


## ARTICLE

## Rapid shifts in migration routes and breeding latitude in North American bluebirds

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## Abstract

Spatial and temporal shifts in the migratory patterns of birds have become more frequent as climate change and habitat alteration continue to impact ecosystems and the species dependent on them. In this study, we used eBird community science data collected over ten years to examine potential changes in the migratory patterns of three North American bluebird species: eastern (*Sialia sialis*), western (*Sialia mexicana*), and mountain (*Sialia currucoides*) bluebirds. Community science datasets such as those provided through eBird are a valuable tool for examining population-level processes, as such data are often costly and time-consuming to collect through other approaches (e.g., directly tracking individuals). Using generalized additive models, we produced smoothed migration paths for all three species over each season from 2009 to 2018. We asked whether there were changes over this 10-year period in the timing of spring and fall migration and migration speed, and the population centroids during breeding and migration. In contrast to many species that are experiencing poleward shifts in their distributions, the population centroids during the breeding period of all three bluebird species appear to have shifted southward over the past decade. Perhaps most surprisingly, we also detected strong longitudinal shifts in the population centroids during migration in eastern and western bluebirds, with both species shifting toward the center of the continent. Despite these changes in migratory routes and breeding distributions, we detected no change in the migratory timing or speed of any of the species. Our analysis indicates that bluebirds are rapidly altering the pattern of their migration, likely in response to changing environmental conditions, but not always in the direction predicted.

## KEYWORDS

bluebirds, breeding, conservation, latitude, longitude, migration, routes, shift, speed, timing

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## INTRODUCTION

Since the mid-1900s, global temperatures have risen by approximately 1°C (Allen et al., 2018), and the Earth has experienced unprecedented anthropogenic changes that have altered ecosystems and disrupted biological processes (Walther et al., 2002). Spring is advancing in the Northern Hemisphere, both in terms of first-leaf and first-bloom dates (Buermann et al., 2013). These advances are forcing insects—and the wildlife dependent on them—to alter their life cycles accordingly (Schwartz et al., 2006). The rapidity of the change in spring phenology can result in a mismatch between peak resource availability and the peak resource demands of many animals, including migratory birds, which may be constrained in their ability to alter the timing of life history events such as migration and reproduction.

With advancing springs, migratory birds may need to arrive on their breeding grounds earlier to take advantage of earlier spring productivity (Mayor et al., 2017; Saino et al., 2011). Individuals may also increase the speed of migration; many bird species already migrate faster during spring compared with fall migration due to the time constraints on arrival to obtain high-quality territories and mates (Nilsson et al., 2013), so changes to migration speed may be physiologically possible in some cases. Speed of migration may also be influenced by environmental conditions experienced en route (Bridge et al., 2016), such as higher wind speeds resulting in earlier arrival to migratory roosts in Vaux's swifts (*Chaetura vauxi*) (Prytula et al., 2021).

In addition to temporal shifts, species may also be undergoing spatial shifts in their distribution as a result of climate change (Huang et al., 2017; La Sorte & Graham, 2020; La Sorte & Thompson, 2007). For instance, in response to increasing temperatures, many northern avian species' ranges are shifting to higher latitudes (Curley et al., 2020; Thomas & Lennon, 1999) and elevations (Tingley et al., 2012). There is also evidence for shifts in the longitudinal distributions of many species, but these studies often focus on species presence or absence at the range margins (Huang et al., 2017), rather than changes in the population centroid of the species across their total distribution. Analyzing a species' entire range may be more informative about changes to their entire longitudinal distribution (Virkkala & Lehikoinen, 2014) than examining the occurrence of small populations, which may be heavily influenced by local events such as land use changes or irregular annual variation in snow-packs or temperature.

Historically, many studies of migratory birds have focused on events occurring during the breeding periods, but to fully understand the annual cycle of a

species, we need to improve our understanding of events occurring outside of its relatively short breeding period (Faaborg et al., 2010). Increasing attention is now being directed toward carryover effects and full annual cycle dynamics (Marra et al., 2015). Recent advances in tracking technology (including satellite tracking, GPS tags, and geolocators) have shed light on individual-level patterns of migration, while large-scale datasets, such as those obtained through community science or weather radar, can be used to examine changes in entire populations (Curley et al., 2020; Kelly et al., 2012; Rushing et al., 2020). Here, we make use of community science data available from eBird (Sullivan et al., 2009) to examine shifts in migration patterns among three closely related migratory bird species.

Specifically, we ask whether eastern bluebirds (*Sialia sialis*), western bluebirds (*Sialia mexicana*), and mountain bluebirds (*Sialia currucoides*) have shifted their migration patterns over the past decade. Each species exhibits different migration life histories: eastern and western bluebirds are considered partial migrants as populations in parts of the range remain as year-round residents (Gowaty & Plissner, 2020; Guinan et al., 2020), while mountain bluebirds are considered fully migratory (Johnson & Dawson, 2020). The species also exhibit varying short-term (2009–2019) population trends based on data from the North American Breeding Bird Survey (BBS) (A. C. Smith et al., unpublished, an update of Environment Canada, 2017). Eastern bluebird populations have declined by 1.14% per year (95% credible interval: −1.61, −0.65), and mountain bluebird populations have also declined, although credible intervals overlap zero (−0.92% per year −2.21, 0.39) (A. C. Smith et al., unpublished, an update of Environment Canada, 2017). By contrast, western bluebirds have shown an increase of 0.77% per year, although again credible intervals overlap zero (−1.02, 2.47). Thus, while closely related, the three species have distinct ecologies and different population trends, and therefore may differ in the degree to which they are impacted by climate change and in the strategies they use to respond.

To examine potential changes in the migratory patterns of North American bluebirds, we used 10 years of community science data from eBird (Sullivan et al., 2009). Large-scale community science datasets such as those available from eBird have allowed researchers to harness millions of bird observations, which can allow for comparisons of year-to-year shifts in migratory patterns (Sullivan et al., 2014; Supp et al., 2015). In response to environmental changes, we expected that bluebirds may have altered aspects of their migratory behavior such as the speed, timing, and routes used, in order to remain in synchrony with advancing spring phenology (Mayor et al., 2017;

Visser & Both, 2005). Based on recent trends observed across a broad range of taxa, we also expected that the three species may be shifting their breeding distributions in response to rapidly changing environmental conditions in North America (Parmesan, 2006; Parmesan & Yohe, 2003). Specifically, we predicted that western bluebirds would demonstrate an eastward shift in population centroids during breeding and possibly also during migration as a result of factors such as changes in fire suppression regimes and increased nesting opportunities through nest box programs, both of which have been linked to the rapid range expansion of the species (Duckworth, 2009; Duckworth & Badyaev, 2007). By contrast, we did not have an ecological reason to expect that eastern or mountain bluebirds would demonstrate a consistent, species-level longitudinal shift during breeding or migration. While migratory timing is often associated with large-scale environmental change, longitudinal shifts may be much more reliant on local conditions en route to or from the breeding and nonbreeding grounds (Stanley et al., 2012). Consistent with studies conducted on other migratory birds, we predicted that as a result of increasing temperatures, all three species of bluebirds would arrive earlier on their breeding grounds (Jonzen, 2006; Parmesan & Yohe, 2003) and/or increase spring migratory speed (Nilsson et al., 2013), and shift the population centroid during breeding toward a higher latitude over time (Rushing et al., 2020).

## METHODS

We obtained presence data for eastern, western, and mountain bluebirds for each day of the year from 2009 through 2018 from eBird (eBird, 2019; Sullivan et al., 2009) and processed these data using the *auk* package (v0.4.0, Strimas-Mackey et al., 2018) for R (v3.6.2, R Core Team, 2020). Following recommended best practices, this processing involved filtering the eBird checklists to include only those that were “Stationary” or “Traveling” (leaving out those that were “Incidental” or “Historical”), had a duration of 0–5 h, a distance of between 0 and 5 km, and that were “complete” (i.e., all species observed were recorded) (Strimas-Mackey et al., 2020). Finally, we “zero-filled” the data, a process that adds counts of 0 for each checklist that did not include any bluebird observations.

We then followed the methodology of Supp et al. (2015) to summarize presence by geographic location using equal-area icosahedron hex grids. Hex grids were created at a resolution of 23,323 km<sup>2</sup> using the *dggridR* R package (v2.0.3, Barnes, 2018). Presence was summarized into daily measures by binning checklists into hexes by date and then calculating the proportion of checklists

that included a bluebird of a given species (number of checklists with a bluebird observed/total number of checklists). For each species we calculated daily weighted mean longitude and latitude using coordinates of the hex centroids. These means were weighted by the proportion of checklists that included observations of a bluebird species. This resulted in a measure of mean species presence per day, per hex. Hexes without checklists were omitted from the analysis.

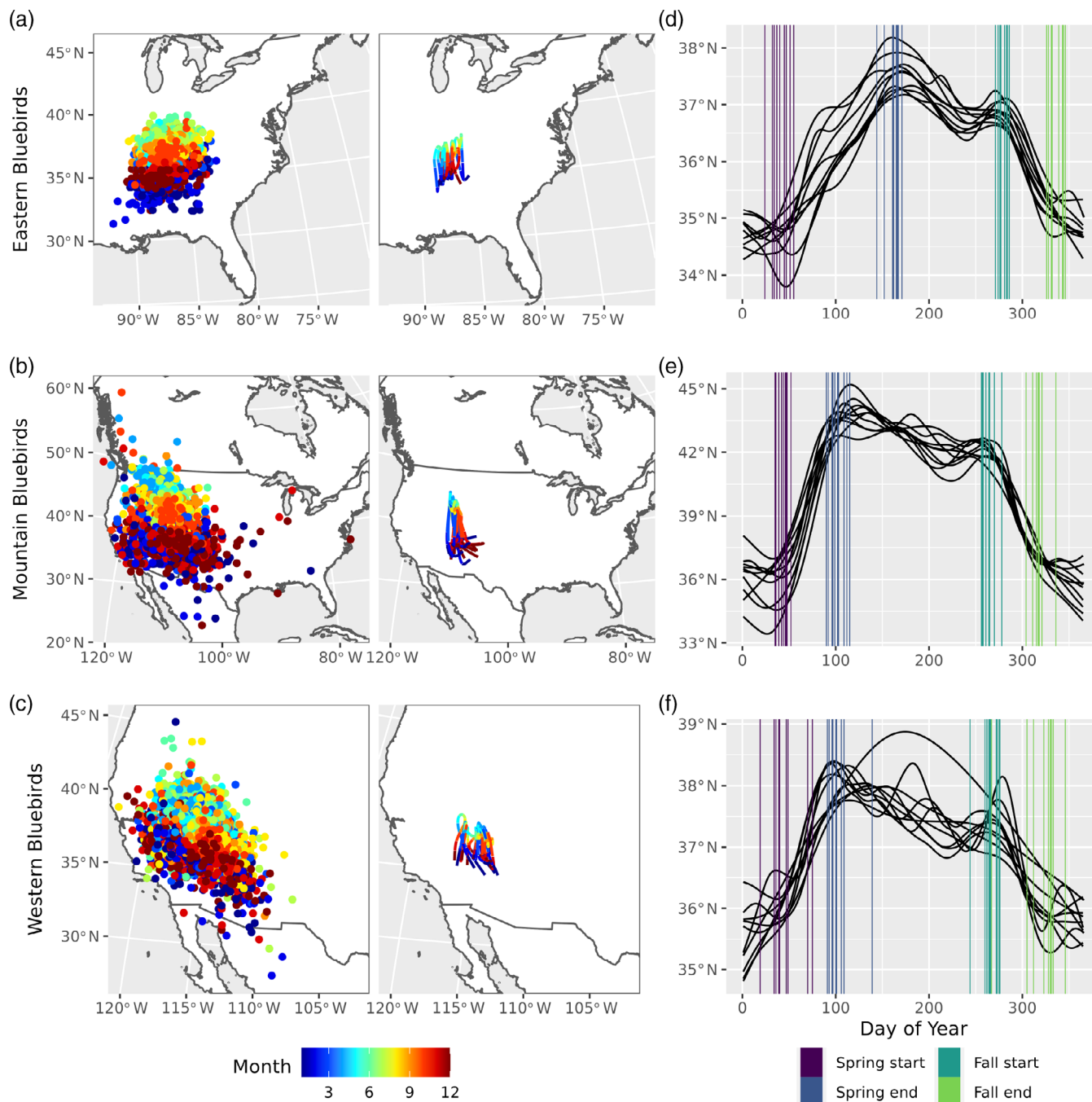
## General additive models of migration

Generalized additive models (GAMs) were used following methodologies from Supp et al. (2015) to model the relationship between daily latitude/longitude and time for each species. GAMs were created with the *mgcv* R package (v1.8-31, Wood, 2011) using a penalized regression spline-based smoothing parameter with a basis dimension of 40 (i.e.,  $k = 40$ ) and a gamma of 1.5 (the degree of smoothing). These models predicted smooth paths from the weighted daily mean locations. These smoothed paths were then used to predict the daily latitude and longitude of the mean population centroid for each species (Figure 1a–c).

## Migration timing

Migration timing was calculated in two steps. First, a coarse migration timing for each species in each year was defined as the date the daily latitudes predicted from the GAMs crossed southern or northern latitudinal thresholds calculated for each season using specific ordinal date ranges. These latitudinal thresholds were defined as the most northerly latitudinal extent during the nonbreeding period and the most southerly latitudinal extent during the breeding period for each species. Specifically, migrations that started or ended in the south (i.e., the start of Northern Hemisphere spring and end of fall migration) used the minimum latitude of the upper limit of the 99% confidence band of predicted daily locations calculated over ordinal dates 1–80 (spring) and 285–345 (fall) (as in Supp et al., 2015). Migrations that started or ended in the north (i.e., the end of Northern Hemisphere spring and the start of fall migration) used the maximum latitude of the lower limit of the 99% confidence band of predicted daily locations calculated over ordinal dates 80–175 (spring) and 225–285 (fall).

Migration timing was then fine-tuned with segmented regressions (segmented R package v1.0-0, Vito & Muggeo, 2008). The date calculated using the thresholds



**FIGURE 1** Mean location of bluebird populations overall (a–c) and by latitude (d–f) over 10 years for eastern (a, d), mountain (b, e), and western (c, f) bluebirds. In the maps (a–c), each point represents the daily mean weighted location of the population, colored by month; lines represent generalized additive model (GAM) smoothed migration paths, one for each year, colored by month. The latitude plots (d–f) show GAM smoothed predicted latitude (of the population centroid; black) overlaid with the calculated starts and ends of spring and fall migration.

in the previous step was used as the starting point, to determine the break point where there was no longer a relationship between predicted latitude and date. This resulted in a more precise calculation of the start and end of migration (as in Supp et al., 2015). We omitted the fall values during 2009 and 2012 for western bluebirds as the migration was too short and gradual for the start and ends to be detected in these years.

## Migration speed

Maximum daily migration speed for each species in each year was calculated for both spring and fall migration as the median distance traveled (in kilometers) over the five fastest days in each period and is expressed as kilometers per day (spring ordinal dates 1–175; fall ordinal dates 225–340; as in Supp et al., 2015). Date ranges extending



into the nonbreeding period were used because there was little movement in the nonbreeding period and to ensure that start and end of migration were not excluded from the calculations. As such, our measure of migration speed should be interpreted as the maximum population-level migration speed, rather than the flight speed of individual birds.

## Maximum latitude and median longitude

The maximum latitude during the breeding season for each species in each year was defined as the maximum predicted daily latitude (of the population centroid) between the end of spring migration and the start of fall migration. The median longitude of both spring and fall migrations for each species and each year was defined as the median predicted daily longitude between the calculated start and end dates of each migration period. The median breeding longitude was calculated as the median predicted daily longitude between the end of spring migration and the start of fall migration. As with migration timing, we omitted the fall values during 2009 and 2012 for western bluebirds as the migration was too short and gradual for the start and ends to be detected in these years.

## Statistical analysis

We ran a series of linear models with explanatory parameters, species, year, and their interaction, with the following response variables: start/end of spring/fall migration, spring/fall migration speed, maximum breeding latitude, median breeding longitude, and median spring/fall migration longitude. If we detected a significant interaction, we ran post hoc analyses as separate linear regressions for each of the three species to examine the relationship between year and the response variable independently. If the interaction was not significant, we removed it from the model. Significant differences among species were explored using post hoc analyses with the emmeans R package (v1.7.5, Lenth, 2018), controlling for multiple testing using the false discovery rate method. Significance was evaluated using an alpha value of 0.05 and analyses were completed using R (v3.6.2, R Core Team, 2020). Model residuals were assessed for normality and heteroscedasticity using the DHARMa R package (v0.4.3, Hartig, 2021). Results are presented as Type III ANOVAs (using the car R package v3.0-8, Fox & Weisberg, 2019), or, where interpretation of the slopes was required, as parameter estimates.

## Maps, data, and scripts

Maps were created using the R packages sf (v0.9-6, Pebesma, 2018) and ggplot2 (v3.3.2, Wickham, 2016), with data obtained from Natural Earth (<https://naturalearthdata.com>) via the rnaturalearth R package (v0.1.0, South, 2017). Raw data are available from eBird (eBird, 2019; Sullivan et al., 2009). Scripts for data summarization, analysis, and figures are available from Zenodo: <https://doi.org/10.5281/zenodo.6885688>.

## RESULTS

### Migration timing

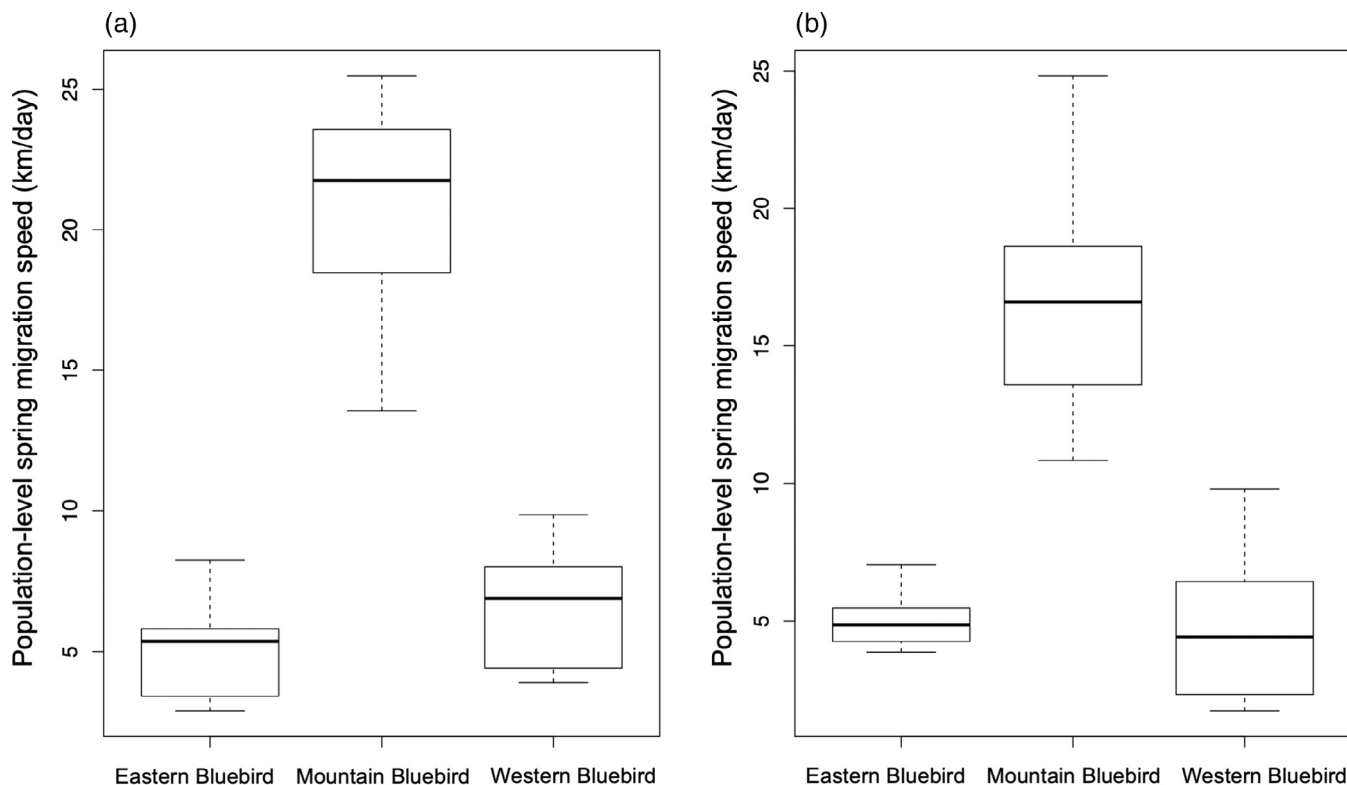
When examining migratory timing (Figure 1d–f), we found no significant year  $\times$  species interaction for the start ( $F_{2,24} = 0.24$ ,  $p = 0.79$ ) and end ( $F_{2,24} = 2.24$ ,  $p = 0.13$ ) of spring migration or the start ( $F_{2,22} = 0.66$ ,  $p = 0.53$ ) and end ( $F_{2,22} = 0.91$ ,  $p = 0.42$ ) of fall migration. Therefore, the interaction terms were removed from subsequent models (Appendix S1: Table S1). We found no effect of year on the start ( $F_{2,26} = 0.08$ ,  $p = 0.78$ ) or end ( $F_{2,26} = 1.02$ ,  $p = 0.32$ ) of spring migration or the start ( $F_{2,24} = 0.38$ ,  $p = 0.54$ ) and end ( $F_{2,24} = 2.75$ ,  $p = 0.11$ ) of fall migration. We found no significant effect of species on the start ( $F_{2,26} = 0.25$ ,  $p = 0.78$ ) of spring migration, but did find a significant effect on the end ( $F_{2,26} = 108.88$ ,  $p < 0.0001$ ) of spring migration as well as on the start ( $F_{2,24} = 11.77$ ,  $p = 0.0003$ ) and end ( $F_{2,24} = 5.68$ ,  $p = 0.010$ ) of fall migration.

### Migration speed

When examining migration speed (Figure 2), the interaction between year and species was not significant in spring ( $F_{2,24} = 0.75$ ,  $p = 0.48$ ) or fall ( $F_{2,24} = 1.02$ ,  $p = 0.38$ ) and was subsequently removed from the models (Appendix S1: Table S1). After removing the interaction term from the model, there remained no effect of year for spring ( $F_{2,26} = 0.94$ ,  $p = 0.34$ ) or fall ( $F_{2,26} = 2.98$ ,  $p = 0.10$ ). There was however an effect of species during both the spring ( $F_{2,26} = 108.44$ ,  $p < 0.0001$ ) and fall ( $F_{2,26} = 58.27$ ,  $p < 0.0001$ ).

### Maximum latitude during breeding

When we examined whether the maximum breeding latitude of the population centroids of the three species



**FIGURE 2** Differences in the spring (a) and fall (b) migratory speed of eastern, western, and mountain bluebirds. Speed of migration was calculated as the mean distance traveled (in kilometers) over the fastest 5 days. Boxplots represent the median value and interquartile range for each species (Q1 below as 25th percentile of data and Q3 above as 75th percentile of data).

changed over time, the interaction between year and species was not significant ( $F_{2,24} = 0.68$ ,  $p = 0.52$ ) and was subsequently removed from the model (Appendix S1: Table S1). We found an overall significant effect of species ( $F_{2,26} = 865.25$ ,  $p < 0.0001$ ) and year ( $F_{2,26} = 4.69$ ,  $p = 0.0396$ ) on maximum breeding latitude. Specifically, maximum breeding latitudes shifted southward by 0.053 degrees per year.

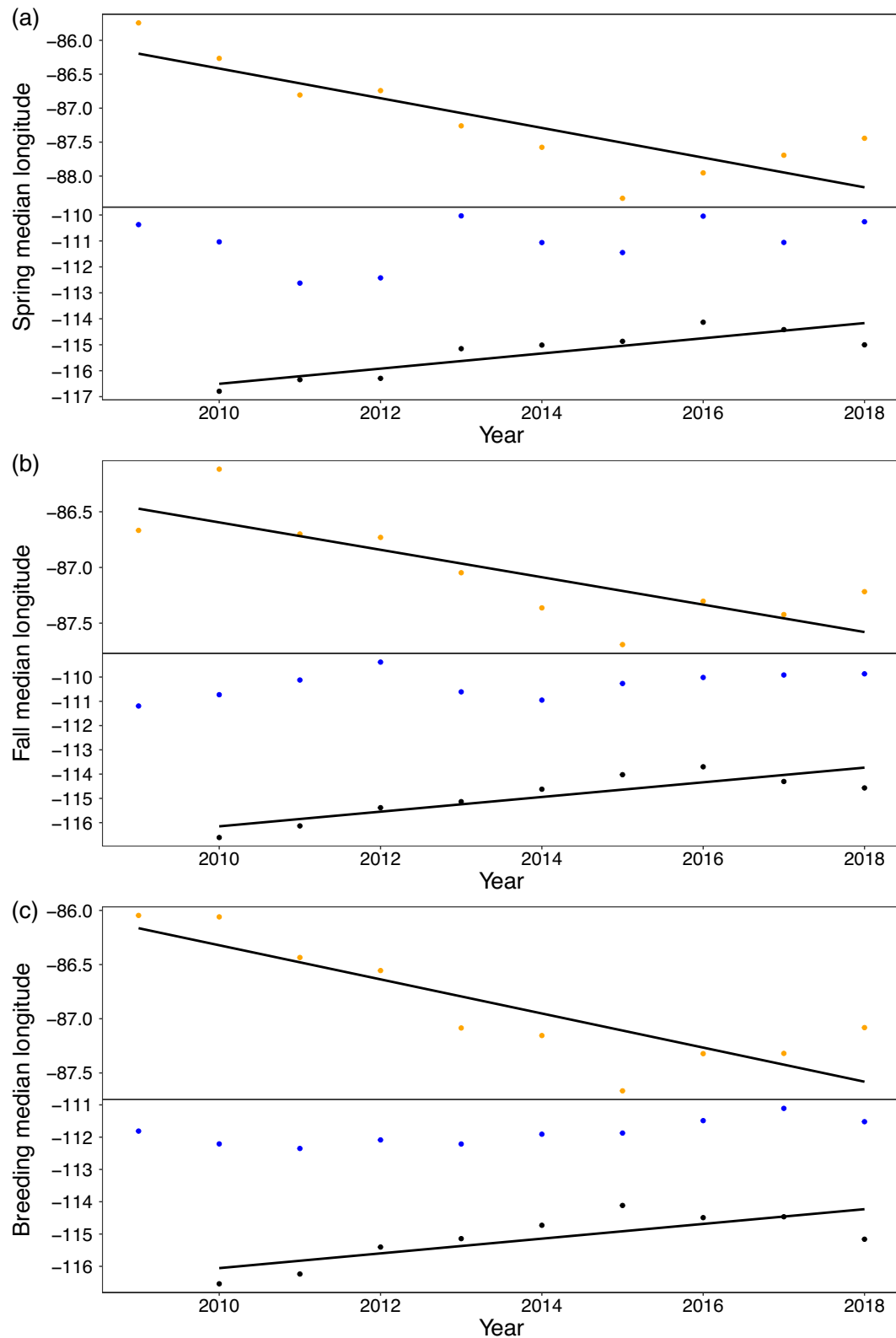
### Median longitude during migration

When we examined median annual longitude during migration, we found a significant year by species interaction for both spring ( $F_{2,24} = 11.05$ ,  $p = 0.0004$ ; Figure 3a) and fall migration ( $F_{2,22} = 14.46$ ,  $p < 0.0001$ ; Figure 3b). We then examined the relationship between median longitude and year separately for each species (Appendix S1: Table S2). The median longitude during spring migration for both eastern ( $r^2 = 0.66$ ,  $p = 0.009$ ) and western bluebirds ( $r^2 = 0.71$ ,  $p = 0.005$ ) changed from 2009 to 2018, with eastern bluebirds shifting their distribution westward by 0.22 degrees of longitude per year and western bluebirds shifting eastward by 0.26 degrees of longitude

per year. By contrast, for mountain bluebirds, the median longitude during spring migration did not change over that time period ( $p = 0.21$ ). Similar to spring migration, the median longitude during fall migration in eastern bluebirds shifted westward by 0.12 degrees of longitude per year ( $r^2 = 0.59$ ,  $p = 0.038$ ), while the median longitude during fall migration in western bluebirds shifted eastward by 0.31 degrees of longitude per year from 2009 to 2018 ( $r^2 = 0.68$ ,  $p = 0.0002$ ). As with spring migration, for mountain bluebirds, the median longitude during fall migration ( $p = 0.09$ ) did not change over time.

### Median longitude during breeding

When examining the median longitude of the population centroid during breeding (Figure 3c), the interaction between year and species was significant ( $F_{2,22} = 17.19$ ,  $p < 0.0001$ ). We then examined the relationship between median longitude and year separately for each species (Appendix S1: Table S2). The median longitude during the breeding period for eastern ( $r^2 = 0.69$ ,  $p = 0.003$ ), western ( $r^2 = 0.52$ ,  $p = 0.0007$ ), and mountain bluebirds ( $r^2 = 0.48$ ,  $p = 0.045$ ) changed from 2009 to 2018.



**FIGURE 3** Changes in the spring (a), fall (b), and breeding (c) median longitude during migration of eastern (black points), western (yellow points), and mountain bluebirds (blue points) from daily population centroid longitudes and latitudes predicted using generalized additive models. Bottom trend line shows western bluebirds shifting eastward whereas top trend line shows eastern bluebirds shifting westward. The horizontal line denotes a split on the y-axis, in order to show all three species efficiently.

We found that eastern bluebirds shifted their distribution westward by 0.16 degrees of longitude per year, western bluebirds shifted eastward by 0.24 degrees of longitude per year, and mountain bluebirds shifted eastward by 0.09 degrees of longitude per year.

## DISCUSSION

Using a 10-year community science dataset, we demonstrated consistent and rapid species-level changes in migration patterns of North American bluebirds, including shifts in migratory routes and breeding latitude and longitude. Somewhat surprisingly, bluebirds do not appear to be advancing the timing of spring migration and, in contrast to northward shifts seen in many other species, the population centroids during breeding appear to be shifting slightly southward. The strongest pattern we detected was a longitudinal shift during spring and fall migration, with both eastern and western (but not mountain) bluebirds migrating closer to the center of the continent. By examining three North American bluebird species concurrently, we were able to examine the differences in how these recently divergent lineages are responding to a rapidly changing planet.

There are some important considerations when interpreting our results, given that we were examining shifts in bluebird population centroids over time based on eBird checklists. While any shifts in population centroids over time could be caused by overall shifts in the population distribution, they could also be the result of changes in abundance or spatial variation in abundance over time. As discussed further below, potential northerly declining population trends could result in a contraction toward the core of the species range, resulting in an apparent southward shift in maximum breeding latitude in our case. Similarly, increases in abundance in certain parts of a species' range would tend to pull the species' centroid toward those areas, assuming increased abundance leads to a higher proportion of checklists including that species. Future studies could incorporate spatial variation in abundance based on BBS data (e.g., Bled et al., 2013) to control for this possibility. Another caveat has to do with the semi-structured nature of eBird data, especially when compared with structured programs such as the BBS that use randomly selected survey routes. While we used standard methods to control for effort level (e.g., only including complete checklists, weighting by proportion of checklists that included observations of a bluebird species, etc.), other sources of variation could include observer effects and imperfect detection of

birds. However, we do not have a strong reason to believe that these factors would change over time to produce a bias in our results.

Arriving early to the breeding grounds has been attributed to competition for mates and territories (Kokko, 1999), and advancements in spring arrival timing have been correlated to changing ecological conditions such as first-leaf and first-bloom dates (Buermann et al., 2013). Youngflesh et al. (2021) examined 56 bird species and found that fluctuations in spring phenology at the breeding grounds were broadly associated with earlier spring arrival dates. By contrast, and contrary to our predictions, we found no changes to the timing of spring migration or the spring arrival of any bluebird species. In addition to changes in breeding ground conditions, nonbreeding ground conditions may also affect the migratory timing of birds (Paxton et al., 2014; Robson & Barriocanal, 2011). Although we did not examine changes to breeding ground conditions, western and mountain bluebirds tend to arrive at their breeding grounds earlier in the season when compared with eastern bluebirds and other passerine species. We found that both species had mean arrival dates as early as March in some years and thus may be able to endure current climate-induced advancements in early spring phenology without yet needing to advance their arrival. Alternatively, interannual variation in environmental conditions, or variation in the strength of phenological adjustments throughout a species range (Youngflesh et al., 2021), could have masked any directional change in range-wide population-level migration timing over the relatively short time period that we examined.

While there were interspecific differences in migration speed (defined as the maximum population-level migration speed), we found that there was no change in the migratory speed of bluebirds over ten years. These interspecific differences in migration speed may be partially the result of divergent migratory strategies resulting from differences in the routes, stopover sites, and stopover durations the three species utilize along their migration paths. Another possibility is that the mountain bluebird population as a whole appeared to be moving more quickly because mountain bluebirds are the only species considered fully migratory. Similar to the issue of spatial patterns in abundance described above, the slower pace of eastern and western bluebirds could be the result of fewer members of these partially migratory populations moving as a proportion of the total population.

Poleward shifts have been observed across many taxa (Parmesan, 2006; Parmesan & Yohe, 2003) and are thought to be an ecological response to warmer



conditions in both winter and early spring at higher latitudes (Buermann et al., 2013; Rushing et al., 2020). A recent analysis of breeding distributions of 73 species of North American migratory birds based on the BBS showed that 55% of shifts were toward the north and 44% were toward the south from 1994 to 2017 (McCaslin & Heath, 2020). In this BBS study, bluebird species either showed no change, or shifted toward the north, depending on the species and region (the analysis examined eastern, central, and western regions of North America separately). Although our analysis is not directly comparable due to different data sources (eBird vs. BBS), time periods, and regional breakdown, our results are contradictory in that they suggest that the population centroids during breeding for the three bluebird species have shifted toward the south. As indicated above, an apparent shift in breeding distributions toward the south could potentially be explained by recently (2009–2019) declining population trajectories, at least for eastern and mountain bluebirds. However, McCaslin and Heath (2020) found that across the suite of species in their study, breeding distribution shifts could not be explained by trends in abundance, although results were variable across species and regions. An additional consideration is that we were unable to examine potential altitudinal shifts in our analysis, and bluebirds could also be responding to changing environmental conditions by shifting their ranges to higher elevations (Tingley et al., 2012). Taken together, our results and those of the above studies suggest that bluebird range edges may be shifting north, but that the center of abundance of their populations may have shifted southward. Another interesting pattern we observed was that population centroids during breeding tended to decline immediately following the end of spring migration in most years (Figure 1d–f). One likely explanation for this pattern is that young will generally fledge earlier at lower latitudes, and thus more bluebirds will be recorded at more southerly latitudes earlier in the breeding season, prior to the onset of fall migration.

The longitudinal shifts we detected during migration, with western and eastern bluebirds shifting toward the center of the continent, could potentially be explained by the Pacific and Atlantic Oceans limiting coastward range expansion, and the movement of human populations toward coastal areas (Neumann et al., 2015; Seto et al., 2011), reducing the available habitat in these regions (Isaksson, 2018). Thus, range expansion during migration could only occur toward the east for western bluebirds and the west for eastern bluebirds. Species' ranges may also shift in response to different population trends occurring in different parts of the range (Virkkala & Lehikoinen, 2017). For example, Hejl (1994)

and Duckworth (2009) proposed that changes in fire suppression regimes, along with nest box programs, have led to improved nesting opportunities for western bluebirds, facilitating an increase in population size—also supported by the BBS (see *Introduction*)—and an eastward range expansion. Potential range expansion of all three species through increased nesting opportunities may be supported by our finding that all three species have experienced shifts to their breeding ground longitude. In contrast to migration longitude where mountain bluebirds experienced no shift, we found that during breeding, mountain bluebird population centroids did in fact shift westward over the ten years we examined. This indicates that there may be shifts in a species' breeding longitude without a concurrent shift in their migration longitude.

With a changing environment due to climatic and other anthropogenic factors, conservation of migratory birds is increasingly critical, yet there is a lack of data on migratory systems, particularly outside of the breeding period (Marra et al., 2015). While standardized surveys such as the BBS focus on breeding bird populations and have been invaluable in estimating population trends, among many other uses (Rosenberg et al., 2019; U.S. Geological Survey and Canadian Wildlife Service, 2020), eBird presents the opportunity to track and monitor the movements and distributions of species throughout their entire annual cycle. Our findings demonstrate that shifting patterns of migration and changes in the mean population centroid (which could be the result of shifts in species ranges) are occurring within bluebirds and potentially other passerine species. For conservation efforts to be effective, we will need to understand how changes to population centroids reflect range-wide patterns of species' distributions and why these changes are occurring—a task that can be difficult using community science data such as eBird. However, data from eBird present an opportunity to address broadscale issues at a low cost, which is beneficial as directed funding can be limited and large-scale, long-term datasets are needed to answer some of the most pressing large-scale conservation issues. In addition to monitoring shifting migrations and breeding population centroids, eBird can identify high priority areas for designation and protection (Cañizares & Reed, 2020) or retroactively determine the effectiveness of conservation efforts (Cazalis et al., 2020).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Sonnleitner & LaZerte, 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6885688>.

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## SUPPORTING INFORMATION

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

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