	2.9452	No
Veery	0.1572	0.1840	-0.2035	0.5178	1.5716	Yes
Swainson's Thrush	0.2261	0.2108	-0.1871	0.6393	2.2609	Yes
American Robin	0.5064	0.2045	0.1055	0.9073	5.0639	No
White-throated Sparrow	0.2377	0.1283	-0.0137	0.4891	2.3768	Yes
Song Sparrow	0.4763	0.1933	0.0974	0.8552	4.7629	No
Ovenbird	-0.5656	0.1184	-0.7976	-0.3335	-5.6557	No
Common Yellowthroat	-0.1341	0.1130	-0.3556	0.0874	-1.3411	Yes
American Redstart	-0.0889	0.2191	-0.5184	0.3406	-0.8888	Yes
Magnolia Warbler	0.0479	0.1243	-0.1958	0.2915	0.4786	Yes
Chestnut-sided Warbler	-0.4313	0.2209	-0.8643	0.0017	-4.3130	Yes