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RESEARCH ARTICLE

Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler

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ABSTRACT

The availability of detailed information that encompasses the geographic range of a species, spans a long-term temporal range, and yields individual information (e.g., age and sex), is a principle challenge in ecology. To this end, the North American Bird Banding Laboratory maintains a unique and underutilized dataset that can be used to address core questions of phenological change in migratory birds. We used records from 1966 to 2015 to quantify how the timing of migration has shifted in a long-distance migrant, the Black-throated Blue Warbler (*Setophaga caerulescens*). Additionally, we examined age and sex differences in the timing of migratory movements. We observed that early spring migrants passed through sites ~1.1 days earlier per decade and the peak of spring migration also occurred earlier over the 50 yr of this study. Additionally, phenological change was more rapid with increasing latitude during peak spring migratory periods. During fall, the peak of migration stayed consistent across the 50 yr studied, but the migratory season showed protraction overall. During spring, males consistently migrated earlier than females and adults migrated earlier than young individuals. During fall, there was no difference in timing between males and females, but young birds migrated earlier than adults. Additionally, migration proceeded faster in spring compared with the fall. This study reveals differential strategies in migrant timing, across seasons, age groups, and by sex, and shows that en route adjustments across latitude may account for changes in migrant timing. This basic information about such a fundamental ecological process is crucial to our understanding of migration and we must utilize these unique data to appreciate critical shifts at relevant scales of migration.

Keywords: banding data, Black-throated Blue Warbler, migration, phenology, songbird

Cambios estacionales específicos en la fenología migratoria de *Setophaga caerulescens* a lo largo de 50 años

RESUMEN

La disponibilidad de información detallada que abarque el rango geográfico de una especie, que cubra un rango temporal de largo plazo y que proporcione información individual (e.g., edad y sexo) es uno de los principales desafíos en ecología. Con este propósito, el Laboratorio de Anillado de Aves de América del Norte mantiene un set de datos único y subutilizado que puede ser usado para responder preguntas clave de los cambios fenológicos en las aves migratorias. Usamos registros de 1966 a 2015 para cuantificar cómo la sincronización de la migración ha cambiado en *Setophaga caerulescens*, un migrante de larga distancia. Adicionalmente, examinamos las diferencias de edad y sexo en la sincronización de los movimientos migratorios. Observamos que los migrantes de inicios de primavera pasaron por los sitios ~1.1 días más temprano por década y que el pico de la migración de primavera también ocurrió más temprano a lo largo de los 50 años de este estudio. Adicionalmente, el cambio fenológico fue más rápido con el aumento de la latitud durante los períodos pico de la migración de primavera. Durante el otoño, el pico de la migración permaneció consistente a través de los 50 años de estudio, pero la estación migratoria mostró en general un alargamiento. Durante la primavera, los machos migraron consistentemente más temprano que las hembras y los adultos migraron más temprano que los jóvenes. Durante el otoño, no hubo diferencias en la sincronización de migración entre machos y hembras, pero los jóvenes migraron más temprano que los adultos. Adicionalmente, la migración se produjo más rápido en la primavera que en el otoño. Este estudio revela estrategias diferenciadas en la sincronización de la migración, entre estaciones, grupos etarios y según el sexo, y muestra que los ajustes en ruta a lo largo de las latitudes pueden explicar los cambios en la sincronización de la migración. Esta información básica sobre un proceso ecológico tan fundamental es crucial para nuestro entendimiento de la migración y debemos utilizar estos datos únicos para apreciar desplazamientos críticos a las escalas relevantes de la migración.

Palabras clave: ave canora, datos de anillado, fenología, migración, *Setophaga caerulescens*

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INTRODUCTION

One of the most conspicuous mass movements of North American fauna is the predictable, seasonal migration of birds between breeding and nonbreeding locations. While some species move relatively short distances of only a few hundred kilometers, others may migrate several thousand kilometers annually, captivating the attention of both ornithologists and bird watchers. These movements have been the subject of numerous studies of the basic ecology, physiology, and behavior of migration. In recent decades, the use of new methodologies like stable isotopes, geo-locators, and Global Positioning System tags, and the collection and availability of citizen science data, have improved the ability to study migration (Kelly and Finch 1998, Bridge et al. 2011, 2013, Sullivan et al. 2014, Brown and Taylor 2017, Taylor et al. 2017). Yet while each of these approaches fills a critical gap towards improving our resolution of migratory movements, few achieve both the detail and scale that bird banding data provide. Additionally, using historical data to characterize large-scale movements is of particular importance to understand these behaviors and how they are changing with shifting environments. For example, among 78 species of birds migrating to and through a banding station in western Pennsylvania, Van Buskirk et al. (2009) found that spring migration became significantly earlier, although autumn migration did not change. In a broad study across 65 species over 42 yr in Western Europe, Jenni and Kery (2003) found that autumn migration was earlier among long-distance migrants and later among shorter distance migrants. The differences observed in these studies may result from pressure to increase the number of offspring produced among short-distance migrants with variable numbers of broods, or from specific changes in environmental conditions experienced by long-distance migrants as a result of change (i.e. North Atlantic oscillation in the Pennsylvania study or increased desertification of the Sahara in the European study), which demonstrates the complexity of avian responses to climate change.

The North American Bird Banding Program is one of the most expansive historical datasets for avian migrants, including over 38 million passerines and near-passerines banded since 1960. These records are data-rich, providing information about the age and sex of individual birds, which is unavailable in other large-scale datasets like Christmas Bird Count, Breeding Bird Surveys, and eBird. While banding records have been used in many projects at local scales (e.g., Moore et al. 1990, Morris et al. 1996, Holzschuh and Deutschlander 2016), their use at large spatial scales are an important method in addressing a variety of questions related to bird biology (e.g., Brewer et al. 2000, Marra et al. 2005, Jackson et al. 2008, Cohen et al. 2014, Morris et al. 2016). Large-scale use of these data requires careful analysis to address potential seasonal or annual differences in effort but are a relatively underutilized resource to study birds at continental scales.

The Black-throated Blue Warbler (*Setophaga caerulescens*) is a long-distance Nearctic–Neotropical migrant with ~3,000 km between its breeding grounds in eastern deciduous forests and its wintering grounds primarily in the Antilles and the eastern coast of Central America (Holmes et al. 2017). This species is common, a relatively widespread breeding bird, and migrates through much of the eastern half of the United States. It is an excellent model for large-scale studies, as demonstrated by numerous studies during the breeding season (e.g., Holmes and Sherry 1992, Nagy and Holmes 2004, Kaiser et al. 2014, Lany et al. 2016) and throughout the annual cycle (e.g., Holmes et al. 1989, Holmes and Sherry 1992, Sliwa and Sherry 1992, Sillett and Holmes 2002). This species has shown varied and complex responses to changes in environmental conditions. In a 25-yr study of the demography of Black-throated Blue Warblers in New Hampshire, Townsend et al. (2013) found that warm springs resulted in higher fecundity as a result of earlier initiation of breeding and increased double brooding among birds that initiated breeding earlier. A related study demonstrated that population changes in this species were linked to both local and global events (Townsend et al. 2016). Population growth was lower after El Niño years than La Niña years regardless of local food abundance, demonstrating population responses to global climate patterns.

While certain patterns of migration, like protandry during spring, have been demonstrated constantly across many studies (Morbey and Ydenberg 2001), other aspects of migration have had highly variable results across different species, locations, and over time (reviewed in Newton 2008, 2011). For example, it is widely documented that migration speed is faster during spring than fall and that during spring migration males migrate before females and adults migrate before young birds (e.g., Morbey and Ydenberg 2001, Morton 2002, Newton 2008, Schmaljohann 2018). However, there has not been similar consistency in demographically driven migration patterns during fall migration (e.g., Murray 1966, Woodrey and Chandler 1997; see also Newton 2008). Additionally, spring migration timing has advanced over time (e.g., Marra et al. 2005, Sparks et al. 2005), but across various studies and species there is little agreement regarding changes to fall migration timing (Ellegren 1993, Wernham et al. 2002 as in Newton 2008). Changes in migratory phenology have been linked to environmental shifts, often attributed to climate change (Knudsen et al. 2011, Pearce-Higgins and Green 2014). However, few studies have both investigated changes over time during spring and fall migratory seasons and across a wide geographic range.

The goal of this study was to investigate whether the Black-throated Blue Warbler migration patterns by demographic groups, across a broad geographic range, and

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across time, are similar to what has been documented in previous studies of spring migration, and to clarify patterns of fall migration, which have inconsistent support in the literature. We do this by leveraging the size and scope of the North American banding dataset to demonstrate how this approach can provide insight into migratory patterns in North American birds. This species is conspicuously sexually dichromatic throughout the year, and researchers can accurately determine age class in males throughout the year and in females during much of the year (Pyle 1997). Thus, demographic data are readily available in the banding program dataset for addressing large-scale questions, including those addressing movement ecology. We addressed the following hypotheses. Migratory phenology would differ across demographic groups (e.g., age and sex) during spring, but not fall (Murray 1966, Woodrey and Chandler 1997, Morbey and Ydenberg 2001, Morton 2002, Newton 2008, Schmaljohann 2018). Migration timing has changed over the last 50 yr such that spring migration is getting earlier and average fall migration timing is not changing. The changes in migration phenology, predicted above, vary latitudinally, such that the effect of earlier spring migration is greater at more northern latitudes along the migratory route (Marra et al. 2005), that is, migration is even earlier at northern migratory sites compared with southern sites, and the change in migration timing will be greatest at southern latitude migration sites during fall (Ellegren 1993).

METHODS

We requested banding data on Black-throated Blue Warblers from the United States Geological Survey (USGS) Bird Banding Laboratory and included all migration records for the 50-yr period from 1966 to 2015. We excluded data from birds banded outside of the expected range for Black-throated Blue Warblers. To define the range of this species, we used BirdLife International shapefiles (BirdLife-International 2016). As a precaution, we also defined a 0.1° buffer around the BirdLife range to capture sites near the periphery of the predicted range estimate. For instance, Appledore Island, Maine, a known migration stopover location, was excluded without this precaution. We defined spring migration as March 1 through June 15 and fall migration as August 15 through November 15, thus excluding birds from outside the migratory seasons. We excluded data from sites that banded extensively during the breeding and wintering periods, removing sites where greater than 50% of the captures occurred between June 15 and August 15 (breeding) and between November 15 and March 1 (wintering). We used age and sex data from these banding records. Because this species is conspicuously sexually dichromatic, we excluded birds that were banded as unknown sex, which accounted for 1.41% or 2,131 total individuals from our initial dataset (further defined below). We also took steps to exclude data from individuals that were not migrating: we removed data from individuals that were captured within the wintering range, south of 25°N latitude, and from young birds that were banded in or near the nest from which they hatched, based on the age code reported to the Bird Banding Lab. In analyses involving age, "young" refers to hatch-year birds during the fall and second-year birds during the spring, "adult" refers to after-hatch-year birds during the fall and after-second-year birds during the spring, and we used the term "unknown" for birds of unknown age during the fall and the imprecise age category of after-hatch year during the spring. We use the terms young, adult, and unknown throughout the remainder of this paper (e.g., Table 1). Data for this study were collected by several independent organizations (Appendix Table 5). All data were obtained by and are available from the USGS Bird Banding Laboratory. All data analyses described below were conducted in R 3.5.2 (2018-12-20).

Within-Season Migration Phenology

To investigate migration phenology differences across demographic groups, we took the following approach for both the spring and fall migratory periods. For both spring and fall migration, we examined latitudinal differences in median passage date by aggregating captures to 0.5° ceiling catchments, and summing the daily number of captures. We quantified peak migration timing by determining the median ordinal date of the cumulative sum of migrants captured across all available years. We only conducted latitudinal assessments if at least 25 unique banding days were available within each 0.5° catchment (the number of total catchments used are reported in Table 2). We used a least squares linear regression with ordinal date regressed on latitude, age, and sex to determine temporal differences in median arrival.

Changes in Migration Phenology Across Years

For analyses investigating changes in migration across time (across years), we used subsets of our data within each season (spring and fall). We defined site as the 10-min block region (~18.5 km, 342.25 km^2) as provided by the Bird Banding Laboratory, which provided consolidation of precision variation in reporting site location across years. Sites were only included to address this question if they had a minimum of 20 yr of data and an average of 10 or more birds per season (spring and/or fall). From this subset and within each season, we only used individual years if 10 or more individuals were banded. To determine changes in timing across years we determined the ordinal date on which the cumulative sum of birds banded exceeded 5%, 50%, and 95% of the total birds banded within each season and year, hereafter referred to as "early", "peak", and "late"

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passage, respectively. We regressed these ordinal dates against year and sex, using location as a random intercept within the *lme4* package (Bates 2010, Bates et al. 2014, Kuznetsova et al. 2017). We used 95% confidence intervals to evaluate the significance of these effects using the R *confint* function and determined mixed-effects R^2 using the *r.squaredGLMM* function in the MuMIn package (Barton 2018). Small sample sizes within age categories precluded the inclusion of age in these analyses. To examine if the rate of change varied across latitude, we extracted site-level coefficients of change using a least square linear regression. Compiling site-level coefficients, we regressed coefficients of phenological change (days year^{-1}) against latitude for early, peak, and late periods.

RESULTS

We used 148,629 records from Black-throated Blue Warblers captured during spring and fall migration in North America from 1966 to 2015. A greater number of individuals were captured during fall migration compared with spring (83.1% of captures occurred during fall) but the sex ratio was approximately even during both seasons (Table 1, Figure 1). For most birds (91.1%), specific age class could be determined; however, during spring migration, specific age class was determined for a smaller proportion of all birds (60.0%; Table 1). The relatively high proportion of unknown age birds in the spring precluded direct comparison between spring and fall migration related to age. In both seasons and among both sexes, young birds were more frequently captured than adults (Table 1).

Within-Season Migration Phenology

Because we found no significant interaction between age and sex in either season (both $P > 0.05$), we ran our final models without the interaction term. Our spring model, which included age, sex, and latitude, accounted for 74.1% of the variation in median passage date ($F = 88.9$, df = 3 and 93, $P < 0.001$). There was a 1.1 day increase in median passage date for each increase in degree latitude, adult individuals migrated 2.9 days earlier than young individuals, and males migrated 5.7 days earlier than females (Figure 2, Table 2). During fall, 68.2% of the variation in median passage date was accounted for by our model with age, sex, and latitude ($F = 102.9$, df = 3 and144, $P < 0.001$). As birds were moving south, for each decrease in degree latitude they passed through 1.6 days later (Figure 2, Table 2). The median passage date for young birds was 2.6 days earlier than for adults (Figure 2, Table 2). There was no difference in migration phenology between males and females during the fall (Figure 2, Table 2).

Changes in Migration Phenology Across Years

Across the 50-yr study period, passage of early individuals, the date at which the first 5% of individuals had been captured, occurred significantly earlier during both spring and fall (~1.1 days per decade in both seasons; Figure 3, Table 3). However, equivalent analyses on peak migration, the date of passage for half the cumulative number of migrants banded, indicated no difference in overall migration timing across years in fall but slightly earlier during spring migration (Figure 3, Table 3). Interestingly, there was no change in passage date of the latest migrants during spring but passage date for the latest fall migrants was significantly later across this 50-yr period (0.9 days per decade; Figure 3, Table 3). Because sex was included in these analyses, we were able to address whether there were sex-related differences in phenology across years. As expected, males arrived earlier than females during spring (see also Within-Season Migration Phenology above); however, we did not consistently see a significant interaction between sex and year (5 of 6, $P > 0.05$), and thus we did not include it in our final model (Figure 3, Table 3). Phenological change was more rapid with increasing latitude during peak spring migratory periods, but other periods did not show spatial dependence on the rate of change (Table 4). There was no relationship between rate of phenological change and latitude during fall migration (Table 4).

DISCUSSION

Developing a more comprehensive understanding of the entire annual cycle of Black-throated Blue Warblers is imperative to appreciate migratory dynamics within this well-studied species. Most long-term studies of migratory phenology have focused only on spring migration (Marra et al. 2005, Mayor et al. 2017). To this end, we present a spatially and temporally broad examination of migratory movements, examining both spring and fall

TABLE 1. Number of Black-throated Blue Warblers captured across the range by season, age, and sex

	Spring				Fall			
	Young [a]	Adult [a]	Unknown [b]	Total	Young [a]	Adult [a]	Unknown [b]	Total
Female	4,576 (69.5%)	2,009 (30.5%)	6,542 (49.8%)	13,127	48,723 (82.2%)	10,547 (17.8%)	2,569 (4.2%)	61,839
Male	4,911 (58.1%)	3,541 (41.9%)	3,501 (29.3%)	11,953	44,602 (73.0%)	16,477 (27.0%)	631 (1.0%)	61,710

[a] Percentage of birds in this age class, compared with other precise age classes (e.g., young vs. adult).
[b] Percentage of birds in the unknown age class, compared with the precise young and adult age classes.

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migratory periods across the range of this species and across a 50-yr time period. During both spring and fall, migration passage date for Black-throated Blue Warblers varied by age, sex, and latitude across sites throughout eastern North America. As predicted, spring migration proceeded more rapidly than fall migration, such that for each degree increase in latitude, the passage date increased by only 1.1 days in spring compared with 1.6 days in the fall. Additionally, our data indicate the timing of fall migration is becoming more protracted with early migration occurring earlier and later migration occurring later across the 50 yr of our study. Previous studies in other species have found that duration of migration by individual birds was shorter in spring than fall, primarily due to seasonal differences in stopover length (Schmaljohann et al. 2012, La Sorte et al. 2013, Nilsson et al. 2013, Horton et al. 2016, Schmaljohann 2018). While our data reflect the difference in the duration of migration by individual birds, they also indicate greater variation in migration timing across individuals. Thus, at the population level, the longer fall migration may be driven both by variation in time spent on the breeding grounds and a longer time spent en route.

TABLE 2. Within-season migration phenology models. Results of linear regressions on median migration date as a function of latitude, age, and sex for Black-throated Blue Warblers are presented. Dates derived from 0.5° latitudinal catchments and all years (1966–2015) were pooled. Individual catchments were only used if at least 25 unique banding days were available within each 0.5° catchment (see Methods)

Coefficients	Estimate	Standard error	*t*-value	*P* (>|*t*|)
Spring (25 latitudinal catchments)				
(Intercept)	90.327	3.004	30.066	<0.001
Latitude	1.099	0.0741	14.836	<0.001
Age (Young)	2.908	0.920	3.161	<0.01
Sex (M)	−5.669	0.919	−6.170	<0.001
Fall (37 latitudinal catchments)				
(Intercept)	328.733	3.597	91.388	<0.001
Latitude	−1.587	0.091	−17.426	<0.001
Age (Young)	−2.561	1.145	−2.237	<0.05
Sex (M)	−0.236	1.145	−0.207	0.837

It is well demonstrated that in passerines males and older individuals tend to arrive on the breeding grounds earlier than females and younger individuals (Spina et al. 1994, Morton 2002), likely driven by competition for territories and mates (Newton 2008). Demographic patterns of migration by Black-throated Blue Warblers in spring were consistent among our analyses of early, peak, and late migration. Across all 3 periods of passage (early, peak, and late) males proceeded females by at least 5 days, supporting our original prediction. Additionally, our results supported our prediction related to age because adults migrated almost 3 days earlier than young individuals. Our spring results are similar to earlier studies of this and closely related species that found earlier migration by males and by adults (Francis and Cooke 1986, Morris and Glasgow 2001, Stewart et al. 2002).

In contrast to the clear pattern in the spring, during fall we found no significant difference in passage date between

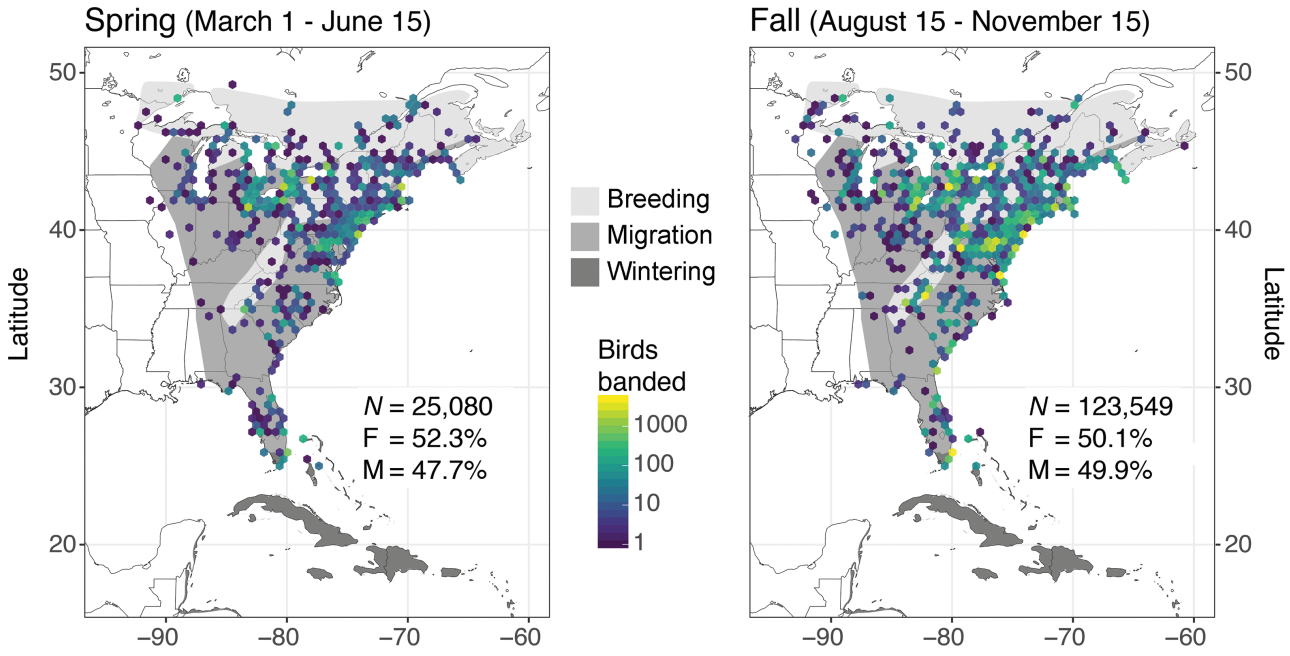


FIGURE 1. Geographic distribution of Black-throated Blue Warblers. Gray shaded areas indicate the breeding, migration, and wintering ranges from BirdLife International (BirdLife-International 2016). Hexagons colored by the log of the total number of captures between 1966 and 2015 during spring and fall migration.

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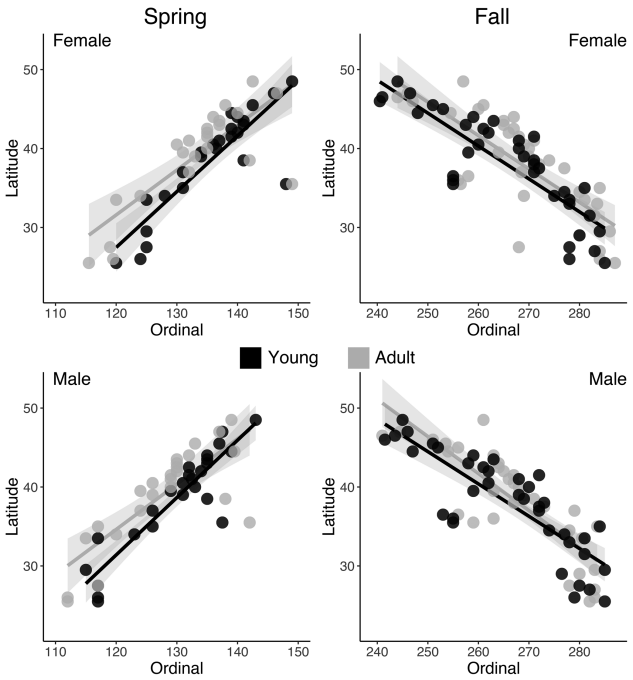


FIGURE 2. Migration phenology by latitude for Black-throated Blue Warblers. Phenology for the (**A**) spring and (**B**) fall migratory seasons using the median date of captures within 0.5° latitudinal catchments. Individual catchments were only used if at least 25 unique banding days were available within each 0.5° catchment (see Methods). Data are provided for males (gray lines) and females (black lines) and for young (broken lines) and adult (solid lines). Shaded areas show the 95% confidence intervals.

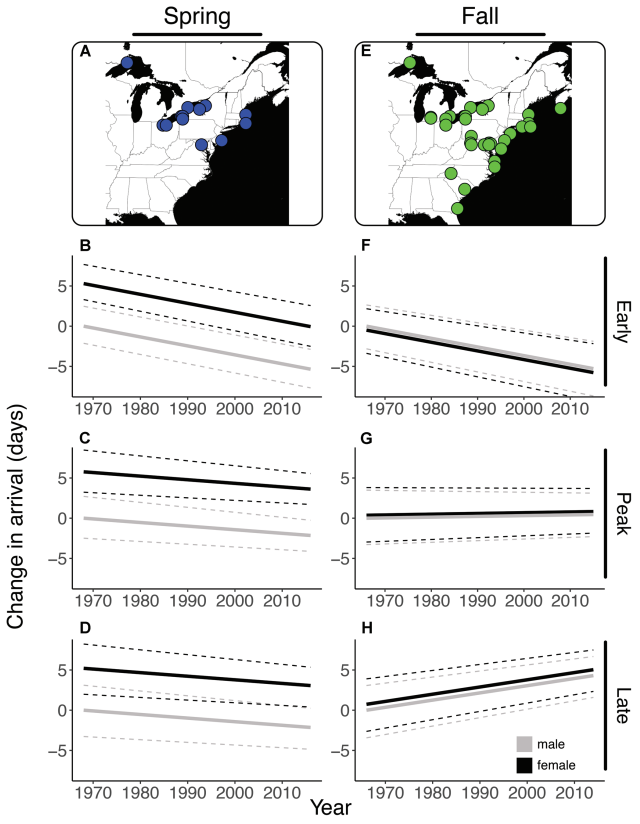


FIGURE 3. Change in migration phenology across years for Black-throated Blue Warblers. Map insets show spring (**A**) and fall (**E**) banding locations that had at least 20 yr of records with an average of at least 10 birds banded per season. Lines show the change in arrival in days for the cumulative passage of 5% (Early; [**B**] and [**F**]), 50% (Peak; [**C**] and [**G**]), and 95% (Late; [**D**] and [**H**]) of captures across the 50 yr. Dates are referenced to the mean arrival date of males in 1966 for males (gray) and females (black). Intervals (dotted lines) show bootstrapped 95% confidence intervals.

males and females. Studies of sex-related patterns of migration timing during fall are not as consistent as those focusing on spring migration (Swanson et al. 1999, Morris and Glasgow 2001, McKinnon et al. 2016). Sex-related timing of departure from the breeding grounds may be dependent upon parental care, reflecting when parental duties are completed by each sex (Newton 2008, 2011). In Black-throated Blue Warblers, both males and females provide parental care through the post-fledging period (Holmes et al. 2017), which is consistent with Newton's assertion above (Newton 2008, 2011). Furthermore, both males and females establish territories during the overwintering period (Holmes and Sherry 1992, Holmes et al. 2017), thus both sexes are experiencing similar pressures during fall, which could lead to similar migration timing in males and females.

Contrary to our original prediction, Black-throated Blue Warblers hatched the previous breeding season (i.e. young) and adults differed in their autumn migration timing. Young Black-throated Blue Warblers migrated 2.6 days earlier than adults during fall, the reverse of the spring pattern, which was similar to Carlisle et al. (2005) and McKinnon et al. (2016) (cf. Ellegren 1993, Woodrey and Chandler 1997, Morris and Glasgow 2001). This age-related difference in the fall may be driven by 2 major activities: reproduction and molt (reviewed in Newton 2008, 2011). For many North American songbirds, adult departure from the breeding grounds occurs after the completion of all reproductive activity and pre-basic molt (Newton 2008, but see Pyle et al. 2018). In young birds, the growth of flight feathers and the subsequent performative molt occurs primarily during the post-fledging period, often while still under parental care (Holmes et al. 2017). Thus, young birds complete their molt prior to their parents, could depart the breeding grounds earlier and precede adults on migration and, therefore, would be captured earlier at migration banding sites.

The effects of changes in migration timing over this 50-yr period have the potential to influence the timing and length of the breeding season, which has been shown to increase fecundity in this species (Townsend et al. 2013).

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TABLE 3. Results of linear mixed models on early (the date at which 5% of the cumulative captures occurred), peak (the median capture date; 50% of cumulative captures), and late (the date at which 95% of the cumulative captures occurred) passage by Black-throated Blue Warblers across years. A total of 13 sites (n = 588 [294: female, 294: male], 1966–2015) met sampling criteria during the spring and 34 sites (n = 1,712 [856: female, 856: male], 1966–2015) during the fall. Confidence intervals that do not overlap zero are shown in bold

Passage	Coefficients	Estimate	Standard error	t-value	R^2 (fixed effects) R^2 (fixed + random effects)	Confidence interval	
						Lower (2.5%)	Upper (97.5)
Spring							
Early	(Intercept)	134.951	1.241	108.729	0.213	**132.418**	**137.736**
	Yearly change	–0.116	0.025	–4.459	0.663	**–0.165**	**–0.060**
	Sex (M)	–5.297	0.309	–17.151		**–5.902**	**–4.691**
Peak	(Intercept)	139.674	1.310	106.603	0.245	**137.019**	**142.548**
	Yearly change	–0.045	0.014	–3.103	0.682	**–0.080**	**–0.016**
	Sex (M)	–5.768	0.276	–20.882		**–6.309**	**–5.227**
Late	(Intercept)	146.655	1.649	88.930	0.152	**143.350**	**150.222**
	Yearly change	–0.045	0.024	–1.847	0.679	–0.097	0.004
	Sex (M)	–5.209	0.319	–16.310		**–5.835**	**–4.582**
Fall							
Early	(Intercept)	249.745	1.585	157.568	0.015	**246.597**	**252.914**
	Yearly change	–0.108	0.036	–2.987	0.578	**–0.179**	**–0.035**
	Sex (M)	0.491	0.366	1.341		–0.227	1.208
Peak	(Intercept)	263.121	1.935	135.986	0.0003	**259.253**	**266.964**
	Yearly change	0.009	0.036	0.261	0.644	–0.062	0.080
	Sex (M)	–0.366	0.328	–1.114		–1.009	0.278
Late	(Intercept)	275.683	1.928	142.978	0.013	**271.839**	**279.515**
	Yearly change	0.090	0.040	2.224	0.678	**0.010**	**0.170**
	Sex (M)	–0.735	0.291	–2.529		**–1.305**	**–0.165**

Overall, we found that not only was the peak of spring migration occurring earlier, but the earliest individuals also migrated earlier. While the peak timing of fall migration has not changed, the earliest individuals are migrating earlier and the latest individuals are migrating later. The combination of the potential for an earlier migration in the spring and a later migration in the fall could result in an overall longer breeding season. Lengthening of the breeding season could allow for double brooding and/or re-nesting after failed breeding attempts, either of which could increase lifetime fitness in this species that is known to double brood (Townsend et al. 2013, Holmes et al. 2017). Additionally, a longer breeding season could translate into our observation of a protracted fall migration. The early fall migrants may reflect young from successful early nesting, allowing earlier departure from the breeding grounds. The later fall migrants may reflect adults and young after successful second broods, or re-nest attempts from which young fledge later than the first nests. Alternatively, the earlier arrival of some individuals on the breeding grounds and later departure of some individuals may be indicative of an increasingly heterogeneous phenology across the geographic breeding range, which would also result in our observed patterns of changing migration phenology.

Black-throated Blue Warblers are long-distance migrants that winter in areas experiencing different environmental conditions than the breeding grounds, and thus will need to respond to changing conditions between wintering, migration, and breeding seasons. Early spring migration is becoming earlier by 1.1 days per decade, peak spring migration is also becoming earlier by 0.5 days per decade, and the rate of change is increasing with latitude. Thus, although we are seeing changes in spring migration phenology over time, the changes are not consistent across the entire migratory range. Examination of flexibility in migration timing is important given the possibility of phenological mismatches between migrants and their prey, especially during the breeding season (Both et al. 2010, Jones and Cresswell 2010). While previous

TABLE 4. Black-throated Blue Warbler site-level coefficients from linear regressions on phenological change on latitude. Early (the date at which 5% of the cumulative captures occurred), peak (the median capture date; 50% of cumulative captures), and late (the date at which 95% of the cumulative captures occurred) passage dates used. A negative coefficient indicates earlier arrival with increasing latitude

Passage	Estimate	Standard error	t-value	P (>|t|)
Spring (n = 13)				
Early	0.0052	0.0059	0.887	0.394
Peak	–0.0081	0.0008	–10.094	<0.001
Late	–0.0027	0.0046	–0.597	0.563
Fall (n = 34)				
Early	–0.0114	0.0073	–1.558	0.129
Peak	0.0054	0.0077	0.704	0.487
Late	–0.0069	0.0100	–0.695	0.492

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researchers have found that the timing of avian migration may be flexible, allowing adjustment to weather and plant phenology en route (Marra et al. 2005), it has also been demonstrated that there may be an increasing phenological asynchrony between spring green-up and arrival of several eastern migrant species (Mayor et al. 2017). Given these results and the potential limits of the degree to which migrants can adjust their timing en route, additional analyses on other species are needed to understand how robust and pervasive this capability is (Schmaljohann and Both 2017). Research on Black-throated Blue Warblers has demonstrated that it is a species that is able to make adjustments to the timing of breeding efforts relative to leaf-out phenology, which allowed for maximum reproductive success (Lany et al. 2016). The earlier onset of spring migration in Black-throated Blue Warblers that we report in this study might be important if changes in prey availability affects reproductive success because it could facilitate a change in overall migration timing. Among European migrants, autumn migration was found to occur earlier among long-distance migrants, but later among short-distance migrants (Jenni and Kery 2003). Our findings of an advanced early fall migration and delayed late fall migration would account for changes in migration in response to climate effects on breeding season activities. Taken together, these results provide evidence of the ability of Black-throated Blue Warblers to shift their phenology of annual cycle events over time.

Using data from Black-throated Blue Warblers from across their migratory range allowed exploration of several hypotheses about migration phenology both across time and among demographic groups in this species. The use of this extensive archive of bird banding data has revealed detailed information about migration at a large scale, including the study of discernable groups (e.g., age and sex) at a scale not possible through other monitoring programs. Building upon this work, comprehensive inclusion of additional migratory species is the next objective to examine how migrants are responding to phenological shifts over the last 50 yr system-wide. This archive and framework could be used to examine testable system hypotheses, including whether migratory distance, foraging guild, body size, and migratory route drive differential responses to large-scale ecological changes.

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APPENDIX TABLE 5. The number of years that banding locations contributed to our long-term study of potential migratory timing changes over the last 50 yr. These stations provided at least 20 yr of data on Black-throated Blue Warblers in spring and/or fall migration with an average of 10 or more birds per season

Location	Spring	Fall
Holiday Beach Migration Observatory, Amherstburg, ON, Canada		20
Long Point Bird Observatory (Tip), near Port Rowan, ON, Canada	41	48
Long Point Bird Observatory (Breakwater), near Port Rowan, ON, Canada		45
Long Point Bird Observatory (Old Cut), Port Rowan, ON, Canada	40	40
Thunder Cape Bird Observatory, Thunder Cape, ON, Canada	23	24
Toronto, ON, Canada	29	30
Waupoos Island, ON, Canada	31	25
Atlantic Bird Observatory, Bon Portage Island, NS, Canada		27
Jekyll Island Banding Station, Jekyll Island, GA, USA		37
Nantucket, MA, USA		26
Darnestown, MD, USA	22	25
Fairlee, MD, USA		27
Mt Nebo Wildlife Management Area, Garrett County, MD, USA		39
Patuxent Wildlife Research Center, Ft Meade, MD, USA		34
Pikesville, MD, USA		20
Manomet Bird Observatory, Plymouth County, MA, USA	46	50
Towson, MD, USA		32
Appledore Island Migration Station, Appledore Island, ME, USA	35	38
Pitsfield Station of the Kalamazoo Valley Bird Observatory, Kalamazoo, MI, USA		26
Kalamazoo Valley Bird Observatory, Kalamazoo, MI, USA		44
Metro Beach Metropark, Macomb County, MI, USA		22
Big Bald Banding Station, near Mars Hill, NC, USA		36
Cape May Bird Observatory, Cape May, NJ, USA		48
Island Beach State Park, Seaside Park, NJ, USA	48	50
Fire Island Inlet, Long Island, NY, USA		34
Braddock Bay Bird Observatory, W Greece, NY, USA	46	31
Black Swamp Bird Observatory, Lacarne, OH, USA	34	35
Black Swamp Bird Observatory, South Bass Island, OH, USA	20	
Presque Isle State Park, Erie, PA, USA	43	41
Powdermill Avian Research Center, near Rector, PA, USA		50
Block Island, RI, USA		50
Black River Swamp Bird Banding Station, Mayesville, SC, USA		25
Coastal Virginia Wildlife Observatory, Kiptopeke, VA, USA		39
Mackay Island National Wildlife Refuge, Knotts Island, VA, USA		22
Allegheny Front Migration Observatory, Dolly Sods, WV, USA		50

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