Differential winter and breeding range shifts: Implications for avian migration distances

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Abstract

Aim: For many migratory avian species, winter and breeding habitats occur at geographically distinct locations. Disparate magnitudes and direction of shifts in wintering and breeding locations could lead to altered migration distances. We investigated how shifts in the centre of abundance (COA) of winter and breeding ranges have changed for 77 species of short-distance migratory birds. We addressed whether species tracked their historical average temperature and precipitation conditions at their winter and breeding COA, using data from 1990 to 2015.

Location: North America.

Methods: We calculated the COA for winter and breeding ranges from the National Audubon Society’s Christmas Bird Count and the North American Breeding Bird Survey. We regressed the annual change in distance (km) between the two annual COAs of each species as a proxy for change in migration distance. We constructed a series of generalized linear mixed models (GLMMs) to evaluate changes in average temperature and precipitation at the wintering and breeding COAs.

Results: Winter shifts in COA were predominantly northward. For most species, average temperature and precipitation that species experienced had not changed. Breeding shifts in COA varied in direction. For breeding season COAs, average temperature warmed, but average precipitation had not changed. Thirty-one species significantly decreased their migration distances, mainly driven by northward shifts in the winter range. Ten species increased their migration distances.

Main conclusions: Winter and breeding range shifts in COA have not occurred at the same magnitude and direction and have therefore impacted migration distance. Our results suggest that wintering and breeding range shifts occur independently and under different climate pressures.

Keywords
Breeding Bird Survey, Christmas Bird Count, migration, migration distance, shifts in abundance
1 | INTRODUCTION

Avian migration is an annual movement across landscapes to take advantage of seasonally variable resources (Alerstam & Lindström, 1990). It is a widely documented behaviour found on all continents and oceans (Alerstam, Hedenström, & Åkesson, 2003). The seasonal movement of migrating individuals has long-term impacts on biodiversity and ecosystem processes (Bauer & H owe, 2014). Understanding how migratory patterns are changing over time is important for conservation planning.

Anthropogenic land use and climate change are altering species distributions (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Hickling, Roy, Hill, Fox, & Thomas, 2006; Parmesan, 2006; Parmesan & Yohe, 2003; Sparks, Roy, & Dennis, 2005; Van der Hoek, Renfrew, & Manne, 2013; Van der Hoek et al., 2015; Walther et al., 2002). Predicting how migratory species might respond to landscape level changes presents additional challenges as breeding and wintering habitats generally occur at geographically disjoint locations (Knudsen et al., 2011). The effects of climate change are projected to be the most pronounced in the winter and at higher latitudes (IPCC, 2013; Virkkala and Lehikoinen 2014). The phenomena that elicit changes in species distributions in one portion of an annual range may not exist in another. Different portions of a migratory species’ range might experience different conditions throughout the annual cycle; therefore, it is necessary to look at each portion of the range independently to understand how distributions are changing throughout an annual cycle. If disparate magnitudes and directions of range shifts are occurring between breeding and wintering locations, the migratory distance between the two will likely change (Doswald et al., 2009; Huntley et al., 2006).

Northward range shifts have been documented in birds in summer (Hitch & Leberg, 2007; Thomas & Lenn on, 1999; Zucker berg, Woods, & Porter, 2009) and winter (La Sorte & Thompson, 2007). However, recent literature has emphasized that species-specific movements are more complex and variable due to the interactions between temperature, precipitation and land use changes (Lenoir et al., 2010; Tingley, Monahan, Beissinger, & Moritz, 2009; Van Der Wal et al., 2013). Multidirectional shifts—shifts having a latitude and longitude component—can be evaluated by incorporating measures of central tendency of a species range. Using central tendency measures, multidirectional shifts have been documented in North America and Europe for various birds, trees and plant species (Ash, Givnish, & Waller, 2017; Currie & Venne, 2017; Fei et al., 2017; Huang, Sauer, & Dubayah, 2017; Pavón-Jordán et al., 2019).

Most knowledge of how migration patterns might be changing in birds comes from ringed-bird data. In the Netherlands, Visser, Perdeck, van Balen, and Both (2009) analysed 72 years of ringed-bird recovery data and found half of the species experienced shortened migration distances. They implicate climate change as the mechanism for birds wintering closer to their breeding grounds. Potvin, Välimäki, and Lehikoinen (2016) found that winter and breeding range shifts do not necessarily occur at equal rates and not all species shift in the same direction, resulting in species-specific changes in migration distance. This research also suggests flexibility in migratory behaviour, influenced by independent environmental changes occurring between ranges.

The availability of high-quality, long-term datasets makes birds good candidates to observe effects of climate on species distributions. In this study, we use two long-term avian monitoring programmes, the North American Breeding Bird Survey (BBS; Pardieck, Ziolkowski, Lutmerding, Aponte, & Hudson, 2015) and National Audubon’s Christmas Bird Count (CBC; National Audubon Society, 2015). These datasets offer continental-scale quantitative data and represent some of the most systematic and complete sampling of any taxa. We examined changes in centre of abundance (COA) for temporally shifting breeding and winter ranges to understand how migration direction and distance is shifting between the two and used COA movement between seasons as a proxy for migration distance.

In this study, we address four complementary hypotheses to examine how species have shifted over time. First, we test the hypothesis that winter and breeding COAs have shifted at the same rate and direction. We expect that winter COA shifts will occur more rapidly northward than their breeding range counterparts. Our expectations are derived from recent studies of North American Birds which have documented northward winter range expansion (La Sorte & Thompson, 2007) but more species-specific variability of movements in the breeding season (Currie & Venne, 2017; Huang et al., 2017). Second, we test the hypothesis that the distance between winter and breeding COAs has not changed; therefore, migration distances have been unaffected. We expect that most species have decreased their distance between winter and breeding COAs and have experienced shortened migration distances driven primarily by northward winter COA shifts exceeding the rates of breeding COAs (Potvin et al., 2016; Visser et al., 2009). We further assessed two additional hypotheses of how temperature and precipitation have changed and evaluate if species have tracked their recent historical climate conditions. We test if temperature and precipitation have changed at the start-year (“stationary”) COA locations. A significant change at the “stationary” COAs provides evidence that species have experienced changes in temperature and precipitation from a previously occupied COA (a potential reason for species to shift away from a location). Last, we test if temperature and precipitation have not changed at the locations that species have annually shifted to (“shifting annual”) COA locations. Our expectation is that temporally unchanged conditions at a species “shifting annual” COA suggests that species have moved to areas with similar historic conditions.

2 | METHODS

2.1 | Winter and breeding range survey data

We calculated centre of abundance (COA) for winter (December-January) and breeding ranges (May-June) for North American short-distance migratory birds from 1990 to 2015 using CBC and BBS,
respectively. As COA calculations are sensitive to spatiotemporal bias, we restricted our analysis to this 26-year period. This helped to standardize the spatial sampling between our two datasets and to avoid artificial shifts in COA, which would be an artefact of the rapid addition of BBS survey routes prior to the years of our study.

The BBS is a network of annually sampled roadside survey routes. Surveys are conducted during the month of June to coincide with the peak of the breeding season for many avian species. Each route is 39.4 km long with 50 census locations spaced throughout. At each census location, a 3-minute point count is taken, where all birds that are seen or heard within a 0.4 km radius are recorded (Pardieck et al., 2015).

CBC censuses are conducted within a 2-week window around 25th December. Each census is annually surveyed in a 24.14 km diameter of a chosen centre point. The centre point of the circle does not vary from year to year. Abundances of all birds seen or heard within the circle are recorded (National Audubon Society, 2015). Effort data (in terms of party hours) can vary within and across CBC circles; therefore, we standardized the overall avian abundances in each CBC circle by the number of party hours for each count circle unit (Raynor, 1975).

To keep the network of routes relatively stationary over time, BBS routes and CBC circles were temporally filtered to exclude all routes missing 2 or more consecutive years of sampling. No routes south of the United States border met the filtering criterion. We eliminated areas where both BBS and CBC surveys were sparsely sampled by only including surveys that occurred below 56.6° latitude and fell between −125 and −75° longitude (as did Currie & Venne, 2017). Using these criteria, we retained 1,326 BBS routes and 1,321 CBC circles for the analysis. To check for any spatial bias between our datasets, we regressed the mean latitude and longitude of CBC and BBS sampling sites over time. For CBC locations, we found a 0.11 km/year shift south and a 0.78 km/year shift to the west. For BBS locations, we found no significant trend in latitude over time. We found a westward shift of 1.66 km/year for longitude. The effect of these shifts on species-specific responses should therefore be small and unbiasing.

### 2.2 Species selection and classification

We followed the migratory guild classification of BBS to obtain a pool of “short-distance migrants”: species whose migratory movements are primarily intra-continental in North America. Neotropical migrants (species that breed in the United States and Canada but overwinter in Mexico, Central America, South America and the Caribbean Islands) were not included in this analysis because most wintering ranges fall outside of the CBC coverage area. We further filtered out species with known irruptive migratory patterns—Pine Siskin (*Spinus pinus*), Red Crossbill (*Loxia curvirostra*), Evening Grosbeak (*Coccothraustes vespertinus*)—and coastal species whose COA for any year was over water—Fish Crow (*Corvus ossifragus*), Osprey (*Pandion haliaetus*), Tree Swallow (*Tachycineta bicolor*) and White-winged dove (*Zenaida asiatica*). In total, 77 species of short-distance migrants met these criteria for inclusion in this study.

### 2.3 Centre of abundance (COA) of latitude and longitude

For each species and range (winter and breeding), we calculated an annual COA. Each COA is an average longitude (x) and latitude (y) calculated from abundance indices from each location. For the winter ranges, the latitudes and longitudes in the calculation were from the centre point of each CBC circle. For breeding ranges, the latitudes and longitudes were from the starting point of each survey route. We used the following formulas to calculate an annual COA abundance for each species:

**Weighted latitude**

\[
\text{Weighted latitude}_t = \frac{\sum (\text{latitude}_i \times \text{abundance}_{i,t})}{\text{total abundance}_t}
\]

**Weighted longitude**

\[
\text{Weighted longitude}_t = \frac{\sum (\text{longitude}_i \times \text{abundance}_{i,t})}{\text{total abundance}_t}
\]

where latitude$_i$ and longitude$_i$ are the latitude and longitude of an individual site i and the corresponding abundance for year t. Total abundance is the sum of all individuals of the species for that year across all the sites (either BBS routes or CBC circles).

Annual COAs were derived from a paired weighted latitude, and weighted longitude:

\[
\text{COA}_t = (\text{weighted latitude}_t, \text{weighted longitude}_t)
\]

### 2.4 Direction of COA shifts

We regressed the annual latitude and longitude components of COA separately against year for each species (degree shift/year, R Core Team 2018). For the latitude component and the longitude component, we identified north and south shifts by regression slopes that were significantly greater or less than 0. Significant shifts to the north-east, south-east, south-west and north-west occurred when both the latitude and longitude components had significant regression slopes (e.g. shifts of COA to the north-east are the results of significant positive latitude and longitude slopes). We report these results in km shift/year.

### 2.5 Temperature and precipitation at COAs

We acquired seasonal temperature and precipitation variables from the CRU-TS 3.22 historical dataset (Mitchell & Jones, 2005) downloadable from the open-source software ClimateNA. v5.21 (http://tinyurl.com/ClimateNA), based on methodology described by Wang, Hamann, Spittlehouse, and Carroll (2016). Climate variables are gridded at a 0.5 × 0.5° resolution. We obtained average winter and summer temperature (°C) and precipitation (mm) for each COA/year combination. To evaluate whether species have tracked
temporal changes in average temperature and precipitation over the study period, we produced two sets of generalized linear mixed models (GLMMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In each of the models, average temperature and precipitation were the response variables and year as a continuous predictor, treating species as a random variable. We included species as a random effect in the model, therefore allowing the y-intercepts to vary among species which helped to account for geographic and species-specific differences in COA. In the first set of models, we used the initial winter and breeding range COA coordinates for each species from year 1990, assumed these COAs would not shift and traced the average temperature and precipitation at this “stationary” COA over time. If COAs do not shift, but climatic properties of those COAs do change, the birds experience changed climatic parameters. In the second set of models, we obtained the average temperature and precipitation at each annual “shifting” COA. If we detected no significant changes in temperature and precipitation at this “shifting” COA, then the birds experienced similar climatic parameters from year to year. We conducted this analysis to show the difference between unchanging conditions (as if the environmental conditions of 1990 remain constant), and what we deduce the birds experienced at shifting COAs. We provide the individual species regressions results in the Appendix S1.

2.6 | Migration distance analysis

As a proxy for migration distance, we calculated the Haversine distance (km) between winter and breeding COA for each year and species using R package ‘geosphere’ (Hijans, 2019). Haversine distance measures the shortest distance between two points on a sphere. This was a more precise measurement for changes between COA while accounting for the curvature of the Earth. Annual migration distance was regressed against year to test whether the slopes were significantly different from zero for each of the species. Significant positive or negative slopes indicate increasing and decreasing migration distance, respectively. Non-significant slope values indicate no change in migration distance. From this analysis, we partitioned species into groups: species with (a) statistically unchanged, (b) increased or (c) decreased migration distances over this time period (Figure 1). To evaluate average change in migration distance over time, we produced a GLMM with migration distance as the response and year as a continuous predictor, treating species as a random factor.

3 | RESULTS

3.1 | Directional shifts in winter versus breeding ranges

In winter, many species (31.1%) have not changed the location of their winter COA. For species with significantly changed COAs, the most frequently observed shift was to the north (29.8%), followed by north-east (11.6%), north-west (10.3%), east (7.9%), south (3.8%), south-east (2.5%), and west (2.5%). No species in this study shifted their winter COA to the south-west (Figure 2a).

During the breeding season, many species (22.0%) did not significantly shift their COA. When shifts in COA occurred, they were comparatively more variable in direction. The most frequently observed shifts were to the north-west (14.2%) and south-west (12.9%), followed by south (11.6%), north (10.3%), west (10.3%), east (7.7%), south-east (6.4%) and north-east (3.8%) (Figure 2b).

3.2 | Latitude shifts between seasons

On average, species in this study shifted the latitude component of their COA northward in winter and slightly southward during the breeding season. In winter, northward shifts occurred at an average rate of 3.09 km/year. In summer, this rate was significantly lower at −0.003 km/year and not significantly different from zero (t = 1.43, df = 76, p-value = 1.811e−05, Figure 3). The difference in these rates was driven by the larger number of species shifting the latitude component of their COA southward during the breeding season (e.g. as shown in Figure 2b).

3.3 | Longitude shifts between seasons

Longitude shifts in COA occurred at the same rate in the winter and breeding seasons and were not significantly different from zero. Winter ranges shifted slightly eastward at a rate of 0.092 km/year and slightly westward in the breeding season at 1.09 km/year (t = 1.43, df = 76, p-value = 0.155, Figure 4). These low rates of close to 0 km/year are driven by almost equal numbers of species shifting eastward and westward within a season. In addition, these shifts occurred at similar magnitudes within and between seasons.

3.4 | Average temperature and precipitation trends at COA

GLMMs showed that the average winter temperature and precipitation at the 1990 (“stationary”) COAs had significantly declined (p < .001) but had not significantly changed at the shifting annual COAs for either variable (Table 1). Average summer temperature had significantly increased at the stationary (p < .001) and shifting annual breeding range COAs (p < .001). Precipitation had not significantly changed at the stationary or shifting annual COA (Table 1).

3.5 | Impacts on migration distances

Across all species, average migration distances have decreased at a rate of −2.985 ± 0.38 km/yr (p = < .001). In this study, 36 (46.8%)
species did not significantly change their migration distance over the time period. In total, 41 species have changed their migration distance, and the majority of these shifts were attributed to significant shifts in latitude, with fewer species exhibiting changes due to shifts in longitude. We found a decrease in migration distance for 31 (40.3%) species and increased migration distance for 10 (12.9%) species (Figure 5). Of the group of species who have decreased their migration distance, 22/31 of these were driven by northward winter shifts of COA exceeding the rate of breeding shifts of COA. Many species demonstrated decreased distances between winter and breeding COA by a combination of southward shifts in breeding COA and northward shifts in winter COA (Appendix S1). For four species, Red-shouldered Hawk (Buteo lineatus), Bald Eagle (Haliaeetus leucocephalus), Western Meadowlark (Sturnella neglecta) and Lesser Goldfinch (Spinus psaltria), the decreased distance between winter and breeding COA are explained by significant shifts in longitude (Figure 5, Appendix S1).

Ten species have increased their distance between their winter and breeding COA (Figure 5). For 6 species, these increases were the result of latitude shifts in breeding COA exceeding the rate of shift in the winter COA counterpart. Shifts in longitude explained the increased migration distance for 4 remaining species; American Crow (Corvus brachyrhynchos), House Finch (Haemorhous mexicanus), Fox Sparrow (Passerella iliaca) and Bewick’s Wren (Thryomanes bewickii) (Appendix S1).
Despite the prevalence of migratory species, literature on migratory systems is disproportionately small (Berger, 2004; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009). Understanding how migratory patterns are changing under climate change is important for long-term conservation planning and management. This study uses broadscale spatiotemporal abundance survey data to examine interseasonal shifts in COA, and how these shifts are potentially altering migratory distances. Assessment of how migration distances are changing is scarce in the literature, but we can speculate that these changes are occurring and have consequences on both individual fitness and long-term population trends for migratory birds.

Recent literature emphasizes species-specific multidirectional shifts in distributions (Currie & Venne, 2017; Fei et al., 2017; Gillings, Balmer, & Fuller, 2015; Huang et al., 2017; VanDerWal et al., 2013). Complex interactions between temperature and precipitation are driving species-specific responses to changes in climate (Garcia, Cabeza, Rahbek, & Araújo, 2014; Tingley, Koo, Moritz, Rush, & Beissinger, 2012; Tingley et al., 2009; VanDerWal et al., 2013). Birds have been shown to geographically track their historical climatic niches (Tingley et al., 2009, Illán, et al. 2014). While most studies focus on temporal changes occurring within a single season, there are few comparative studies looking at species-specific shifts between two distinct periods (but see Potvin et al., 2016; Zurell, Graham, Gallien, Thuiller, & Zimmermann, 2018). We offer evidence that environmental variables are differentially tracked between seasons and that distributions throughout the annual cycle are independent. These temporal and disjunct seasonal changes in distributions suggest flexibility of migratory behaviour, at least at the macroecological scale.

We found that winter movements in COA were primarily occurring in a northward direction, with 51.9% of the species having a significant northward shift in the latitude component of their COA. Our results are consistent with the pole-ward shifts documented in North American birds during the winter (La Sorte & Thompson, 2007) and in Europe (Potvin et al., 2016; Visser et al., 2009). Our reaffirmation of northward winter shifts was therefore not surprising, as birds are known to be physiologically constrained by winter temperatures (Root, 1988) and temperature-driven northward shifts of wintering birds have been widely documented (La Sorte & Thompson, 2007; Lehikoinen et al., 2013; Pavón-Jordán et al., 2019). Although our finding that winter temperatures have declined at the stationary COAs appear to be at odds with the current global warming trends (United States Global Change Research Program, 2018), cooling trends in the south and south-eastern United States have been documented since the 1950s. This large area of declining temperatures is referred to as the U.S. "warming hole" (Pan et al., 2004). The "warming hole" is likely the product of increased temperatures in the Arctic and the cool air of melting of sea ice being driven southward by air currents, creating cooler than expected temperatures in parts of the United States during the winter (Partridge et al., 2018). Of our 77 "stationary" COAs, 45 occur east of −100°W longitude and fall approximately within the warming hole as mapped by Partridge et al. (2018). Though our cooling trend is significant, the slope of this relationship is very small, representing a 0.26°C cooling over the 26-year time period (Table 1).

In this study, average winter temperature and precipitation have remained consistent at the shifting annual COA for most species. Climate conditions as a whole appear to be an important factor for wintering locations for migratory birds (Pérez-Moreno, Martínez-Meyer, Soberón Mainero, & Rojas-Soto, 2016; Somveille, Rodrigues, & Manica, 2015). Despite northward shifts in winter COAs, we did not detect many instances where temperature was significantly changing at these shifting annual COAs. From the resolution of our data, it appears that species are shifting their winter COAs in a manner consistent with the pattern of climate change (Chen et al., 2011; Parmesan & Yohe, 2003).

We found that breeding season movements of COA were more variable in direction in comparison with winter movements. Despite
this variability, most species experienced warming at both their 1990 "stationary" and “shifting annual” COA. Average precipitation, however, was unchanged at the 1990 “stationary” and “shifting annual” COAs. Maintaining consistent annual precipitation might be important as precipitation during the breeding season is known to limit survivorship in birds (Sillett, Holmes, & Sherry, 2000) and is indirectly linked to food resource availability (Carroll, Cardinale, & Nisbet, 2011).

Avian species distributions appear to be susceptible to environmental changes along longitudinal gradients, as well as latitudinal ones. Westward shifts were common; 37.6% of the species had significant westward longitude shifts in their breeding COA. Our results are consistent with two recent analyses of North American birds that also found high occurrences of avian abundances shifting west during the breeding season (Currie & Venne, 2017; Huang et al., 2017). Additionally, Fei et al. (2017) examined 86 tree species across the eastern United States and most commonly observed westward range shifts over the course of 30 years. Sapling recruitment was highest at the western edges of ranges, particularly for drought-resilient species with the ability to exploit increasing moisture patterns within drier, western areas. Interaction between warming temperature and changing precipitation patterns offers the potential to differentially impact species via their individual tolerances, which might explain our observed variability in summer.

While significant shifts in COA were evident between seasons, 46.8% of the species in this study have not shifted their winter and summer COAs enough to impact migration distance. We categorize these results in three ways: (a) neither summer nor winter COA has shifted (seven species), (b) winter and summer COA shifts have occurred in roughly equal magnitudes and directions (five species), or (c) direction and magnitude of a COA shift in one season are not large enough to significantly affect migration distance (24 species). This last point highlights that measurements of COA shifts and migration distance are occurring at independent scales. In addition, the coarse scale of the data might not provide an adequate resolution to detect the smallest of movements.

When species significantly changed the distance between their COAs, we found a propensity towards shortened migration
distances. The primary driver was winter COA shifts occurring more northward compared to breeding COA shifts. Studies using banded-bird data have reported similar results (Siriwardena, Wernham, & Baille, 2004; Fiedler, Bairein, & Köppen, 2004; Potvin et al., 2016; Visser et al., 2009). In total, 40.3% of species decreased the distance between winter and summer COA; similar proportions have been reported for European birds (Visser et al., 2009). Shortened migration distance in response to climate change may offer a competitive edge, particularly for short-distance migrants by allowing migrants to more quickly track seasonal conditions between their wintering and breeding grounds (Coppack & Both, 2002). The advancement of spring phenology has been well documented in the Northern Hemisphere (Cayan, Kammerdiener, Dettinger, Caprio, & Peterson, 2001; Schwartz, Ahas, & Aasa, 2006), which has resulted in resource mismatches for migratory birds (Both & Visser, 2001; Møller, Rubolini, & Lehikoinen, 2008; Saino et al., 2011). In response, earlier arrival of short-distance migrants has been documented with North American birds (Butler, 2003), a pattern consistent with northward shifts in wintering range and decreased migration distances (Visser et al., 2009).

We infrequently observed species that increased migration distance: only 10 (9.2%) species. Visser et al. (2009) found that no bird in their study had significantly increased migration distances; however, Potvin et al. (2016) found more variability in migration distance change over a similar time period. Longer migration distances are presumably disadvantageous. The risk of mortality during the annual cycle is most likely the highest during migration (Klaassen et al., 2014; Sillett & Holmes, 2002), and increased migration distances will likely increase energy expenditure during an already physiologically taxing journey. As a result, birds might remain at stop-over sites for longer periods of time (Goymann, Spina, Ferri, & Fusani, 2010) or increase en route travelling times between wintering and breeding grounds.

Though the coverage of the CBC and BBS is extensive, they are not without limitations. For example, they do not sample the entirety of each species’ range, even for species that occur within the boundaries of survey coverage. However, these datasets still provide the most consistent geographic and temporal coverage for our study period. We completed the COA analysis on a more conservative species pool, where we only incorporated species with greater than 50% of their breeding and winter ranges within CBC and BBS coverage (as estimated by their range maps in Birds of North America species accounts). Our results from this smaller species pool are fundamentally similar to those we report here (see highlighted species in the Appendix S1). Differences in longitude shifts between seasons are likely due to the small sample size of the smaller data set. We believe that although coverage might be limited for some species, the incorporation of our larger species pool is more representative of the multispecies geographic trends that are occurring.

The focus of this study was to evaluate changes in migration distances under climate change; however, species-specific shifts as a result of other ecological phenomena were also captured by analysing COA shifts. For example, House Finches (H. mexicanus)—a species endemic to the western United States—were introduced to New York in the 1940s (Elliott & Arbib, 1953). Since then, they have experienced a rapid, and continuing, westward expansion (Bock & Leptine, 1976; Veit & Lewin, 1996). Similarly, Bald Eagles (H. leucocephalus), which were historically widespread and endemic to North America, rapidly declined in the continental United States in the early 1900s due to the rampant agricultural use of dichloro-diphenyl trichloroethane (DDT). Following the Federal ban of DDT, as well as the effectiveness of Federal protection programmes, Bald Eagles have recolonized much of their historical range, particularly in the eastern United States (Watts, Therres, & Byrd, 2007). We emphasize that although climate might be a primary driver of COA shifts, other ecological phenomena, such as invasion and re-colonization, may be helping to drive shifts.

To be successful, migratory birds will ultimately have to respond to environmental changes that vary throughout their annual cycle. Our results suggest that winter and breeding range shifts are occurring independently, and under different climate pressures. Therefore, conservation programmes should emphasize impacts that occur during all parts of the avian cycle.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the USGS North American Breeding Bird Survey [https://www.pwrc.usgs.gov/bbs/RawData/] and the National Audubon Society’s Christmas Bird Count [http://netapp.audubon.org/cbcobervation/].

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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