



Avian Behavior, Ecology, and Evolution

Long-term changes in arrival timing and site functionality in two passerine species during spring migration in northeastern Pennsylvania, USA

Cambios a largo plazo en el tiempo de llegada y funcionalidad del sitio en dos especies de aves paseriformes durante la migración de primavera en el noreste de Pennsylvania, EE. UU.

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ABSTRACT. Although there is abundant evidence that migrant landbirds have modified their migratory timing in response to climate change, few studies have looked for evidence of long-term changes in site use or function, while even fewer studies have looked for differential effects on demographic groups within a species. Here, we analyze 18 years of daily weather data and 17 years of Gray Catbird (*Dumetella carolinensis*) and Common Yellowthroat (*Geothlypis trichas*) capture data to look for evidence of long-term changes in temperature and precipitation as well as arrival timing by species, sex, and age during spring migration in northeastern Pennsylvania, USA. We also determined whether there was evidence of protandry in Gray Catbirds, a sexually monochromatic species. Additionally, we investigated changes in site use, as indicated by long-term change in capture rates or rates of mass gain by age or sex in both species. Although average daily temperatures did not change, we found long-term changes in the amount and probability of precipitation during the spring migratory period (April–May). We also found that both species advanced their arrival timing (Gray Catbirds ~6.6 d/decade, Common Yellowthroats ~2.8 d/decade) and that advances in arrival timing varied by sex or age in both species. We found no evidence of protandry in Gray Catbirds. Further, we found evidence that site functionality changed for both species, as demonstrated by sex-related differences in yearly mass gain for birds using the study site. Understanding the phenological response of migratory species to climate change requires consideration of climate change effects across multiple temporal and geographic scales, and, as our results suggest, consideration of differential effects of climate change by demographic groups within species.

RESUMEN. A pesar de que tenemos evidencia abundante que las aves terrestres migratorias han modificado el tiempo de migración en respuesta al cambio climático, pocos estudios han buscado evidencias de cambios a largo plazo en el uso de sitios o su función, mientras que aún menos estudios han estudiado el efecto diferencial sobre grupos demográficos dentro de una especie. En este estudio, analizamos 18 años de datos climáticos diarios y 17 años de datos de capturas de *Dumetella carolinensis* y *Geothlypis trichas* en busca de evidencias de protandria en *D. carolinensis*, una especie sexualmente monocromática. Adicionalmente, determinamos si existe evidencia de cambios en el uso del sitio, como lo indican los cambios a largo plazo en las tasas de captura o ganancia de masa por edad o sexo en ambas especies. A pesar de que el promedio en la temperatura diaria no cambió, encontramos cambios a largo plazo en la cantidad y probabilidad de la precipitación durante el periodo de migración de primavera (Abril-Mayo). También encontramos que las dos especies han adelantado el tiempo de llegada (*D. carolinensis* ~6.6 d/década, *G. trichas* ~2.8 d/década) y que el adelantamiento en los tiempos de llegada varía por sexo y edad en ambas especies. No encontramos evidencia de protoandria en *D. carolinensis*. Mas aún, encontramos evidencia que la funcionalidad del sitio ha cambiado para las dos especies, como lo demostraron las diferencias relacionadas con el sexo en la ganancia anual en la masa de las aves utilizando nuestro sitio de estudio. Entender las respuestas fisiológicas de especies migratorias al cambio climático requiere consideración de los efectos del cambio climático a través de múltiples escalas temporales y geográficas, y, como nuestros resultados sugieren, consideración de efectos diferenciales del cambio climático por grupos demográficos dentro de especies.

Key Words: *avian migration; climate change; demographic groups; phenology; protandry*

INTRODUCTION

There is abundant evidence that migrant landbirds modify migratory timing in response to both annual variation in temperature (Balbontín et al. 2009, Haest et al. 2018, Smith et al. 2022) and longer term warming, i.e., climate change (see Lehikoinen and Sparks 2010, Ambrosini et al. 2019 and references therein), though there is considerable variation in responses among species and even among populations (Both and Visser 2001, Gordo et al. 2005, Rubolini et al. 2007). For example, numerous species arrive earlier at the breeding grounds (Saino et

al. 2004, Miller-Rushing et al. 2008, Smith et al. 2009) and leave earlier or later from the breeding grounds on fall migration (Jenni and Kéry 2003, Mezquida et al. 2007, DeLeon et al. 2011). While work continues in an attempt to understand this variation, research to date has mostly focused on the timing of arrival and relationships between arrival timing and changing climatic conditions at the breeding grounds (Fontaine et al. 2015). Fewer studies have looked for evidence of long-term changes in arrival timing combined with changes in site use or the energetics of site use as the climate changes (VanTol et al. 2021).

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Further, climate change and its consequences vary in both space and time (Ambrosini et al. 2019, Trenberth and Hurrell 2019), and this spatial and temporal heterogeneity may be especially problematic for migratory songbirds because of their dependence on spatially, temporally, and climatically disparate habitats during the migratory period and other stages of the annual cycle (Calvert et al. 2009, Fontaine et al. 2015). Thus, understanding the phenological response of migratory species to climate change requires the consideration of effects across multiple temporal and geographic scales (Calvert et al. 2009). Moreover, because conditions during any period of the migratory cycle have implications for subsequent periods (Marra et al. 1998, Norris et al. 2004, Rockwell et al. 2012), particular attention must be paid to how changing climatic conditions at locations throughout the migratory cycle are interrelated to understand how individuals and species will respond (Both 2010, Fontaine et al. 2015).

Because the energetics of migration are substantial (Moore 2018), the ability for a migrant to deposit fat while using a stopover site is critical (Schaub et al. 2008, Moore 2018). Migrant landbirds using high-quality stopover habitat will deposit fat, causing them to gain mass over the progression of the morning (Dunn 2002, Bontar et al. 2007) as they prepare for a subsequent night's migration (Moore and Kerlinger 1987, Moore 2018). Although estimating the direction and rate of mass change of individuals captured over the course of a morning is a commonly used metric to evaluate both the energetics at a stopover site (Winker et al. 1992, Newton 2008, Moore 2018) and the quality of that site (Dunn 2002, Smith and Hatch 2017), few studies have looked for changes in the energetics of site use by examining long-term changes in rates and direction of mass change as a consequence of climate change (VanTol et al. 2021).

Even fewer studies have looked for differential effects of climate change on migratory timing by age and sex within a species, as well as age- or sex-related differences in site use or function, even as sex- and age-related wintering and en route ecology may result in these different demographic groups experiencing the consequences of climate change differently (Neate-Clegg and Tingley 2023). For example, if a certain sex or age class is forced to use winter habitat that is more severely affected by climate change, these age or sex categories may suffer greater climate change consequences, in turn influencing factors such as overwinter survival, timing of departure from the wintering grounds, speed of migration, and timing of arrival and condition upon arrival at the migratory destination (Marra et al. 1998, Norris et al. 2004, Studds and Marra 2007, Rockwell et al. 2012). Further, climate-driven advances in migratory timing at the level of a species or among different demographic groups within a species might influence site use if birds eliminate some stops or choose alternate locations (VanTol et al. 2021), whereas climate-driven changes within a site (e.g., increasing precipitation) may influence site quality, in turn influencing a bird's ability to deposit fat.

Long-term avian capture and banding efforts provide information on species arrival and passage dates, rates of capture, fat stores, and mass (see VanTol et al. 2021). These efforts may also provide information on age and sex, which permits evaluation not only of species-specific long-term effects, but also by age and, depending upon the species, sex within a species. Similar to VanTol et al. (2021), we used a long-term (17-year; 2004–2019, 2021) avian

capture data set collected in northeastern Pennsylvania, USA to test for evidence of long-term change in (1) arrival dates by age and sex, (2) mass gain by age and sex, and (3) capture rates by age and sex in Gray Catbirds (*Dumetella carolinensis*) and Common Yellowthroats (*Geothlypis trichas*), the two most commonly captured species at our study site. Further, although there is substantial research (e.g., Morbey and Ydenberg 2001, Rubolini et al. 2004, Kokko et al. 2006) providing evidence that spring-migrating males precede females (protandry) in sexually dichromatic species, including Common Yellowthroats (Smith et al. 2022), much less is known about protandry in sexually monochromatic species such as Gray Catbirds. Our data set included a large number of Gray Catbirds of known sex, permitting us to look for evidence of sex-based differences in the timing of Gray Catbird arrival at our site. Finally, we used a long-term (18-year; 2004–2021) daily temperature and precipitation data set collected during the spring migratory period to look for evidence of changes in temperature or precipitation in northeastern Pennsylvania.

METHODS

Study area, field methods, and species

We collected data on Gray Catbirds and Common Yellowthroats using upland shrub-dominated habitat both within (2014–2019, 2021) and immediately adjacent (2004–2013) to Lackawanna State Park, Lackawanna County, Benton Township, northeastern Pennsylvania, USA (41.55° N, 75.71° W). We chose these species because we captured ≥ 9 individuals across all years of study. Study sites (area sampled by our nets) ranged from approximately 0.7–1.0 ha, all sites were within 1.8 km of each other, and elevation ranged from 305–360 m. Shrub habitat was approximately 25–40 years post agriculture, contained a mix of exotic (primarily honeysuckle *Lonicera* spp.), native shrubs (primarily dogwood *Cornus* spp. and, prior to infestation by exotic viburnum leaf beetle *Pyrrhalta viburni* in 2007, arrowwood viburnum *Viburnum dentatum*; Smith and Hatch 2017), and a few saplings of most tree species found in nearby forested habitat. We captured birds through both the spring migratory period and into the breeding season (from the third week of April through the second week of June). This approach permitted us to estimate arrival day at our site and, for some Gray Catbirds, determine sex based on breeding morphology (see *Methods: Gray Catbird sex determination*). We operated between 10 and 16 permanently positioned mist-nets, checking nets at 30-min intervals. Nets were opened by sunrise and remained open until between 10:00 and 11:00 am. We did not capture birds when the air temperature was below 3°C or when there was rain. For each individual captured, we recorded species, age, and sex (Pyle 1997), mass, visible subcutaneous fat using the 6-point scale of Helms and Drury (1960), along with wing cord, tail length, weigh time, and date. Weigh time was recorded as the time a bird was weighed just prior to release. Birds were banded with a U.S. Geological Service aluminum leg band, and recaptures were measured without reference to previous records. Similar to numerous other studies (e.g., Dunn 2002, Holzschuh and Deutschlander 2016, Neate-Clegg and Tingley 2023), our data set does not permit us to discriminate individuals arriving and breeding in the area (local breeders) from birds using the sites prior to continuing migration.

Table 1. Mixed models used to evaluate arrival timing and mass change rates for Gray Catbirds and Common Yellowthroats captured in and around Lackawanna State Park, Lackawanna County, northeastern Pennsylvania, USA, in 2004–2019 and 2021. Bird band number was included as a random effect to control for repeated captures across years. We previously reported sex-related (Common Yellowthroat) and age-related (Common Yellowthroat, Gray Catbird) effects on arrival timing, so we only include sex as a main effect in the Gray Catbird model.

Species	Response variable	Model
Gray Catbird	Arrival day	Arrival day ~ year + sex + year:age + year:sex
Common Yellowthroat	Arrival day	Arrival day ~ year + year:age + year:sex
Gray Catbird	Yearly mass change rate	Mass ~ sex:minutes since sunrise:year + age:minutes since sunrise:year
Common Yellowthroat	Yearly mass change rate	Mass ~ sex:minutes since sunrise:year + age:minutes since sunrise:year

Gray Catbird sex determination

Because Gray Catbirds are sexually monochromatic, we used a combination of morphological evidence and DNA to assign sex. First, extending our field season into the breeding period permitted us to use morphological evidence (presence of a brood patch for females or an obvious cloacal protuberance for males) to determine sex. Beginning in 2015, we augmented this approach by using DNA collected from blood sampling. Blood samples collected in the field were kept on ice until they could be preserved with Queen's buffer (Seutin et al. 1991) and stored at -20°C . DNA was extracted using Qiagen DNEasy Blood & Tissue kits (Venlo, Netherlands; Covino 2015). Birds were sexed by amplifying a marker from the chromodomain helicase DNA-binding (CHD) gene, located on the sex chromosomes of birds (resulting in two distinct products for the heterogametic females and one for the homogametic males; Griffiths et al. 1996, 1998). We used the P2 and P8 primers (Griffiths et al. 1996, 1998), and PCR was performed using Promega GoTaq DNA Polymerase (Madison, Wisconsin, USA), with each reaction including 5 μL Green GoTaq Reaction Buffer, 2.5 μL MgCl_2 , 1 μL $10\times$ P2 primer, 1 μL $10\times$ P8 primer, 0.1 μL Taq, and 13.4 μL deionized water. The PCR cycle started with 4 min at 95°C followed by 34 cycles of 30 s at 95°C , 30 s at 50°C , and 45 s at 72°C , finishing with 4 min at 72°C . PCR products were run out on a 1.5% agarose gel stained with SYBRSafe, and bands were visualized using a Bio-Rad Gel Doc XR+.

Statistical analyses

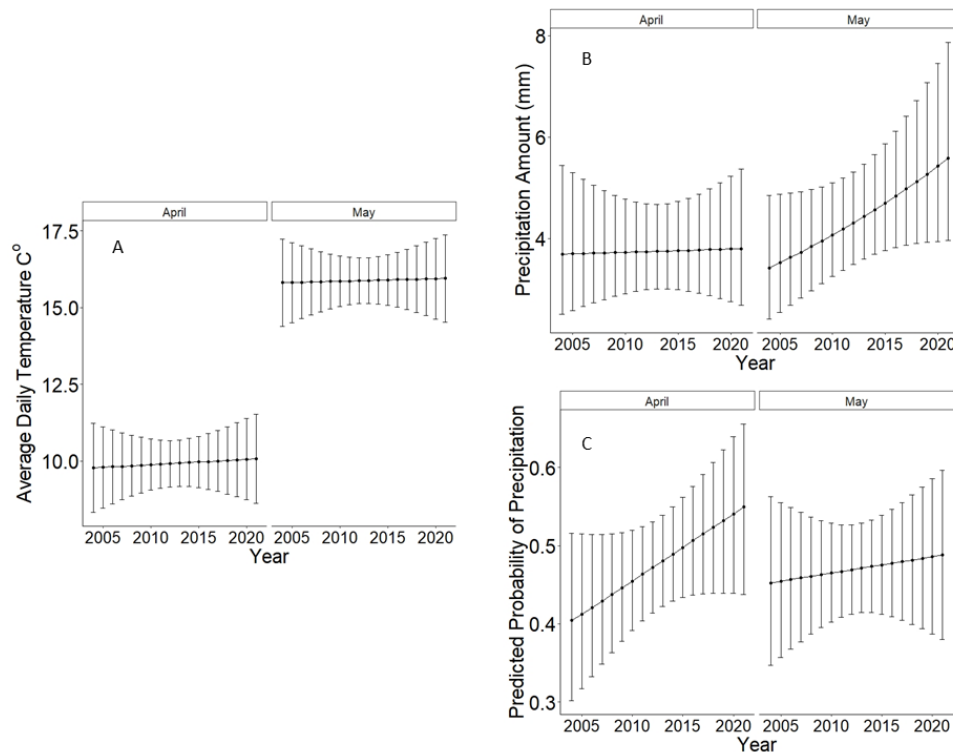
We used R version 4.1.2 (R Core Team 2021) to download daily weather summary data and to perform all statistical analyses. We used the GSODR package (Sparks et al. 2017) to access daily temperature and precipitation data (Global Surface Summary of the Day, U.S. National Centers for Environmental Information) from 2004 through 2021, April and May (Gray Catbirds and Common Yellowthroats begin arriving at our site in late April, although most birds arrive in early May), collected at the Scranton Wilkes Barre Airport in Avoca, Pennsylvania, USA, approximately 25 km south of the study location. We used generalized linear mixed-effects models to summarize average daily temperature for the months of April and May via the glmmTMB package (Brooks et al. 2017), which permitted us to incorporate a first-order autoregressive covariance structure through a random effects term (all temperature and precipitation data were temporally autocorrelated). To summarize precipitation, we used a hurdle modeling approach (Zuur and Ieno 2016), again using the glmmTMB package to correct for temporal autocorrelation, modeling days with and without precipitation using a generalized mixed model with binomial

distribution. Separately, we used a generalized mixed model with gamma distribution to model daily precipitation amount for only those days during which precipitation occurred. For all models, we included the cumulative days from the first day of the study (scaled to a mean of zero), month (April or May), and an interaction between time and month as the predictor variables.

We used a linear mixed-model approach (lme in the nlme package, Pinheiro et al. 2022) to evaluate the effect of year on arrival day and rate of mass gain in Gray Catbirds and Common Yellowthroats captured during the spring migratory period. To interpret the scale of effect sizes more directly, we shifted the year variable in each model to start at zero. This procedure preserved the distance of one year, that is, the scale of change in time between values in the independent variable, while allowing for a direct interpretation of change over time starting from time zero. We delineated the endpoint of spring migration for each species by examining histograms of first captures, determining the date when first captures dropped to zero (Smith et al. 2022). Further, we only used data collected the first time an individual was captured within a year, and entered band number as a random effect because we captured a small proportion of individuals in multiple years (Cadahía et al. 2017). Using first captures within a season is commonly used when studying landbird migration (e.g., Dunn 2002, Marra et al. 2005, Bonter et al. 2007, Van Buskirk et al. 2009, Ramirez et al. 2022), maximizing the likelihood of capturing birds soon after their arrival at a site. Because we previously reported on sex (Common Yellowthroat) and age-related (Common Yellowthroat, Gray Catbird) differences in arrival timing at our site in northeastern Pennsylvania (Smith et al. 2022), we did not include age or sex as main effects in the models looking for effects of year on arrival day in Common Yellowthroats, nor did we include age as a main effect when evaluating arrival timing in Gray Catbirds (Table 1).

To test for long-term changes by age and sex in the rate of mass gain at our site (VanTol et al. 2021), we first used the StreamMetabolism package (Sefick 2016) to obtain daily sunrise times, then calculated a new variable to represent the time elapsed since sunrise (minutes since sunrise) by subtracting sunrise time from an individual's weigh time. Because we were interested in modeling change in mass change rates across years by age and sex, we only included two three-way interactions in models (Table 1). If birds gained mass at our site, we expected a positive relationship between mass at first capture and the time elapsed since sunrise (Dunn 2000). Further, if there were changes in the energetics of site use by sex or age, we expected that rate of mass gain by year would vary among these demographic groups. Using

Fig. 1. Yearly average daily temperature (A), amount of precipitation (B) and probability of precipitation (C) in April and May, 2004–2021 at Scranton Wilkes Barre Airport, northeastern Pennsylvania, USA. Whiskers represent $\pm 95\%$ confidence intervals.



the lme approach permitted us to account for heterogeneity and temporal autocorrelation as necessary (Zuur et al. 2009). Finally, we set up null models with either arrival day or mass as the dependent variable and band number as a random effect. We then compared each null model against the more complete (biological) model (Table 2), evaluating the fixed effect estimates if the more complete model was better than the null.

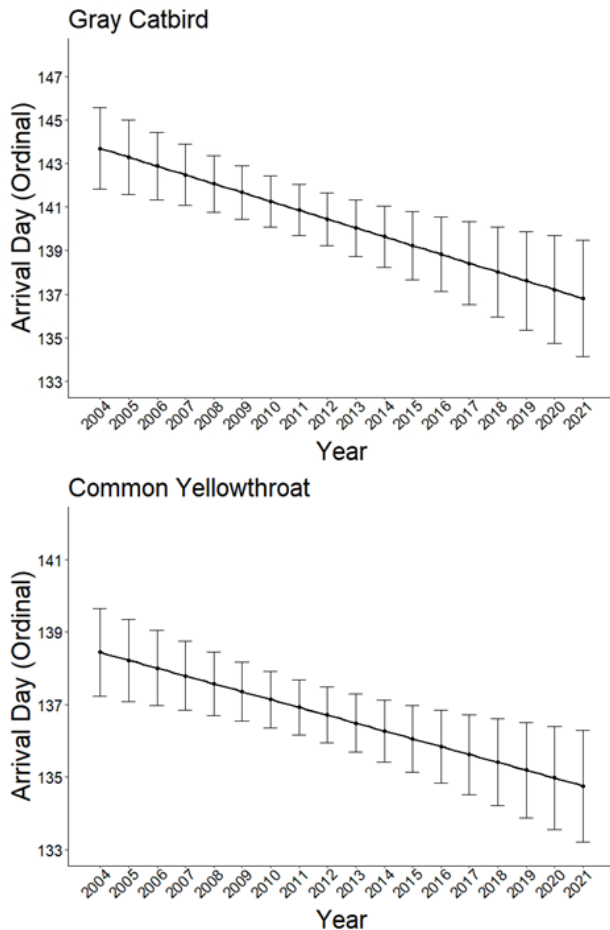
We used the mgcv package (Wood 2006) to run generalized additive models (GAMs) to look for long-term changes in capture rate by age or sex across years. For this analysis, we used capture rates (birds per 100 net-hours) estimated for each category (age, sex) for Gray Catbirds and, separately, Common Yellowthroats. Each year, we began capturing birds (species other than Gray Catbird or Common Yellowthroat) in mid-April, before Gray Catbirds or Common Yellowthroats arrived at the site. Consequently, there are a number of days for which capture rate was zero because individuals had yet to arrive at the site. For this analysis, we removed those days and used the date we captured the first individual, within a year, to demark the beginning of migration for each species. Following the approach of Gavin Simpson (Modelling seasonal data with GAMs: <https://fromthebottomoftheheap.net/2014/05/09/modelling-seasonal-data-with-gam/>), we created a time variable by converting date to a numerical variable and dividing by 1000. We also created a seasonal variable that represented month and day as a numerical value to account for seasonal variation. Both the time and seasonal variables were included as smoothing terms using thin plate splines by age and sex to account for seasonal or long-term trends and to address nonlinearity. For each species, we ran

Table 2. Comparisons of null models to more complete (biological) models used to test for evidence of long-term change in arrival day and yearly mass change rate for Gray Catbirds and Common Yellowthroats captured in and around Lackawanna State Park, Lackawanna County, northeastern Pennsylvania, USA, in 2004–2019 and 2021. AIC = Akaike information criterion.

Species	Model type	Response variable	<i>K</i>	AICc	Δ AICc
Gray Catbird	Biological	Arrival day	8	3374.0	6.0
	Null	Arrival day	3	3380.0	
Common Yellowthroat	Biological	Arrival day	7	3501.3	46.6
	Null	Arrival day	3	3548.0	
Gray Catbird	Biological	Mass	55	1830.3	113.4
	Null	Mass	3	1943.7	
Common Yellowthroat	Biological	Mass	51	875.0	59.0
	Null	Mass	3	934.0	

gamma models using only those days with positive capture rates. We included linear parametric terms for sex and age to look for differences in capture rate, as well as an interaction between age and scaled time and another interaction between sex and scaled time to look for long-term changes in capture rate by each demographic category. We evaluated model assumptions for mixed models as suggested by Zuur et al. (2009) and used the DHARMA package (Hartig 2022) to evaluate model assumptions for generalized mixed models and GAMs. We used the emmeans package (Lenth 2023) to calculate parameter estimates, and the

Fig. 2. Change in arrival day over time in Gray Catbirds and Common Yellowthroats, northeastern Pennsylvania, USA. Whiskers represent $\pm 95\%$ confidence intervals.



emmeans function in emmeans to estimate and compare trends in arrival timing. Finally, we use the language of evidence, as suggested by Muff et al. (2022), when interpreting our statistical results.

RESULTS

Average temperatures did not appear to change over the years encompassed by our study (Fig. 1A). Although the amount of precipitation did not change in April, it increased in May (Fig. 1B), when most Gray Catbirds and Common Yellowthroats were captured. Further, the probability of precipitation increased across years and did so at a higher rate in April than in May (Fig. 1C).

We captured 441 Gray Catbirds and 500 Common Yellowthroats of identifiable age and sex, and recaptured 92 Gray Catbirds and 56 Common Yellowthroats in subsequent years. For Gray Catbirds, there was no evidence of a difference between male-to-female ratio identified via morphology vs. DNA ($\chi^2 = 2.0$, $df = 1$, $P = 0.16$). In all instances, the more complete model was better than the null (Table 2). We found very strong evidence that Gray

Catbirds arrived earlier in later years ($F_{1,89} = 10.9$, $P = 0.001$; Fig. 2), although there was no evidence that sex influenced arrival timing ($F_{1,347} = 1.4$, $P = 0.23$). Our results provide weak evidence that older birds advanced their arrival timing faster than did younger birds ($F_{1,89} = 3.4$, $P = 0.07$; Table 3) though there is little evidence that female Gray Catbirds advanced arrival timing faster than males ($F_{1,89} = 2.3$, $P = 0.11$; Table 3). We found very strong evidence both that Common Yellowthroats captured in later years arrived earlier ($F_{1,53} = 9.2$, $P = 0.004$; Fig. 2) and that older birds advanced their arrival timing faster than did younger birds ($F_{1,53} = 22.3$, $P < 0.001$; Table 3). Further, we found strong evidence that Common Yellowthroat males advanced their arrival timing faster than did Common Yellowthroat females ($F_{1,53} = 7.2$, $P = 0.01$; Table 3).

Table 3. Interaction results from mixed-model analyses evaluating change in arrival day by age (ASY = after second year or SY = second year) and sex for Gray Catbirds and Common Yellowthroats using habitat in and around Lackawanna State Park, Lackawanna County, northeastern Pennsylvania, USA, in 2004–2019 and 2021. β = slope parameter estimate, SE = standard error, t = test statistic for the comparison of slope of change across years.

Species	Category	<i>N</i>	$\beta \pm SE$	<i>t</i>	<i>df</i>	<i>P</i>
Gray Catbird	ASY	207	-0.529 ± 0.146	1.9	89	0.07
	SY	234	-0.283 ± 0.119			
	Female	171	-0.576 ± 0.187	1.5	89	0.14
	Male	270	-0.237 ± 0.132			
Common Yellowthroat	ASY	284	-0.409 ± 0.077	4.7	53	< 0.001
	SY	216	-0.025 ± 0.081			
	Female	154	-0.101 ± 0.085	2.7	53	0.01
	Male	346	-0.332 ± 0.075			

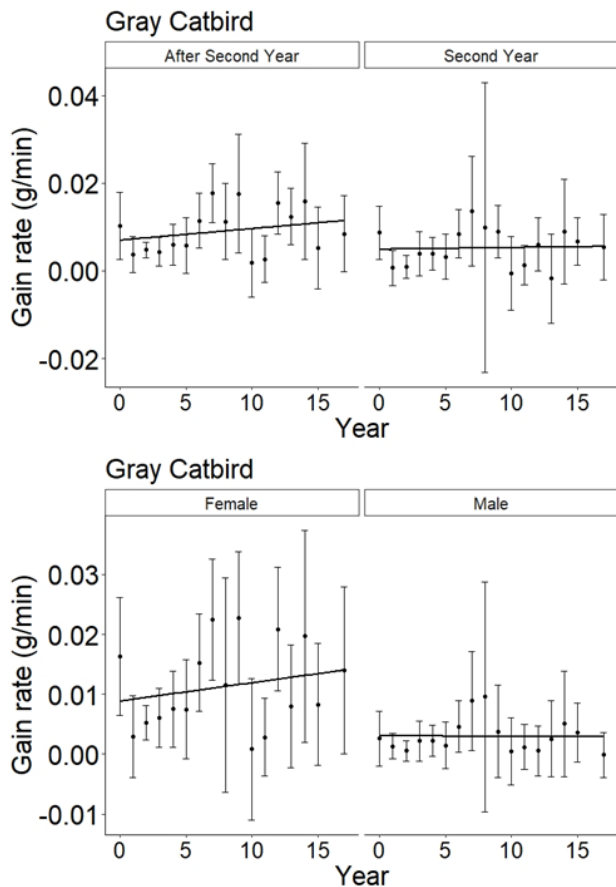
We found very strong evidence that female Gray Catbirds increased their mass gain rate across years, whereas males did not ($F_{34,40} = 3.6$, $P = 0.0001$; Fig. 3) and weak evidence that gain rates differed by age ($F_{17,40} = 1.8$, $P = 0.06$; Fig. 3). We also found moderate evidence that mass gain rates increased across years in Common Yellowthroat males ($F_{32,5} = 4.9$, $P = 0.04$) but not in females (Fig. 4). Finally, we found no evidence that mass gain rates were differentially influenced by age across years ($F_{16,5} = 2.0$, $P = 0.24$).

Although we found evidence of nonlinear effects of time since the start of the study on capture rate in Gray Catbirds, we found no evidence that capture rates differed by age or sex (Table 4). We also found evidence of nonlinear effects of time on capture rate in Common Yellowthroats (Table 4). For this species, capture rate was higher for older than younger birds and higher for males than females (Table 4).

DISCUSSION

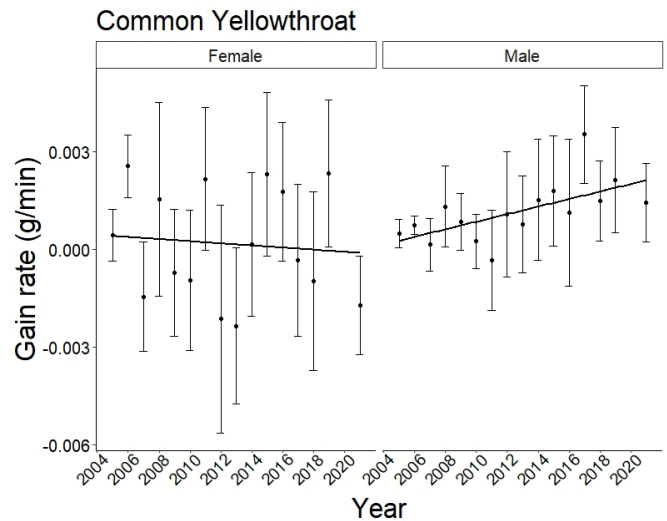
We found evidence that spring arrival at the site advanced by ~6.6 d/decade for Gray Catbirds and ~2.8 d/decade for Common Yellowthroats, and that changes in arrival timing varied by sex and/or age in both species. Although we found no evidence that site use in either species changed in time (capture rates by age and sex for each species did not change in time), we did find evidence for sex-related differences in yearly mass gain rates.

Fig. 3. Average yearly mass change rates by sex and age in Gray Catbirds, northeastern Pennsylvania, USA. For these analyses, year was shifted to start at zero to facilitate modeling, i.e., year 0 = 2004, year 15 = 2018. Whiskers represent \pm 95% confidence intervals.



We previously demonstrated that, on average, spring migrating male Common Yellowthroats arrived at the site before females did (protandry; Smith et al. 2022), though we found no evidence of protandry in Gray Catbirds known to have nested at the site (Hatch and Smith 2009). We also found age differences in arrival in both Gray Catbirds and Common Yellowthroats such that older birds arrived before younger birds (Smith et al. 2022), similar to numerous other studies (Stewart et al. 2002, Newton 2008, Cadahía et al. 2017). Protandry is well documented in dimorphic species (Rubolini et al. 2004), though much less is known about arrival timing by sex in sexually monochromatic species (Rubolini et al. 2004, Edwards and Forbes 2007, Newton 2008), likely because of the difficulty in determining the sex of a sexually monochromatic species arriving on breeding grounds or passing through a stopover site. Our study methods (capturing birds early in the breeding season and using breeding morphology to assign sex combined with using DNA to determine sex) provided the opportunity to evaluate arrival timing in a sexually monochromatic species (Smith et al. 2020). Here, we use a much larger data set (171 vs. 27 females, 270 vs. 56 males) over a much longer period (17 yr vs. 3 yr) to obtain results similar to those of

Fig. 4. Average yearly mass change rates by sex in Common Yellowthroats, northeastern Pennsylvania, USA in 2004–2019 and 2021. Whiskers represent \pm 95% confidence intervals.



Hatch and Smith (2009), i.e., no evidence that males and females differ in their timing of arrival at the site. Our results support the hypotheses that the degree of sexual dichromatism is related to protandry (Rubolini et al. 2004) and that selection for early arrival in Gray Catbirds occurs similarly in both sexes (Edwards and Forbes 2007).

Our overall findings that both Gray Catbirds and Common Yellowthroats using the site advanced their spring migratory timing add to the substantial literature demonstrating advanced spring migration timing in European (Rubolini et al. 2007, Thorup et al. 2007, Horton et al. 2020) and North American landbirds (Van Buskirk et al. 2009, Zaifman et al. 2017, Horton et al. 2020, Neate-Clegg and Tingley 2023). Our estimates of advancing migratory timing in Gray Catbirds and Common Yellowthroats are similar to the recently published estimates of Mayor et al. (2017; Gray Catbirds ~4 d/decade), Jones and McCormick (2021; Gray Catbirds ~6 d/decade), Mills (2005; Common Yellowthroats ~4 d/decade), and Jarjour et al. (2017; Common Yellowthroat ~2 d/decade); they differ somewhat from the findings of Miller-Rushing et al. (2008; Gray Catbird ~1 d/decade and Common Yellowthroat ~0.8 d/decade) and Jones and McCormick (2021), who found no evidence that Common Yellowthroats advanced their arrival timing.

Estimates of advanced timing in spring migration often show variation among studies, with at least some variation attributable to differences in study methods, e.g., using first arrival date vs. estimated median or mean arrival date, or the temporal scale of the study (Kolářová et al. 2017). For example, studies covering shorter time spans may identify stronger signals of advancement if those studies sampled birds in recent years, when there has been an acceleration in climate warming (Mayor et al. 2017, Neate-Clegg and Tingley 2023). Regardless, despite the variation in magnitude of individual trend estimates when comparing our results to those of other studies, most studies found evidence for advanced phenology in both species and attributed these advances to climate change.

Table 4. Model output from a generalized additive model of parametric variables relative to capture rate for Gray Catbirds and Common Yellowthroats during spring migration, northeastern Pennsylvania, USA, in 2004–2019 and 2021. The time variable was scaled in the analysis and represents the number of days from the first day of the study. β = slope parameter estimate, SE = standard error, t = test statistic.

Species	Parametric variables	$\beta \pm SE$	t	P
Gray Catbird	(Intercept)	0.978 \pm 0.073	13.5	< 0.001
	Age (After second year)	0.090 \pm 0.065	1.4	0.17
	Sex (Female)	-0.035 \pm 0.063	-0.6	0.58
	Age (After second year):Time	0.005 \pm 0.064	0.1	0.93
	Sex (Female):Time	-0.0132 \pm 0.065	-0.2	0.84
Common Yellowthroat	(Intercept)	1.081 \pm 0.062	17.5	< 0.0001
	Age (After second year)	0.144 \pm 0.068	2.1	0.04
	Sex (Female)	-0.245 \pm 0.071	-3.5	0.0006
	Age (After second year):Time	0.017 \pm 0.067	0.3	0.81
	Sex (Female):Time	0.019 \pm 0.070	0.3	0.79
	Smooth terms	Effective df	F	P
Gray Catbird	s(Time)	1.685	0.9	< 0.001
	s(Year)	8.0 $\times 10^{-5}$	1.2 $\times 10^{-6}$	0.89
	s(Year,Time)	4.8 $\times 10^{-6}$	5.0 $\times 10^{-9}$	0.87
Common Yellowthroat	s(Time)	1.978	4085.5	< 0.0001
	s(Year)	3.77 $\times 10^{-5}$	5.0 $\times 10^{-9}$	0.99
	s(Year,Time)	2.93 $\times 10^{-6}$	7.0 $\times 10^{-7}$	0.81

Even as advanced timing of spring migration is one of the most documented responses of migratory landbirds to global climate change, little work has assessed whether these advances are consistent across different demographic groups such as age classes or sexes (Neate-Clegg and Tingley 2023). Not only did we find evidence that Gray Catbirds and Common Yellowthroats advanced their arrival, we also found evidence of differences by age in both Gray Catbirds and Common Yellowthroats such that timing advanced faster in older than younger birds and in male than female Common Yellowthroats. Our findings are similar to those of Neate-Clegg and Tingley (2023), who provide a number of hypotheses to explain why migration may advance faster in males than females and in older than younger birds. For example, males or older birds may winter farther north than females or younger birds and thus be exposed to different migratory cues (Komar et al. 2005, Coppack and Pulido 2009). Further, if temperatures in the northerly part of the wintering range better correlate with breeding ground temperatures, individuals wintering in those areas may be better able to track increasing temperatures. Males and older birds often depart the wintering grounds before females and younger individuals (Coppack and Pulido 2009, Briedis et al. 2019). Such differential departure by sex or age might permit more time to adjust migration speed en route (Neate-Clegg and Tingley 2023).

If climate change causes conditions on the wintering grounds to change, consequent changes in competition by sex or age could result in larger differentials in body condition, in turn causing age- or sex-dependent differences in departure from the wintering grounds and thus in migration timing (Marra et al. 1993). Additionally, differential effects of climate change across a species' wintering range combined with demographic groups wintering in different parts of that range may result in differences in departure timing. For example, we have evidence (see Smith et al. 2022) that Gray Catbirds and Common Yellowthroats using the study site may winter in southern Florida and islands in the

Caribbean (Ryder et al. 2011, Somveille et al. 2021) and, for Common Yellowthroats, possibly the eastern coast of Central America (Milá et al. 2005); these areas have been differentially affected by climate change (Karl et al. 2009, Cuervo-Robayo et al. 2020).

Finally, evidence suggests that protandry results in fitness advantages, perhaps because of advantages in access to the highest quality territories (Lozano et al. 1996, rank advantage hypothesis), more mating opportunities (Kokko et al. 2006, mate opportunity hypothesis), and differences in sex-specific fitness costs and benefits of arrival timing (Møller et al. 2009, sexual conflict hypothesis), or some combination of these (Samplonius and Both 2017). Of course, protandry is likely to occur under balancing selection between costs (e.g., low food abundance, higher thermoregulatory costs) and benefits (e.g., increased opportunity for multiple clutches and other factors that increase seasonal reproductive performance) of early arrival (Neate-Clegg and Tingley 2023). Climate change, through reducing the costs of arriving earlier, may be increasing the degree of protandry (Møller 2004, Neate-Clegg and Tingley 2023) in Common Yellowthroats using the study site.

We found evidence that the functionality of the site changed in terms of mass gain, although not in capture rate, perhaps because of birds encountering better environmental conditions in later years. Although our results suggest no change by sex or age in the number of individuals using the site, yearly mass gain rates increased in both female Gray Catbirds and male Common Yellowthroats, implying that site quality increased, at least with respect to these demographic groups' ability to deposit fat. Further, although average daily temperatures at the site did not appear to change, i.e., temperature-related thermoregulatory costs remained similar, the amount of precipitation in May increased, which is when most individuals of both species were captured. Though more work is necessary to understand better

the sex-related differences in yearly mass gain rates, our results suggest that long-term changes at the site, perhaps via the influence of increased spring precipitation on vegetation productivity (Xiao and Moody 2004), positively influence arthropod abundance, perhaps by improving food resources or reducing water stress (Crossley et al. 2021). An alternative hypothesis is that enhanced mass gain is a result of fewer birds using the site, reducing competition (VanTol et al. 2021). However, our capture rate results suggest that site use was stable, at least with respect to Gray Catbirds and Common Yellowthroats.

Our results add to the growing body of literature demonstrating that birds are advancing their migration phenology, presumably in response to the effects of climate change experienced during one or more phases of the annual cycle. Our results also highlight the need for more species-specific studies to understand if, how, when, and where the effects of climate change are having effects. For example, our estimates of advancing migratory timing in Gray Catbirds and Common Yellowthroats were similar to some studies examining the same species but differed from other studies. These between-study differences suggest differential intra-specific responses, likely because climate change and its consequences vary in space and time (Ambrosini et al. 2019, Trenberth and Hurrell 2019). Further, our results suggest sex- and age-related differences in how individuals are responding to climate change, both prior to arrival and when using the site. For example, even though we found evidence that both species advanced their arrival day over the course of the study, they did so at different rates. We also found evidence of differences in how quickly different demographic groups within each species advanced their arrival timing, perhaps because these groups experienced different environmental factors on the wintering grounds or en route. Further, we found evidence that environmental conditions at the site influenced mass gain rates in some, though not all, of the demographic groups we examined, and did so differently in Gray Catbirds and Common Yellowthroats. Understanding the phenological response of migratory species requires consideration of climate change effects not only across multiple temporal and geographic scales (Calvert et al. 2009), but also on different demographic groups within a species.

Author Contributions:

R. J. S. is responsible for conceptualization, field data collection, some statistical analyses, and writing of the initial manuscript draft. J. M. G. conducted most statistical analyses. M. I. H. was involved in conceptualization and assisted with field data collection. E. L.-N. and A. M. R. analyzed DNA to assign sex in Gray Catbirds. All authors reviewed and provided input on manuscript drafts and gave final approval for publication.

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Data Availability:

The data are available from Zenodo <https://doi.org/10.5281/zenodo.7699039>.

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