

3-2020

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This is the peer reviewed version of the following article:

McCaslin, H.M. & Heath, J.A. (2020 March). Patterns and Mechanisms of Heterogeneous Breeding Distribution Shifts of North American Migratory Birds. *Journal of Avian Biology*, 51(3), e02237. which has been published in final form at <https://doi.org/10.1093/auk/ukaa051>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley's version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

Patterns and Mechanisms of Heterogeneous Breeding Distribution Shifts of North American Migratory Birds

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Abstract

There is widespread evidence that species distributions are shifting in response to climate change. Warming temperatures and climate niche constraints are hypothesized drivers of northward shifts in temperate migratory bird breeding distributions, but heterogeneity in the direction of distribution shifts suggests that the climate niche hypothesis does not explain all changes in distributions. We propose that: 1) changes in migration costs and benefits related to dampened seasonal differences between breeding and winter areas, 2) sensitivity to supplemental cues that affect duration of migration and onset of reproduction, 3) a latitudinal mismatch-driven fitness gradient, or a combination of these drivers may explain southward distribution shifts. We examined latitudinal shifts in breeding distribution centroids for 73 species of migratory birds from 1994 - 2017 across eastern, central, and western regions of North America using Breeding Bird Survey data and tested if life history characteristics related to the above hypotheses and population status were associated with shift patterns. We found that 44% of regional centroid shifts were southward, 55% were northward, and several species shifted in different directions in different regions. Migratory strategy and protandry predicted breeding distribution centroid shifts, although they tended to be more predictive of northward shifts than southward shifts. There was evidence that supplemental cues explained some southward shifts because herbivorous birds tended to shift southward compared to insectivores, or raptors that shifted northward. Shifts in centroids were not explained by trends in abundance, suggesting that centroid shifts were not attributable to population declines or increases at distribution margins. Our results show the prevalence of heterogeneous breeding distribution shifts, including often overlooked southward shifts, and suggest that more work is needed to develop alternative hypotheses that would explain southward shifts in distributions.

Keywords: Breeding bird survey, distribution centroid, global change, migration, range shifts

Introduction

Species distributions are shaped by complex interactions among many factors, including physiology, phylogeography, competition, and dispersal. Climate change has had widespread effects on species distributions because temperature directly affects energy budgets and physiological tolerances (Somero 2010, Rapacciuolo et al. 2014) and indirectly affects species interactions (e.g. Renner and Zohner 2018). In the Northern hemisphere, it has been frequently hypothesized that species distributions will shift northward to track suitable climate niches (Lawler et al. 2013, Hovick et al. 2016). However, some studies of North American migratory birds have reported southward shifts in distribution (Zuckerberg et al. 2009, Hovick et al. 2016) suggesting that additional factors may contribute to distribution changes (Lenoir et al. 2010, Currie and Venne 2017). Changes in the distribution and abundance of migratory bird species are likely to have cascading effects on ecosystem function and structure (Bauer and Hoyer 2014). Therefore, it is important to better understand patterns of distribution shifts and the underlying mechanisms that drive these changes. Given that distribution shifts are variable across taxa (Lenoir et al. 2010, Rapacciuolo et al. 2014), more work is needed to understand how different mechanisms may be driving distribution changes in different locations or for species with different life histories.

In the Northern hemisphere, wintering distributions of many migratory bird species have shifted northward. La Sorte and Thompson (2007) found that winter range boundaries and centers of abundance for 254 migratory species in North America were shifting north. Northward shifts in wintering distributions are associated with shorter migration distances between breeding and wintering sites (Visser et al. 2009) and warming winter temperatures (MacLean et al. 2008, Heath et al. 2012). This shift may confer fitness benefits because closer proximity between non-breeding and breeding ranges may allow individuals to better anticipate conditions in breeding areas, facilitating earlier arrival on breeding territories, which may improve reproductive performance (Heath et al. 2012). Thus, for winter distributions, the combination of reduced migratory costs and reproductive benefits of shorter migrations may act synergistically to shift centroids north.

Compared to the relative consistency of northern shifts in winter distributions, the direction and magnitude of recent shifts in breeding distributions have been more heterogeneous among species. In New York state, 57% of avian species' mean breeding latitude shifted northward and 43% of species' mean breeding latitude shifted southward from 1980 to 2005 (Zuckerberg et al. 2009). In the central United States, northward shifts in breeding distributions were shown in 52% of avian species, and southward shifts were shown for 24% (Hovick et al. 2016). Despite this evidence for southward breeding distribution shifts, few hypothesized mechanisms have been proposed to explain these patterns (though see Lenoir et al. 2010, Chen et al. 2011, Lawler et al. 2013).

We propose three non-mutually exclusive hypotheses to explain southward shifts in breeding distribution centroids. First, migratory movement is an adaptive response to seasonal environments and strong seasonal resource peaks in temperate areas have been a driver of greater migration tendency and distance throughout avian evolutionary history, resulting in the northward expansion of breeding distributions (Cox 1968, Alerstam et al. 2003). Prolonged growing seasons (Peñuelas and Filella 2001, Richardson et al. 2013) and rapidly warming winters (Vitasse et al. 2018, Zohner and Renner 2019) associated with climate change are dampening the seasonal differences between breeding and wintering grounds and may change the costs and benefits of migration, leading to decreased migration distances (Austin and Rehfish 2005). If changes in seasonality and migration affect distribution shifts, we predicted short-distance migrants or species with overlapping breeding and wintering distributions would shift southward, contracting their breeding range and shortening migration distance, because these species are likely to be facultative migrants and adjust migratory programs in response to environmental factors (Ramenofsky et al. 2012). Second, supplemental cues (e.g. temperature, presence of conspecifics, vegetation green-up) influence migratory timing, cessation, and the onset of reproductive readiness (Gwinner 1977, Wingfield et al. 1992). Up to this point, most studies that have investigated avian migratory responses to changes in supplemental cues have focused on temporal adjustments to migration (e.g. Bridge et al. 2010, Studds and Marra 2011), but we expect that changes in cues likely have spatial effects as well. For example, climate-driven advancement of growing seasons may alter supplemental cues such as resource availability that in turn, affect migration duration (Bridge et al. 2011, Studds and Marra 2011), resulting in southward shifts. We expected that diet would influence species' distribution shifts because spring phenology is shifting at different rates for plants, invertebrates, and vertebrates (Visser and Both 2005). Specifically, we predicted that herbivorous species would shift southward faster than insectivorous or carnivorous species because of the rapid advancement of green up, which is a likely cue for food availability and the start of the breeding season. Additionally, we predicted that species that migrate diurnally and with conspecifics would be more likely to respond to changes in supplemental cues. Diurnal migration may facilitate visual cues that provide information on food resources and environmental conditions (Ward and Raim 2011). Social information mediates responses to supplemental cues and can result in changes to migratory progress and timing (Helm et al. 2006, Ramenofsky et al. 2012, Teitelbaum et al. 2016). Finally, migration strategies can evolve or change quickly in response to environmental changes (Pulido 2007). Climate change is altering seasonal phenology and has rapidly advanced the onset of growing seasons causing mismatch between the availability of prey resources and the arrival and breeding of migratory birds (Visser and Both 2005, Saino et al. 2011). Northern populations may be more vulnerable to mismatch compared to southern populations (Sanz 2003), which may result in a latitudinal fitness gradient leading to southward distribution centroid shifts. Here, we predicted that specialists, territorial species, or protandrous species would be more likely to experience negative consequences of mismatch (Julliard et al. 2003, Helm et al. 2006, Jonzén et al. 2007, Day and Kokko 2015, Pearce-Higgins et al. 2015) and more likely to exhibit southward shifts in breeding distribution centroids compared to generalists, non-territorial species, and non-protandrous species.

We examined shifts in the center of abundance (distribution centroids) for migratory birds in eastern, central, and western regions of North America over a 23-year period (1994 - 2017) coinciding with anthropogenic climate change. We use life history traits of species to assess the hypotheses to explain centroid shifts (supplementary material). We

used migration type (complete or partial), migration distance, overlap of breeding and wintering range, and average wintering latitude to examine whether climate-driven changes in seasonality explained southward shifts in centroids. We used diet (herbivore, insectivore, carnivore), circadian migration patterns (nocturnal or diurnal), and conspecific group size during migration to examine whether changes in supplementary cues were associated with distribution shifts. We used habitat specialization, territoriality, and presence of protandry (i.e. if males tend to arrive earlier on the breeding grounds) to examine whether phenological mismatch in northern breeding areas created a latitudinal selection gradient. Finally, we explored whether shifts in centroids were the result of trends in abundance by using population status to explain changes in distribution.

Methods

We used a two-step approach for estimating centroid shifts of migratory birds. First, we used data from the North American Breeding Bird Survey (BBS) to estimate annual abundance of 73 species of migratory birds from 1973-2017. Then, we used linear models for each species to analyze latitudinal abundance centroid shifts by year for 1994-2017, a period of rapid climate change, and assessed associations between shifts and life history traits. We analyzed shifts in abundance centroids separately for eastern, central, and western regions in North America (Fig. 1) because many species that occur over a large area can occur in different habitats, express different phenotypes, and are exposed to different patterns of climate change across the continent. Therefore, species may exhibit different distribution dynamics in different portions of their range.

The BBS is a large scale avian monitoring project in which each breeding season, observers sample designated 40 km routes throughout the United States and Canada using a series of three-minute point counts. Since its inception in 1966, the BBS has established over 5,200 unique routes, but observers vary in their ability to detect species on routes and detect fewer birds their first year than in subsequent years (Link and Sauer 2002). As a result, BBS counts are biased by combinations of observers and routes, observer experience, and variation in effort through space and time. Therefore, BBS counts adjusted for sampling effort, experience, and spatial and temporal heterogeneity are a useful index of species abundance (Link and Sauer 2002), and the abundance centroid is useful for addressing distribution questions over a large-scale (Huang et al. 2017, Hovick et al. 2016). Centroid (center of mass, weighted latitudinal/longitudinal mean, or center of abundance) describes overall distribution patterns without being heavily influenced by changes at the range margins. Thus, it is a good metric to assess the central tendency of a distribution, and changes to the abundance centroid may not mirror behavior at the range margins (Huang et al. 2017, Virkkala and Lehikoinen 2014, Massimino et al. 2015).

We restricted our study to the contiguous United States and Canada below 52 degrees North, because 97.5% of unique route runs have occurred below 52 degrees North. We selected migratory species that represented a range of broad life history traits and that were each recorded in a minimum of 10 BBS strata within a given region during the study period to ensure an adequate sample size for each species (Huang et al. 2017). Additionally, for each species, we removed records from any strata in which the species was detected on fewer than four routes to ensure enough samples per stratum (Huang et al. 2017). We maintained the distinction used by the BBS between subspecies of Northern flickers (*Colaptes auratus auratus* and *C. a. cafer*) and dark-eyed juncos (*Junco hyemalis hyemalis*, *J. h. oreganus*, and *J. h. caniceps*) throughout analyses, but combined one record of Harlan's hawk (*Buteo jamaicensis harlani*) with records for red-tailed hawks (*B. jamaicensis*).

We obtained data from the BBS for all years and species available at the BBS FTP site (Pardieck et al. 2018) and filtered the data to include only surveys on which at least one of the 73 species included in our analysis was detected. We used the species total (total observations of a species across all stops) for each route as the species counts in the analyses. We defined 'strata' as the intersections of Bird Conservation Regions (BCRs, Bird Studies Canada 2016) and state or province boundaries, similar to Link and Sauer (2002) and Huang et al. (2017). We calculated annual species centroids within these spatial units because BCRs represent areas with similar biogeographical characteristics, and when intersected with political boundaries, also represent management units for wildlife, so sampling effort and habitat is roughly homogenized within these units (Huang et al. 2017).

We used a hierarchical model to compute annual abundance indices in each stratum for each species from the raw route totals. For species that occurred in more than one region, we ran this model separately for each region because BBS counts are affected differently by sampling through time and space, so region-specific sampling parameters may be more accurate than continent-wide estimates (Link and Sauer 2002, Link and Sauer 1998).

$$\text{Count} \sim \text{neg binomial}(\lambda_{i,j,t}, \epsilon_{i,j,t}) \quad (1)$$

$$\log(\lambda_{i,j,t}) = S_i + \beta_i t + \omega_j + \eta I(j, t) + \gamma_{i,t} \quad (2)$$

$$N_{i,t} = A_i z_i \exp(S_i + \beta_i \hat{t} + \gamma_{i,t}) \quad (3)$$

$$Y_t = \frac{\sum_i N_{i,t} y_i}{\sum_i N_{i,t}} \quad (4)$$

We used the hierarchical model shown in Equations 1 and 2 to calculate adjusted stratum-specific annual species abundance indices to adjust counts for route-, observer-, and stratum-level sampling effects, which is a modification of the model for BBS counts presented by Link and Sauer (2002). In the model, in which i indexes stratum, j indexes unique observer-route combinations, and t indexes year, the raw counts are modeled by the stratum-specific intercept (S_i) and a stratum-specific slope (β_i) multiplied by centered year (\hat{t}). A term for observer and route specific effects (ω_j), a binary term for first year sampling effects ($\eta I(j, t)$), and interactive year-stratum effects ($\gamma_{i,t}$) were included to account for bias associated with sampling and observers. We modeled route abundance using a negative binomial distribution with overdispersion term $\epsilon_{i,j,t}$, because BBS counts are overdispersed relative to a Poisson distribution. All hyperparameters were given weakly informative, normally-distributed priors with mean zero, and variances for all hyperparameters were allowed to vary independently. We calculated abundance indices in R using the Bayesian package INLA, which is an alternative to Markov Chain Monte Carlo (MCMC) for fitting Bayesian models that can include georeferenced and spatial point data in models (Lindgren and Rue 2015, Rue et al. 2009). In Equation 3, A_i is the area of stratum i divided by the total area of all the strata in the region that the species is present in, calculated independently for each region, and z_i is the number of routes in stratum i that the species was present on divided by the total number of routes in the stratum (Link and Sauer 2002). We used the posterior means of the abundance indices ($N_{i,t}$) and the geographic centers of the strata ($y_{i,t}$), calculated in ArcGIS, to calculate yearly regional abundance centroids for each species (Eq. 4).

In the second step of analysis, we used the annual centroid estimates to analyze latitudinal shifts in regional center of abundance by modeling the locations of the annual centroids against year (centered) in a linear model for each species. We restricted our study to years between 1994 and 2017 because evidence of anthropogenic climate change and biological responses began to appear in the early 1990s (Hughes 2000, Easterling et al. 2000). We categorized shifts as northward if 95% of posterior samples for the regression slope were positive, and shifts as southward shift if 95% of posterior samples were negative and summarized shifts as mean velocity (km per year) of region-specific species estimates. We ran the centroid regressions using Hamiltonian Monte Carlo sampling in Rstanarm (Carpenter et al. 2017, Stan Development Team 2017), running each model with four chains for 1000 burn-in and 1000 sampling iterations per chains and assessed model convergence with Rhat and by visually assessing chain blending.

We assigned species values for the following life history traits according to species records on Birds of North America Online (Rodewald 2015) and grouped traits according to our three hypotheses: migration type, migration distance, overlap of breeding and wintering range, and average wintering latitude to test our hypothesis about changes in seasons affecting migratory strategy; diet, circadian migration patterns, and conspecific group size during migration to test the role of supplemental cues in shifts; and habitat specialization, territoriality, and presence of protandry to test the influence of mismatch-driven latitudinal fitness clines (details about trait assignment and predictions in Supplemental Material). Within each region, we used linear mixed models to estimate the effect of life history characteristics on estimated average yearly shift velocities. We first compared all single covariate models within each hypothesis group to select the most predictive covariates because covariates within hypothesis groups tended to be correlated and therefore could not be included in the same model. Then, we used the most predictive covariate from each hypothesis to construct models with covariates from two or three hypotheses, combined both additively and interactively, and compared these to single covariate models to find the most predictive model overall. We included a random effect of taxonomic family in all models to control for the effect of phylogeny (similar to Acampora et al. 2016, Donald et al. 2018). We implemented these models in a Bayesian framework using Rstanarm (Carpenter et al. 2017) with weakly informative priors for the covariate parameters. We included all estimated shift velocities in our linear mixed models, including those for species for which the shifts were not significant, because there were relatively equal nonsignificant shifts in both northward and southward directions and because their inclusion did not affect interpretation.

We calculated population status in each region for each species over the 23-year period by modeling the regional annual abundance indices (\tilde{N}_t , Eq. 5) by year in linear models in Rstanarm. We classified regional species status as “Increasing” if 95% of posterior samples for the regression slope were positive, “Decreasing” if 95% of posterior samples for the regression slope were negative, and “No change” otherwise. We used population status as the predictor and the estimated centroid shift velocities (regression slopes) as the response in one linear model per region to assess if population abundance trends over the study period predicted shift magnitude and direction.

$$\tilde{N}_t = \sum_i N_{i,t} \quad (5)$$

We used efficient leave-one-out cross validation (LOO-CV) via the R package loo (Vehtari et al. 2018) for model selection, and verified that LOO-CV model selection was not biased by small group sample sizes by comparing LOO-CV results with Bayesian model stacking model weights (Yao et al. 2018), because using LOO-CV to select a single best model from a set of many models can sometimes cause overfitting with small sample sizes (Piironen and Vehtari 2017, Supplemental Material). We used Bayesian stacking weights to compare the relative importance of the models in our model sets, and the weights mirrored the LOO-CV results, suggesting models did not have high support because they were overfit.

Results

We found shifts in breeding distribution centroid in at least one region for 54 of the 73 North American migratory bird species and subspecies (Fig. 1). The average velocity of northward centroid shifts was 3.67 km per year, suggesting an average northward shift over the 23-year period of approximately 84 km. The average velocity of southward centroid shifts was 2.72 km per year, suggesting an average southward shift over the 23-year period of approximately 63 km. Yellow-breasted chats (*Icteria virens*) and barn swallows (*Hirundo rustica*) exhibited the greatest southward shifts, moving an average of 10 km per year and 9 km per year, respectively, between 1994 and 2017, with projected total centroid shifts of over 200 km over the 23-year period.

Some species occurred and were analyzed in multiple regions, resulting in a total of 142 centroids analyzed across all regions. Sixty-one percent ($n = 86$) of all region-specific centroids shifted, and of these region-specific centroid shifts, 44% percent ($n = 38$) were southward and 55% ($n = 48$) were northward (Fig. 2). Of the 43 species analyzed in two or three regions, 14 species shifted the same direction across all regions, 25 species had a shift in one region and no shift in another region, and six species had shifts in opposite directions in different regions (Tables 1-3). Only three species showed shifts in the same direction across all three regions: barn swallows and yellow-breasted chats both shifted south across all three regions, and purple martins (*Progne subis*) shifted north across all three regions.

There was some evidence that migratory strategy (partial or complete migrant) explained centroid shift velocity and direction in the central region (Fig. 3), but not in the eastern or western region. Partial migrants were 18% more likely to shift northward than complete migrants, though neither group shifted substantially in either direction (95% CIs: complete [-10.30, 9.76], partial [-8.09, 11.83]).

Diet (carnivorous, insectivorous, or herbivorous) predicted centroid shift velocity in the eastern and western regions, but not in the central region. In the eastern and western regions, centroids of primarily carnivorous species (birds of prey) have shifted north more than those of insectivores or herbivores. Average shift velocities for carnivores were 7.53 km per year in the eastern region and 2.47 per year in the western (Fig. 4). The probability that a carnivorous species had shifted north in the eastern region was over 0.99, and in the western region was 0.75. Centroid shifts for insectivores varied, leading to an average shift velocity near zero in both regions (95% CIs: eastern [-4.52, 5.66]; western [-6.86, 6.65]). Herbivores also had average shift velocities near zero in both the eastern and western regions (95% CIs: eastern [-5.10, 5.86]; western [-8.66, 6.35]), but in the western region, the probability that an herbivorous species shifted south was 0.63.

In the eastern region, the best-performing model included whether or not a species displayed protandrous spring arrival. Species with protandry were about 15% more likely to shift northward than those that do not have differential arrival (Fig. 3).

The direction of shifts was not correlated with whether a species was increasing, decreasing, or stable in regional population abundance over the study period (Table 4).

Discussion

We found that latitudinal shifts in breeding distribution centroids of migratory bird species were not uniform in direction, nor were shifts of one species consistent across regions. We found some support that life history traits explained directional velocity of centroid shifts, though several results were in the opposite direction of what our hypotheses would predict. For example, if dampened seasonality between breeding and wintering grounds resulted in southward shifts, we predicted that partial migrants would be more likely to shift south. In the central region, however, partial migrants were more likely to shift northward than complete migrants. We did find that in the eastern and the western regions, carnivorous species shifted northward, insectivorous species did not shift consistently in one direction, and herbivorous species showed a tendency to shift southward. These results were consistent with the prediction that species sensitive to supplemental cues (i.e., vegetation green-up) may shift southward because of advancing growing seasons. In the eastern region, protandry tended to predict a weakly northward shift. Trends in abundance were not correlated with centroid shifts, suggesting that directional shifts were not the result of a change in the population declines overall. Thus, life history was an important component of breeding distribution centroid shifts for many migratory birds. The best-supported model differed by region suggesting that mechanisms of distributional centroid shifts were complex and likely the result of several factors.

Distribution centroids of partial migrants in the central region were more likely to shift north, while centroids of complete migrants were more likely to shift south. We had predicted that partial migrants would be more likely to shift south than complete migrants because partial migrant populations contain both migratory and resident individuals. Thus, resident behavior may develop more quickly if benefits of migration decrease as seasonal differences between breeding and wintering ground dampen. While this result does not support the dampened seasonality hypothesis, it may provide insight into another potential mechanism. Migrants within partial migrant populations tend to be relatively short-distance migrants compared to migrants from completely migratory populations. Short-distance migrants may rely more on supplemental cues and be better able to track resources on breeding grounds compared to long-distance migrants that rely on predictive cues, such as photoperiods (Sullivan et al. 2016) and are constrained by more ‘hard-wired’ migratory schedules (Ramenofsky et al. 2012). These patterns are consistent with Hovick et al.’s (2016) analysis of bird species occurring in the central United States which showed that short-distance migrant distributions have shifted north and neotropical migrant distributions have not shifted.

Diet explained centroid shifts in eastern and western regions of North America. Carnivorous species consistently exhibited greater northward shifts than species with primarily insectivorous or herbivorous diets. This may be because this group consisted predominantly of raptors, which tend to have larger body sizes and relatively longer nesting and brood-rearing periods than smaller species (Lack 1968), so they may benefit from breeding farther north and advancing the timing of reproduction (Heath et al. 2012, Martin et al. 2014) in response to earlier springs at higher latitudes where short breeding seasons previously constrained reproduction.

If changes in supplemental cues affected migration cessation and onset of reproduction, we predicted that distribution centroid of insectivores and herbivores would shift southward because these species are likely to use emergence of vegetation as a supplementary cue for reproduction during a relatively short period of resource abundance (Ramenofsky et al. 2012), and earlier springs with less latitudinal gradient in onset would cause them to encounter these cues earlier during migration. This prediction was supported for some insectivorous species, like bobolinks, which shifted southward and have been shown to track primary productivity with migration movements (Renfrew et al. 2013), and yellow-breasted chats and swallows, which showed large southward centroid shifts across all regions, but was not supported for insectivores as a whole. Herbivorous species showed a higher tendency to shift south. Some of these species may use primary productivity to time migration, moving northward with the progression of spring so that they can breed during peak resource availability (Shariatinajafabadi et al. 2014, Thorup et al. 2017), and advancing springs may cause individuals to encounter vegetation cues to initiate breeding prior to returning the full distance to their original breeding grounds.

We found some evidence that protandry predicted northward breeding distribution shifts in the eastern region, where protandrous species were slightly more likely to shift north than non-protandrous species. However, the high amount of variation within both groups suggests that there are more factors interacting with protandrous migration to affect distribution shifts, and we did not find strong evidence for our hypothesis that a fitness advantage of more southern territories is a driver of centroid shifts.

Population status did not predict the direction of centroid shifts, indicating that southward shifts in abundance centroid cannot be attributed to declines in abundance in the northern portion of the range with steady populations throughout the rest of the range. Rather, the lack of a relationship between population trends and centroid shifts suggests redistribution of abundance within a species distribution in a region, and, when considered with the regional variation in shift direction for many species, indicates that drivers of distributional change act on species and populations across multiple scales.

Our results highlight that distributional responses to global change are highly variable, and that southward shifts are a possible strategy for coping with change, despite a lack of hypotheses in the literature predicting southward shifts. Our results that 55% of centroid shifts were northward and 44% of shifts were southward are similar to other multispecies studies of distribution shifts (Zuckerberg et al. 2009, Currie and Venne 2017, Huang et al. 2017). We did not find strong predictors of southward shifts in breeding distribution centroid, similar to other studies that have shown southward shifts in distributions without clear evidence of an effect of life history (e.g. Zuckerberg et al. 2009). Therefore, it seems that as a whole, we do not have a grasp on drivers of changes to breeding distributions, likely because it is difficult to study the complex processes underlying these changes, and it is important that we broaden our perspective in the study of breeding distributions and global change to consider the multitude of possible responses shaped by many interacting factors, including processes during other parts of the annual cycle.

Maximizing the benefits of reproducing in a seasonal environment and minimizing the costs of annual long-distance movement is a key determinant of distributions for migratory birds (Cox 1985, Alerstam et al. 2003, Winger et al. 2018), and current climate change may cause migratory tendency to decrease in some species (Austin and Rehfisch 2005, Pulido and Berthold 2010). Selection for shortening migration distances as a result of warmer temperatures has been documented in fall migrations as many species are short-stopping to winter closer to the breeding grounds (Visser et al. 2009, Heath et al. 2012, Paprocki et al. 2014). Shortening of migration has not been expected to impact breeding distributions because philopatry is an important factor in breeding distributions (Winger et al. 2018). However, anecdotal evidence of migratory birds establishing breeding populations outside of their historical breeding ranges by shortening spring migration (Yeh and Price 2004, Van der Jeugd et al. 2009, Macias-Duarte 2011, Garcia-Perez et al. 2013, Winkler et al. 2017) indicates that migratory birds may respond to environmental change in a way that decreases philopatry. In this study, we provide evidence of southward shifts in breeding distribution centroids, which may indicate a tendency towards shortening spring migration and could compound the fitness benefits of shortening migration via shifting wintering distributions. There is still much to understand about the dynamics of breeding distributions, especially southward shifts in abundance, and we encourage more hypotheses and investigation into drivers of these shifts given overwhelming evidence of heterogeneous distributional responses to global change.

Acknowledgements

We thank the Breeding Bird Survey staff at the USGS Patuxent Wildlife Research Center for maintaining and coordinating survey efforts and data, and to the volunteers who conduct surveys for the BBS. We are also grateful to Bryce Robinson and Casey Lott for their feedback during the development of this project and for reviewing an earlier draft, and to Håvard Rue for his help with the INLA code.

Author Contributions: Both authors conceived the study idea and design, analyzed the data, and wrote the manuscript.

Data Availability: The data associated with this manuscript will be archived in an institutional repository at the time of publication of the manuscript.

Declarations: The authors declare that they have no conflict of interest.

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Table 1 Summary of eastern region breeding distribution centroid abundance shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift Direction	Shift Velocity	Projected Total	Population
		(km/yr)	Shift (km)	Status
Osprey	North	6.66	153.24	Increasing
Red-tailed Hawk	North	2.13	48.88	Increasing
Northern Harrier	North	11.67	268.50	Increasing
Sharp-shinned Hawk	North	9.67	222.40	No change
Killdeer	South	-3.81	-87.56	Decreasing
Chimney Swift	North	1.99	45.68	Decreasing
Ruby-throated Hummingbird	North	4.30	98.92	Increasing
Northern Flicker (Yellow-shafted)	North	4.91	112.90	Decreasing
American Kestrel	North	2.32	53.46	Decreasing
Acadian Flycatcher	No shift	0.05	No shift	Increasing
Least Flycatcher	No shift	1.04	No shift	Decreasing
Eastern Phoebe	South	-4.06	-93.32	Increasing
Eastern Kingbird	South	-1.32	-30.32	Decreasing
Loggerhead Shrike	No shift	0.84	No shift	Decreasing
Red-eyed Vireo	North	1.83	42.06	Increasing
White-eyed Vireo	No shift	0.21	No shift	Increasing
Yellow-throated Vireo	No shift	0.17	No shift	Increasing
Warbling Vireo	South	-0.64	-14.69	Increasing
Bell's Vireo	No shift	0.98	No shift	Increasing
Purple Martin	North	1.48	34.14	Decreasing
Barn Swallow	South	-4.02	-92.48	Decreasing
Tree Swallow	South	-5.43	-124.94	Decreasing

Red-breasted Nuthatch	No shift	1.25	No shift	Increasing
Sedge Wren	North	1.73	39.69	Decreasing
Marsh Wren	No shift	-0.62	No shift	Decreasing
House Wren	No shift	0.16	No shift	Increasing
Blue-gray Gnatcatcher	No shift	0.19	No shift	No change
Ruby-crowned Kinglet	North	2.33	53.69	Increasing
Eastern Bluebird	No shift	0.00	No shift	Increasing
Wood Thrush	South	-2.18	-50.22	Decreasing
American Robin	South	-1.64	-37.80	Increasing
Cedar Wax wing	No shift	-1.23	No shift	Decreasing
Pine Warbler	North	5.34	122.83	Increasing
Yellow Warbler	North	2.73	62.74	Decreasing
Common Yellowthroat	North	3.34	76.72	Decreasing
Kentucky Warbler	No shift	0.17	No shift	Decreasing
Yellow-throated Warbler	North	0.61	13.94	Increasing
Black-and-white Warbler	No shift	0.26	No shift	Decreasing
Chestnut-sided Warbler	No shift	-0.99	No shift	Decreasing
Worm-eating Warbler	No shift	-0.22	No shift	Increasing
Hooded Warbler	North	1.97	45.34	Increasing
Prairie Warbler	South	-1.72	-39.50	Decreasing
American Redstart	No shift	0.77	No shift	Decreasing
Black-throated Blue Warbler	North	2.13	49.03	Increasing
Canada Warbler	North	3.15	72.38	Decreasing
Nashville Warbler	No shift	1.50	No shift	No change
Yellow-breasted Chat	South	-0.65	-14.91	Decreasing
Henslow's Sparrow	South	-1.77	-40.69	Increasing
Song Sparrow	North	1.39	32.05	Decreasing

Dark-eyed Junco (Slate-

colored Junco)	North	3.68	84.60	No change
Bobolink	South	-1.62	-37.18	Decreasing
Baltimore Oriole	South	-1.11	-25.44	Decreasing
Purple Finch	No shift	1.57	No shift	Decreasing
American Goldfinch	No shift	0.18	No shift	No change

Table 2 Summary of western region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift	Shift Velocity	Projected Total	Population
	Direction	(km/yr)	Shift (km)	Status
Osprey	No shift	0.79	No shift	Increasing
Red-tailed Hawk	North	0.83	19.07	Increasing
Golden Eagle	No shift	1.47	No shift	Decreasing
Northern Harrier	No shift	1.80	No shift	Increasing
Swainson's Hawk	No shift	0.04	No shift	Increasing
Sharp-shinned Hawk	North	11.35	261.02	Decreasing
Killdeer	South	-2.40	-55.27	Decreasing
Long-billed Curlew	No shift	0.97	No shift	Increasing
Vaux's Swift	No shift	-2.76	No shift	Decreasing
Northern Flicker (Red-shafted)	No shift	-0.98	No shift	Decreasing
American Kestrel	South	-2.31	-53.21	Decreasing
Prairie Falcon	No shift	1.03	No shift	Increasing
Dusky Flycatcher	South	-3.58	-82.38	Decreasing
Gray Flycatcher	South	-1.58	-36.29	Increasing
Western Wood-Pewee	South	-1.04	-23.90	Decreasing
Say's Phoebe	No shift	0.81	No shift	Increasing
Eastern Kingbird	North	0.77	17.74	Increasing
Loggerhead Shrike	North	3.07	70.70	Decreasing
Red-eyed Vireo	No shift	-0.30	No shift	Decreasing
Warbling Vireo	North	4.81	110.70	Increasing
Purple Martin	North	9.52	219.05	Increasing
Barn Swallow	South	-9.04	-208.01	Decreasing

Tree Swallow	No shift	-0.60	No shift	Decreasing
Red-breasted Nuthatch	No shift	0.14	No shift	Decreasing
Marsh Wren	North	2.37	54.57	Increasing
House Wren	North	2.42	55.69	Increasing
Blue-gray Gnatcatcher	No shift	-0.60	No shift	Increasing
Ruby-crowned Kinglet	No shift	1.73	No shift	Decreasing
Western Bluebird	North	2.54	58.40	Increasing
Mountain Bluebird	North	2.14	49.20	No change
American Robin	North	1.11	25.42	Decreasing
Sage Thrasher	No shift	-0.34	No shift	Decreasing
Cedar Wax wing	No shift	-1.57	No shift	Decreasing
Yellow Warbler	South	-3.06	-70.30	Decreasing
Common Yellowthroat	No shift	0.20	No shift	Increasing
Nashville Warbler	North	4.69	107.90	No change
Black-throated Gray Warbler	South	-1.83	-41.99	Decreasing
Yellow-breasted Chat	South	-1.64	-37.70	Increasing
Song Sparrow	South	-1.66	-38.25	Decreasing
Dark-eyed Junco (Oregon Junco)	South	-4.13	-94.97	Decreasing
Dark-eyed Junco (Gray- headed Junco)	South	-3.17	-72.81	No change
Purple Finch	No shift	0.12	No shift	Decreasing
American Goldfinch	South	-2.96	-68.19	Decreasing
Cassin's Finch	No shift	-0.72	No shift	Decreasing

Table 3 Summary of central region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift	Shift Velocity	Projected Total	Population
	Direction	(km/yr)	Shift (km)	Status
Red-tailed Hawk	South	-1.32	-30.33	Increasing
Golden Eagle	North	17.62	405.35	Increasing
Northern Harrier	No shift	0.98	No shift	Decreasing
Swainson's Hawk	South	-2.55	-58.61	Increasing
Sharp-shinned Hawk	No shift	6.93	No shift	No change
Killdeer	No shift	0.05	No shift	Decreasing
Long-billed Curlew	No shift	-1.16	No shift	Decreasing
Chimney Swift	North	5.49	126.24	Decreasing
Ruby-throated				
Hummingbird	No shift	-2.61	No shift	No change
Northern Flicker (Yellow-shafted)	North	2.08	47.73	Decreasing
Northern Flicker (Red-shafted)	North	3.88	89.21	Decreasing
Northern Flicker (unid. Red/Yellow shafted)	No shift	4.97	No shift	Increasing
American Kestrel	No shift	-1.26	No shift	Decreasing
Prairie Falcon	No shift	-0.23	No shift	Increasing
Least Flycatcher	South	-1.72	-39.53	Increasing
Western Wood-Pewee	North	1.74	39.93	No change
Say's Phoebe	North	2.27	52.17	No change
Eastern Phoebe	South	-2.28	-52.50	Increasing
Eastern Kingbird	North	1.51	34.81	Decreasing

Loggerhead Shrike	North	6.37	146.52	Decreasing
Red-eyed Vireo	North	3.23	74.39	Increasing
Yellow-throated Vireo	No shift	-6.54	No shift	Increasing
Warbling Vireo	South	-2.91	-67.03	Increasing
Bell's Vireo	No shift	0.27	No shift	Increasing
Purple Martin	North	1.38	31.71	Decreasing
Barn Swallow	South	-2.63	-60.54	Decreasing
Tree Swallow	South	-2.62	-60.26	Increasing
Sedge Wren	No shift	0.68	No shift	No change
Marsh Wren	North	0.81	18.74	Increasing
House Wren	North	1.66	38.16	Decreasing
Blue-gray Gnatcatcher	No shift	0.14	No shift	Increasing
Mountain Bluebird	No shift	-1.94	No shift	Decreasing
Eastern Bluebird	No shift	-0.88	No shift	Increasing
American Robin	North	1.35	31.06	Increasing
Cedar Wax wing	South	-3.54	-81.36	Increasing
Chestnut-collared				
Longspur	No shift	-0.22	No shift	Decreasing
Yellow Warbler	No shift	-0.28	No shift	Increasing
Common Yellowthroat	North	4.29	98.61	Decreasing
American Redstart	North	1.29	29.75	Increasing
Yellow-breasted Chat	South	-10.01	-230.30	Increasing
Song Sparrow	No shift	0.13	No shift	Increasing
Bobolink	South	-0.34	-7.87	Increasing
Baltimore Oriole	South	-4.06	-93.33	Decreasing
American Goldfinch	South	-0.84	-19.28	Decreasing

Table 4 Ninety-five percent (95%) credible intervals for breeding distribution centroid shift velocity (km per year) by regional population status for East, West, and Central regions from 1994-2017. Population status did not predict shift velocity, except in the east region, where species with no change or an increase in abundance index were slightly more likely than species with a decreasing population abundance to shift north.

	East	West	Central
No change	(-3.51, 9.49)	(-6.60, 8.61)	(-7.81, 10.86)
Increasing	(-4.34, 7.35)	(-5.22, 8.03)	(-9.28, 8.33)
Decreasing	(-5.65, 5.99)	(-7.42, 6.09)	(-7.80, 9.55)

Figure 1. Map illustrating regions, strata, and centroids for 73 species and subspecies of North American migratory birds. Strata, outlined in black, are the intersections between Bird Conservation Region boundaries and state or province boundaries. Dots are regional species centroids in 1994 and color represents whether regional species abundance, estimated using a hierarchical model to account for stratum, route, and observer sampling bias, decreased (orange), increased (green), or did not change (yellow) from 1994-2017. Fifty-four regional species centroids shifted over the 23-year period, and black arrows illustrate the projected latitudinal shift of the species centroid, based on the average shift velocity (km per year) for the species over the 23 years. Note that these arrows do not illustrate longitudinal shift in centroid, which is outside the scope of this study.

Figure 2. Significant shifts in breeding distribution centroids for North American migratory bird species by region from 1994 – 2017. Counts above the horizontal axis (pink) are northward shifts, and counts below the horizontal axis (blue) are southward shifts.

Figure 3. Relationship between (a) presence of protandry in the eastern region and (b) migratory strategy in the central region and species' breeding distribution shift velocities from 1994-2017. Box plots represent posterior distributions of the best performing model for each region, and open circles are the data. (a) In the eastern region, species with protandrous migration were slightly more likely to shift northward than those that do not display protandry. (b) In the central region, partial migrants were more likely to shift northward and complete migrants were more likely to shift southward, although neither group shifted substantially in either direction.

Figure 4. Relationship between primary diet and species' breeding distribution shift velocities in the (a) western and (b) eastern regions from 1994-2017. Box plots represent posterior distributions of the best performing model for each region, and open circles are the data. Vertebrate-eating species shifted northward with average velocities of 2.5 and 7.5 km per year in the western and eastern regions respectively. Species with primarily invertebrate diets did not shift in either direction, and plant-eating species were slightly more likely to shift southward than northward.

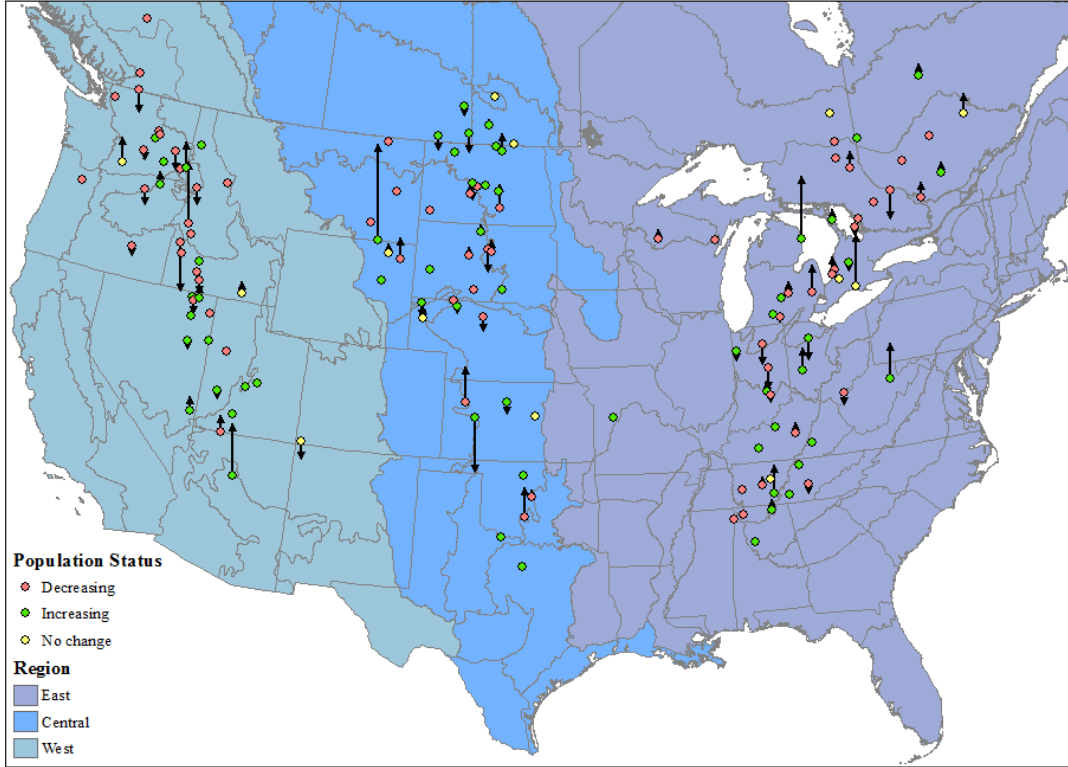


Figure 1

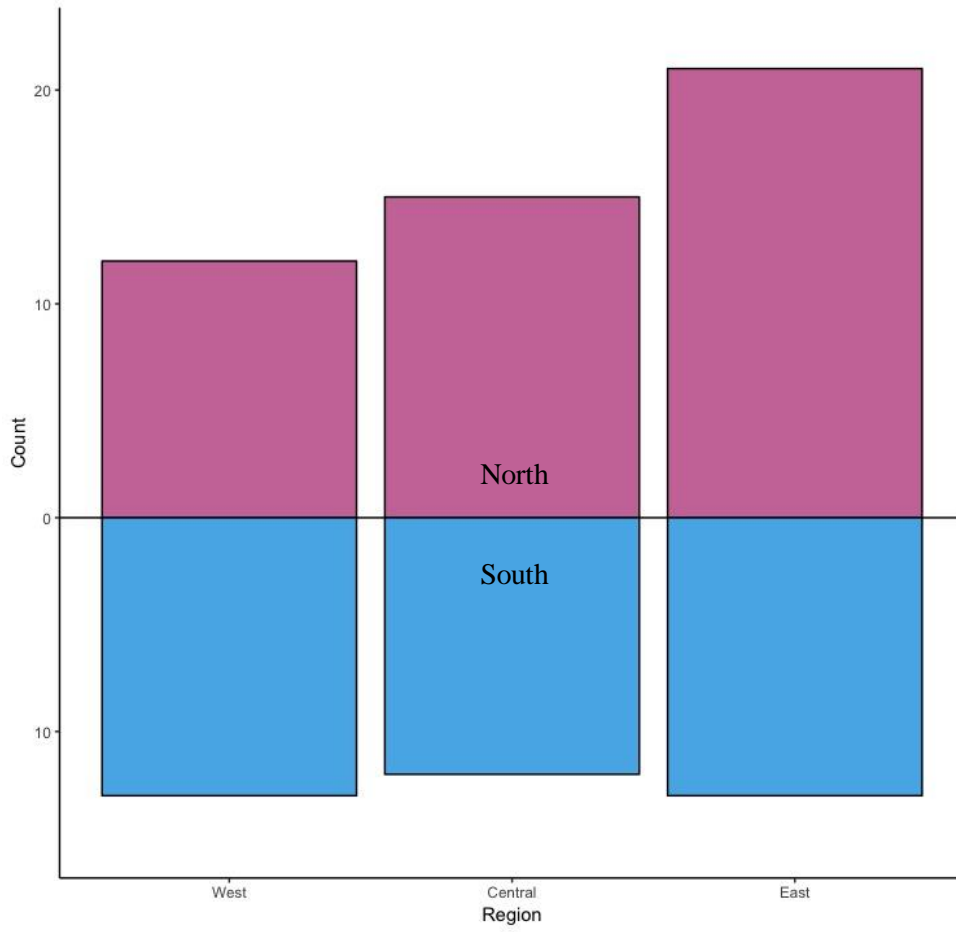


Figure 2

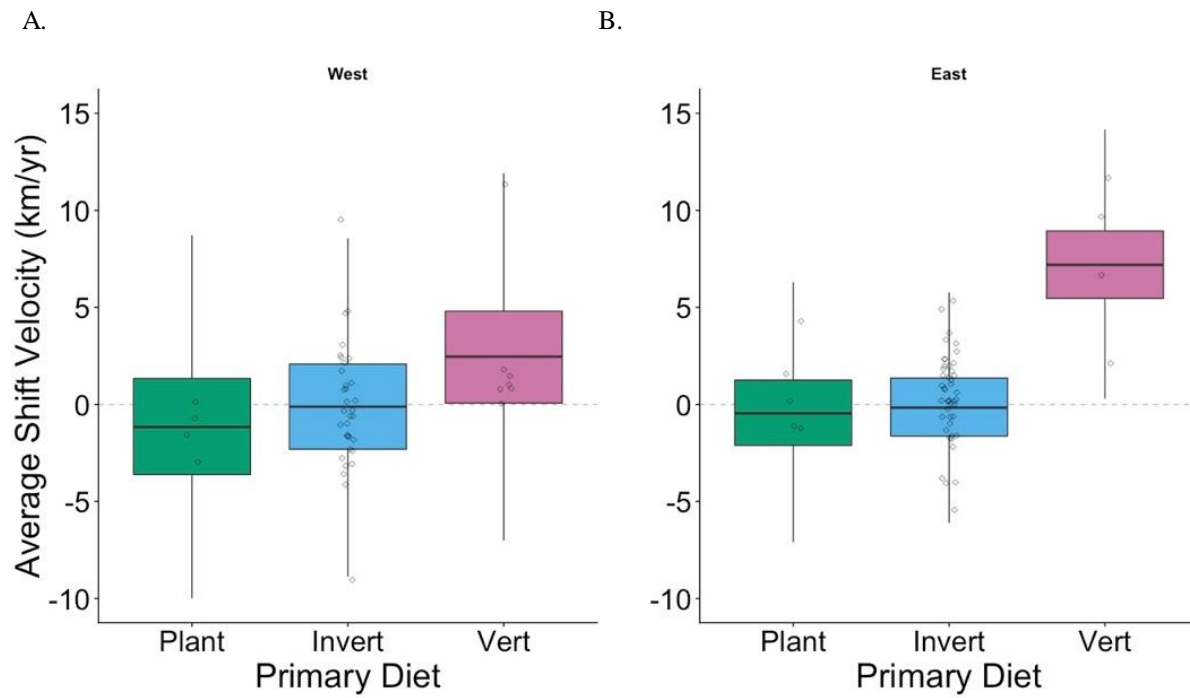
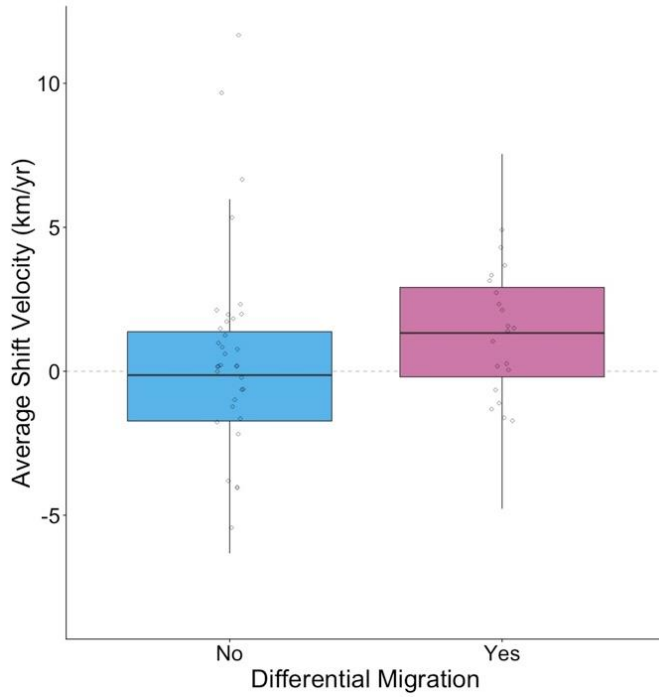


Figure 3

A.



B.

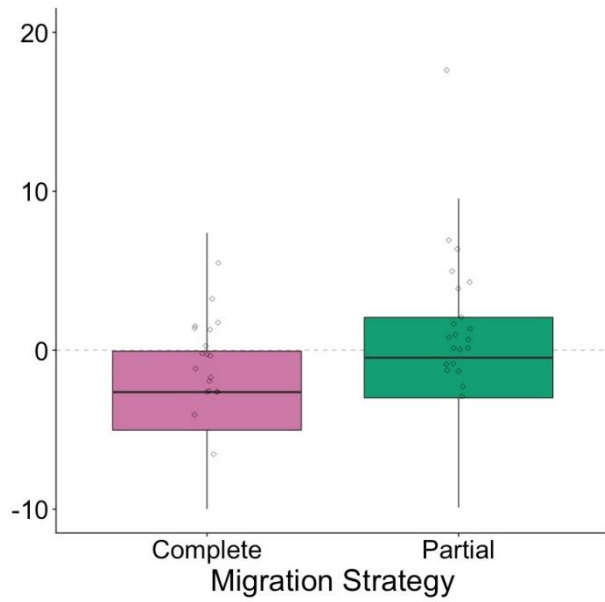


Figure 4