AN ABSTRACT OF THE DISSERTATION OF

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Title: Are Bird Habitat Associations Consistent Across Space and Time?

Abstract approved: ____
Matt G. Betts

The concept of the fundamental niche is frequently used in ecology to define the set of environmental conditions needed by a species to survive and reproduce (Hutchinson 1957). In contrast, the realized niche constitutes the locations where a species actually occurred, which is a function of both the environmental (abiotic) conditions and biotic interactions (e.g., predation, competition, mutualisms; Soberon and Peterson 2005). Up to now, the realized niche of most species has been mostly examined during breeding seasons and researchers have long assumed that niches should remain constant across species' ranges and across the avian annual cycle. If this assumption is valid, then the conservation of each species across their full annual cycle is made easier because each species is associated with a single niche. However, if species have more than one realized niche, then we risk misleading conservation efforts by protecting the wrong habitat in some regions or seasons.

In this dissertation, I aim to identify whether most species exhibit a single realized niche, or rather, that species have multiple niches that change depending on age and sex (Ch.2), geographic location (Ch. 3) or the stage of the annual cycle (Ch.4).

More specifically, in chapter 2, I assembled a large dataset representing the capture (and release) of Rufous Hummingbirds (*Selasphorus rufus*) and calculated migration routes and timing across age and sex categories. The data showed that adult males, adult females and juveniles tend to migrate using different migration corridors. A greater number of young birds migrated south through California in comparison to the adults which migrated largely through the Rocky Mountain states. Moreover, migration timing also varied across age and sex categories

with adult males departing first and young of both sexes departing last – on average one month after the adult males. Overall, the results of this chapter suggest that Rufous Hummingbirds likely encounter and use slightly different sets of environmental conditions during their fall migration across demographic groups.

The goal of chapter 3 was to determine if species exhibit consistent habitat relationships across their breeding range. In other words, are niches sufficiently predictable that predictive models can be readily transferred from one location to another? This property is termed "stationarity". I used Breeding Bird Survey data from across North America, land cover and climate data from remote sensing, and a model transferability methodology to predict avian abundance across space for 131 species. I also assessed whether species' traits were correlated with levels of stationarity in distributions. Lastly, I tested whether prediction accuracies between modeled regions decreased with 1) geographical distances, 2) level of extrapolation, and 3) were affected by a 'core-boundary' effect. The results suggest that, for most species, habitat relationships change across species' breeding ranges. Species with large distributions, with distributions in regions with less topographic relief, and species with shorter life spans were more likely to have non-stationary distributions. Moreover, results show that predicting across long geographical distances or to novel environments decreases prediction accuracies. Overall, these results suggest that caution should be used when assuming stationarity in models, because the habitat used by birds across regions sometimes differed in measurable ways within a species' range. These results are important for conservation planning because many conservation efforts such as forecasts of biological invasions, prioritization of land protection, and translocation of endangered species relies on accurately predicting abundance across space (Guisan et al. 2013).

Lastly, in chapter 4, I tested whether 83 migratory bird species are consistent in their niches throughout the annual cycle. Here, I used year-round data from the citizen science program, eBird, along with land cover and weather data from remote-sensing sources to calculate niches for each species in four different seasons in each year (2005 – 2020). I compared niches across years (within season) and across seasons (within years) and calculated the percent niche overlap and the drivers of niche dynamics between pairs of niches. As expected, niche overlap was higher across years than across seasons. Consistent with the *niche plasticity hypothesis*, the niches of migratory birds were largely stable across species' annual life cycles, but with some small and significant differences among them. These results suggest that migrants have the most similar niches between spring and fall migrations, and most different niches between breeding and over-wintering grounds. Moreover, migratory birds seem to have the most constrained niches during the breeding season. These results suggest that while most migratory birds may rely on common sets of environmental conditions across seasons, the seasonal niches also contracted and expanded significantly throughout the year.

Taken all together, the results of these three chapters suggest that each bird species is associated with differing sets of environmental conditions among demographic groups, and across space and time. As such, species are better represented by multiple realized niches, which overlap to different degrees within their fundamental niche. These results highlight the need to identify each species' collection of realized niches in order to successfully conserve their populations and protect their habitat throughout their full life cycle. Doing so is likely essential to reversing the negative trends observed in our bird populations (Rosenberg et al. 2019).

Are Bird Habitat Associations Consistent Across Space and Time?

by
Josée S. Rousseau

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APPROVED:

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Josée S. Rousseau, Author

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Chapter 3 – Matt Betts helped develop the project ideas and research design. He also provided edits and comments on numerous drafts.

Chapter 4 – Matt Betts helped develop the project ideas and research design. Zhiqiang Yang provided remote sensing summaries for all species and advice on methodology. Rebecca Hutchinson also helped with the methodology. Matt Betts and Rebecca Hutchinson provided edits and comments to the manuscript.

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DEDICATION

I dedicate my dissertation to my husband Donald T. Ashton and our son Thomas R. Ashton. Its completion would not have been possible without your love, dedication, and support. A heartfelt thank you to both of you.

CHAPTER 1 – General introduction

The successful conservation of bird populations relies on being able to accurately define species' relationships to the environment - their habitat - at different scales, both spatial and temporal. Early studies in ornithology that examined bird-habitat relationships were primarily based on relatively fine-scale studies, completed in a few, at best dozens of locations, and usually limited to breeding seasons (Faaborg et al. 2010). Within these fine-scale studies, researchers assumed, likely correctly, that a species would exhibit the same relationship with its environments throughout the study. Today, with the advances in computer science and availability of big data, we are now able to piece together information from thousands of local surveys, spanning countries and often completed across seasons, to determine if birds do in fact use the same habitat across broader spatial and temporal scales. If the assumption that a species has a constant relationship with its environment is still valid across large scales, then conserving each species is made easier because one species equals one set of environmental conditions to protect, regardless of place and time. But if species do not retain the same relationship with their environments throughout their range and across their full annual cycle, then conserving one set of habitats could seriously misguide conservation efforts.

This idea that each species has a set of preferences in terms of habitat emerged from the concept of the niche (Hutchinson 1957, 1978). Under this concept, each species selects the set of environmental conditions that best allows them to survive and reproduce. If we were to represent each environmental variable in a plot, each variable would be represented as an axis, where a species would prefer a specific range of values. By combining these axes to an n-dimensional plot, we obtain a "hypervolume", often represented by a sphere, which symbolizes the conditions that allow a species to 'exist indefinitely' (Hutchinson 1957). This hypervolume is called the *fundamental niche* and is extremely hard to measure. Most fundamental niches can only be determined through experiments where one would obtain a mechanistic understanding of the links between a species fitness and its environment (Soberon and Peterson 2005, Kearney 2006, Soberón and Arroyo-Peña 2017). To accurately determine the fundamental niche of a species, the interacting effects of many environmental variables would need to be assessed. These experiments would inform us on the full range of environmental conditions individuals of a species can sustain and allow better predictions of the impact of climate change for example (Morin and Thuiller 2009). However, these experiments are seldom completed due to their complexity. As such, fundamental niche of very few species have been measured and are known.

However, we *are* able to measure the *realized niche* of a species. Realized niches are most often quantified through correlations between occurrence data and a few environmental variables measured at the time and place of survey (Soberon and Peterson 2005, Kearney 2006). The realized niche can also be represented by a hypervolume which represents the range of environmental conditions sustained by a species, but its size is reduced by biotic interactions such as competition (Hutchinson 1957). A realized niche is often smaller and included within the fundamental niche of a species (Hutchinson 1957, Soberón and Arroyo-Peña 2017). The concept of realized niche has many values and is used extensively in ecology. One of its well-known applications is in species distribution models (SDMs). By recording the presence of birds, their location, and the environmental factors associated with each location, one can model and predict the presence of a species over space and time (Austin 2002; Guillera-Arroita et al. 2015). Such models have been used to forecast biological invasions, identify critical habitats, prioritize the purchase of reserves, and guide translocation of endangered species (Guisan et al. 2013). However, the concept of realized niche is scale dependent, and exemplifies relationships between species and environments at a place and time.

The value of this concept depends on whether a realized niche, measured at a place and time, can be representative of the entire species across their range and throughout their full life cycle. On one hand, what defines a species is a group of individuals capable of exchanging genes, but these individuals typically have a set of physical attributes in common. As such, each species should be adapted to optimize a specific (or not so specific) relationship with its environment. This would support having one realized niche per species, which is mainly what Hutchinson (1957) intended. On the other hand, each species has life events that may change with season, age, and sex. Most migrant birds breed during the summer months and often rely on an abundance of insects. Their behavior, diet, and even physiology may change during migration (Hedenstrom 2008, Weber 2009, Swanson 2010, MacPherson et al. 2018). As such, different life events across the annual life cycle could be associated with different habitat requirements, and thus necessitate different niches across seasons. Moreover, while individuals should be more similar within a species then between species, a species can often consist of several populations, or even subspecies, across its range, with each population being adapted to their local environmental conditions (Peterson and Holt 2003). Lastly, adding yet another level of complexity, habitat requirements, habitat segregation, or differences in behavior may cause different age or sex categories within a species to be associated with different habitats during some life events, such as over-wintering (Lynch et al. 1985, Ornat and Greenberg 1990, McCloskey and Thompson 2000, Marra 2000). In each of these cases – different habitats between seasons, across a range, and between demographic groups – would represent the possible existence of more than one realized niche per species.

In this dissertation, I aim to identify whether most bird species exhibit a single realized niche, or rather that species have multiple niches that change depending on age and sex (Ch.2), geographic location (Ch. 3) or the stage of the annual cycle (Ch.4). The following three chapters each assess a situation in which a species could rely on multiple realized niches. In chapter 2, I compared fall migration patterns across ages and sexes for rufous hummingbird (*Selasphorus rufus*). In chapter 3, I tested whether niches change across the breeding range of 131 North American bird species, which would result in non-stationarity in SDMs. Lastly, in chapter 4, I compared the niche of 83 migratory species across seasons of the entire annual cycle throughout the Americas.

More specifically, in the second chapter I used data from the capture (and release) of Rufous Hummingbirds to determine if the different age and sex categories migrate at the same time and use the same fall migration corridor. Hummingbirds, because of their small size and high energetic demands rely on their environment to provide food and shelter at every stage of their long migration. If young and adult male and female hummingbirds migrate at different times and through different corridors, then the combination of high reliance on their environment and the presence of different climates and habitats throughout their migration would suggest they use different niches across demographic groups.

The goal of my third chapter was to assess whether North American bird species (n = 131) use the same habitat throughout their breeding ranges. In other words, are niches sufficiently predictable that predictive models can be readily transferred from one location to another? This property is termed “stationarity.” If a species has a stationary distribution, the relationship between abundance and habitat should be constant across their breeding distribution. To address this question, I used data from the Breeding Bird Surveys (Sauer et al. 2013) and remote sensing data representing land cover and climate, in combination with a model transferability methodology. I first created a stationarity index per species, which represents the level of consistency in their relationship with habitat across their range. I expected a gradient in stationary across species. I used this index to determine if some species, or more specifically some species traits, are more likely to be associated with non-stationary distributions. Lastly, I investigated the distribution of each species to assess if models predicted across regions had prediction accuracies affected by 1) geographical distances, 2) level of extrapolation, and 3) were affected by a ‘core-boundary’ effect. I then provide recommendations about which species are more likely to have non-stationary distributions and what causes the reduction in stationarity across their range. In particular, species having a different relationship between abundance and habitat across their range would perhaps be better represented by more than one realized niche.

The objective of chapter four was to determine if migratory birds (n = 83 species) use the same niche throughout their annual life cycle. Here, I used data from the citizen science program eBird, which includes millions of records, spanning the Americas, and represents year-round occurrences. I also used land cover and weather data from remote sensing sources. I first calculated a realized niche for each species, season (4 seasons) and year (2005 to 2020). I then compared niches across years (within seasons) and across seasons (within years) and calculated a percentage niche overlap between each pair of niches. Here, I expected niches to have a greater percent overlap across years than across seasons because birds tend to have high site fidelity and reuse the same locations across years. I also identified the drivers of niche dynamics, or change, across seasons by calculating the proportion of each pair of niches that remained stable (was used in both niches) and the proportion that changed (either contracted or expanded). These metrics were used to determine if the seasonal niches of each species were the same throughout the year, changed slightly but significantly across seasons, or changed drastically within the annual life cycle.

My goal, in these three chapters, was to determine if bird species tend to be associated with one, or multiple, realized niches across demographic groups, space and time. In other words, if they were associated with different environmental conditions across their full annual cycle. This information is essential if we are to conserve the right habitat at the right place and time for each species.

USING CONTINENTAL-SCALE BIRD BANDING DATA TO ESTIMATE DEMOGRAPHIC MIGRATORY PATTERNS FOR RUFOUS HUMMINGBIRD (*SELASPHORUS RUFUS*)

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CHAPTER 2 – Using continental-scale bird banding data to estimate demographic migratory patterns for Rufous Hummingbird (*Selasphorus rufus*)

ABSTRACT

The effective conservation of birds requires knowledge of species-specific population dynamics. Yet these dynamics during migration and across age and sex categories are poorly understood for small birds. The goal of this study was to assess large-scale fall migration patterns of Rufous Hummingbirds (*Selasphorus rufus*). Because the age and sex categories of this species depart from the breeding grounds and arrive from migration on different weeks, we predicted that each might use different migration routes, differ in migration speeds, and vary in their weekly distributions. Rufous Hummingbirds are among a few declining species for which a large amount of banding data is available during migration and across the migration corridor. We assembled a large hummingbird capture dataset (28,948 captures; 459 unique locations; fall migrations from 1998 to 2013) and used the centroid location of each age-sex-year-week group to calculate migration routes, timing, and speed. We used a utilization distribution kernel to measure distributions during migration. Adult females tended to have a southbound migration route parallel to and between those of young and adult males. Moreover, a greater number of young birds migrated south through California in comparison to adult females and adult males. Our results suggest that the migration of each age-sex category is separated by approximately two weeks with adult males migrating first, followed by adult females, and then the young of both sexes; yet migration speed was not statistically different among categories. Last, adult males were captured within a smaller geographic distribution, i.e., the area during any given week of migration, compared with adult females and young. We conclude that different age-sex categories of Rufous Hummingbirds use alternative routes and differ in migration phenology and distributions. Our results suggest that the age-sex categories could be affected differentially by habitat loss, phenological changes, and climates during migration. Considering such demographic migratory dynamics could improve conservation outcomes.

INTRODUCTION

Knowledge of bird population dynamics is essential for effective species conservation. Yet, during migration, these dynamics are poorly understood for small birds such as hummingbirds (Faaborg et al. 2010). Although recent advances have allowed us to determine migration trajectories for many species (La Sorte et al. 2016), a finer picture of the demographic patterns present within these migrations is needed. These demographic patterns include differences in migration timing, speed, and routes between age and sex categories. Understanding demographic dynamics during migration may improve conservation outcomes because annual migration is associated with high mortality rates (Sillett and Holmes 2002, Holmes 2007, Paxton et al. 2017).

Although most demographic migration studies have been completed using relatively small study areas, geolocators have recently allowed scientists to determine migration routes and timing for a few individuals at broad spatial scales (Stutchbury et al. 2009, McKinnon et al. 2013, DeLuca et al. 2015, Woodworth et al. 2016, Cooper et al. 2017). These geolocators are now enabling the study of migration for small birds such as passerines (McKinnon et al. 2013). However, even though the technology is improving (Robinson et al. 2010), geolocators are still too heavy to accommodate the small sizes of many species, especially hummingbirds, and will remain so for some time. Such studies are also sample-limited compared to other capture and marking techniques such as constant-effort mist netting and banding. Although some broad-scale studies use banding data to study movements, these studies tend to rely on multiple captures of the same individuals (Thorup et al. 2014). To date, no studies have considered demographic migration patterns of a small species at broad scales using a large sample size (thousands of individuals) of (first) captures, especially for species as small as hummingbirds.

A few demographic patterns, referred to here as general behaviors associated with specific age and sex categories, have been documented for migrating songbirds. Ralph (1971) documented a coastal effect where juvenile birds of three species tended to migrate along a large body of water while adults used a more inland route. Carlisle et al. (2005) observed a difference in the timing of juvenile versus adult migration among species and suggested that this may be driven by molt strategy. For land birds, differences in timing of migration between sexes has been documented for both spring and fall migration (Briedis et al. 2019), but more so in the spring. The early arrival of males in most species seems related to the acquisition of higher quality territories and associated increases in fitness (Morbey and Ydenberg 2001).

The use of relatively different migration routes and timing among age and sex categories implies that birds are potentially facing different conditions during migration. These conditions may include differences in habitat, phenology, and climate. Although species have evolved to survive migration, the projected increase in novel climates during fall migration (La Sorte et al. 2018) and localized changes in habitat may impact the survival rate of each demographic category differently. This highlights the importance of understanding the influence of demographic categories on migration dynamics.

Such a study would not be feasible for most small bird species because of the small amount of demographic data available during migration and at broad scales. We selected the Rufous Hummingbird (*Selasphorus rufus*; authority: Gmelin, 1788) because it is one of the few species in North America with a southbound migration that overlaps (at least in part) with the breeding season of most other bird species. The fall migration of Rufous Hummingbirds spans from the end of June to September (Healy and Calder 2020). Therefore, many of the biologists studying breeding bird demographics throughout North America collect substantial records representing the southbound migration of this species. Moreover, this species is declining (North American Bird Conservation Initiative 2014, Rosenberg et al. 2016, Sauer et al. 2017) at a yearly rate of 1.8% (Sauer et al. 2017) and there is a need to learn more about its biology in order to prioritize conservation efforts (Alexander et al. 2020). Last, the age and sex of this species can readily be determined from captured birds (Pyle 1997, Williamson 2001).

It is well documented that Rufous Hummingbird adult males migrate before adult females, and adult females before the young of both sexes (Stiles 1972, Phillips 1975, Kodric-Brown and Brown 1978, Wethington and Russell 2003). It is also well understood that Rufous Hummingbirds rely on flower nectar as a source of food during their migration (Phillips 1975, Kodric-Brown and Brown 1978, Carpenter et al. 1993). Given these observations, and differing availability of food plants in space and time over the migration period, we expected each age and sex category to select different migration routes and to migrate at different speeds. We also expected the distribution, i.e., the area occupied by the captures of each age and sex category, to vary among demographic categories during migration.

METHODS

Data

The capture and banding of birds provide accurate demographic information for a large number of individuals at continental scales, e.g., North America. We used Rufous Hummingbird banding data from Canada, the United States, and Mexico archived by the Avian Knowledge Network (AKN; n = 3578), Institute for Bird Populations, Monitoring Avian Productivity and Survivorship program (IBP; n = 13,370), and the USGS Bird Banding Laboratory in the United States and Bird Banding Office in Canada (BBL and BBO; n = 99,485). We combined the data from these three sources and removed duplicates and records without a date, latitude, longitude, or demographic information (age and sex). The combined dataset included 87,197 capture records from Canada (24.5%), the United States (75.4%), and Mexico (< 0.1%) representing 3044 different locations. These locations often represent capture stations for which locations were determined haphazardly, and therefore are not randomly distributed over the landscape. We selected records from 1998 to 2013. We chose this span because data were requested from BBL/BBO in early 2014 and few records were available before 1998. The three sources of data varied in terms of the metadata available with each capture record. For example, the BBL/BBO source did not document the effort associated with each sampling date. This presents limitations associated with possible sampling bias that are discussed below and reviewed by Thorup et al. (2014). Most records represent the first (and only) capture of an individual bird. Hummingbird recaptures and recoveries are very rare during migration (0.2% of the records used in our analysis). It could be argued that these recaptures and recoveries are not independent from the original capture, however, their low numbers in relation to the total sample size (172 individuals total) is highly unlikely to have influenced the results. The analysis also included unbanded Rufous Hummingbirds (1.9% of the records used), mainly from IBP and AKN.

Although adult male Rufous Hummingbirds can be distinguished in the field from other species of hummingbirds and from female and young Rufous Hummingbirds, adult female and juvenile Rufous Hummingbirds are difficult to age and sex visually and can be easily confused with Allen’s Hummingbirds (*Selasphorus sasin*) where distributions overlap (Stiles 1972, Healy and Calder 2020). Capturing birds and using a combination of tail feather width, color and shape, gorget pattern, morphometrics, and bill striations allow for more accurate identification of species and associated age and sex (Ortiz-Crespo 1972, Pyle 1997, Williamson 2001). The ageing accuracy is considered > 95% during fall migration, the sexing accuracy of adults is similarly high, while the sexing accuracy of young is considered > 75% based on the criteria provided by Pyle (1997).

We categorized the capture records based on age, sex, and capture date. Age categories are hatching year (referred to young), after hatching year (referred to adult), and unknown. The young category contains all birds hatched within the calendar year of capture. Adult birds were hatched in a calendar year previous to the one of capture. Unknown-age birds are the individuals for which age was not determined; we excluded these records from the analysis. Our sex categories were female, male, and unknown. As with age, the unknown sex category contains birds for which sex identification was not determined. Records with unknown sex were also excluded from our analysis. This resulted in a total of four age and sex categories for the analysis of demographic movements: adult males, adult females, young males, and young females.

We used eBird data (Sullivan et al. 2014) to assess and compare the number of Rufous Hummingbirds observed by birders versus the numbers captured by banders. We extracted eBird observations that spanned the same geographical and temporal range as the captures. However, eBird observations are typically not aged or sexed, and were thus summarized at the individual level.

Analysis

We assessed differences in migration routes, timing, speed, and distributions among age and sex categories of Rufous Hummingbirds. All records were grouped in an age-sex, year, and week category, e.g., adult male, year 2010, week 29. Weeks were assigned starting on 1 January of each year, e.g., 1 to 7 January = week 1. For each age-sex-year-week category, we used the latitude and longitude of the captures to calculate a mean and a median center point (centroid). Each centroid represents the mean location of a unique hummingbird category.

We defined the onset and end of migration for each age-sex category by selecting centroids located within our migration corridor. When weekly centroids occurred south of the breeding distribution (BirdLife International and Handbook of the Birds of the World 2016), 150 km north of Mexico, and west of the Texas Panhandle, the associated age-sex group was considered to be in migration. That is, we assumed that a hummingbird was migrating regardless of its location if it was associated with a centroid located within the migratory corridor. We used a 150- km buffer north of Mexico to remove bias caused by the unknown number of birds having moved into or remaining in Mexico. We did not extend the migration route east of Texas because it is unknown what percentage of the population uses that route to winter in the southeast United States (most Rufous Hummingbirds winter in Mexico). This selection process resulted in 28,948 captures during fall migration and 548 during spring migration. Because we deemed spring sample size to be too small, we focused our analysis exclusively on fall migration.

We observed a large difference in the number of fall migration records available for each age-sex category, with adult males (n = 4787) having 1.8 times fewer captures than adult females (n = 8524), and 1.9 and 1.4 times fewer captures than young males and females (n = 8939 and 6698, respectively). To avoid introducing biases in migration speed and distribution extents due to differences in sample size, we drew 100 random subsample datasets from the adult female and young records to match the number of adult male records. We recalculated the centroids for each of 100 subsamples, made sure the centroids were within the migration corridor, and selected those with a minimum of 5 capture locations and 20 individuals. The following statistics represent the mean and standard deviation from the 100 subsamples for the adult females, young males, and young females. For our analysis, we used a total of 4485 adult males, a mean number of adult females of 4278 ± 108 (SD) per subsample, a mean number of young males and females of 4264 ± 85 (SD) and 4313 ± 57 per subsample, respectively. These subsamples represented approximately 292.57 ± 3.36 (SD) centroids (age-sex-year-week categories), covering 459.27 ± 5.49 (SD) unique locations. The number of captures per age-sex-year-week categories ranged from 20 to 218 with a mean of 59.29 ± 32.83 (SD) captures per centroid. For each of the following analyses (beside kernel distribution and age ratio), we used the mean value from the 100 subsamples per age-sex category as input in the model.

The fall migration centroids calculated using the mean and median were highly correlated (Spearman's r = 0.81–0.92, max $p < 0.001$). We kept the mean centroids for our analysis because they were more spatially centered and were less biased toward locations with very high abundances of hummingbirds (which are known for their high number of surveys).

To calculate a mean migration route per age-sex category, we first combined all subsamples to obtain a mean centroid location (referred to hereafter as centroid) per age-sex-year-week category and assessed whether migration routes among age-sex categories changed across years. This was first visually assessed (Appendix A, Figure A.1). We also used a generalized least square linear model (GLS) with mean longitude as a response variable and age, sex, year, and the interaction of age × year and sex × year as the independent variables. We accounted for temporal (weekly) autocorrelation across capture locations within each year and age-sex category using correlation matrices. We checked the assumptions associated with linear models (here and with the other similar analyses below) by graphical assessment ensuring that the variance of the standardized residuals was proportionate across fitted values. We also checked for normal distribution in model residuals. If either the age × year or sex × year interactions was supported statistically, then we would conclude that different age-sex categories were not only migrating using different longitudes, but that this effect varied over the years. However, the interaction terms were not significant (age × year $F(15,283) = 0.97$, $p = 0.49$; sex × year $F(15,283) = 0.52$, $p = 0.93$; Appendix B, Table B.1), which allowed us to combine all years to assess relative differences in migration routes among age-sex categories. We used the centroid of each age-sex-year-week category to calculate a mean and standard error per age-sex-week, using year as a replicate.

The pattern observed in mean migration routes raised additional questions about the number of hummingbirds observed in two different geographical regions (east versus west) during the breeding season (April to July) and the corresponding number of hummingbirds migrating through eastern, i.e., east of the Rockies, vs western regions from July to Sept. The percentage of young observed in each region during the breeding season could help us determine if productivity was responsible for the pattern observed in mean migration routes. To explore this, we compared abundances derived from two independent datasets, those from capture data and those from eBird observation data (Sullivan et al. 2014). Using eBird data had the advantage of covering more locations within the distribution than the banding data. We calculated the total number of individuals per eBird location (unique combination of latitude and longitude) and per capture location. We then summarized the total number of Rufous Hummingbirds on the breeding grounds and on migration for the eastern and western regions to compare the totals between eBird and captures. Moreover, using the capture data, we also calculated the percentage of young at each capture location, and summarized the results to obtain a mean percent of young per region (east and west) and period (breeding and migration). The eastern regions included all locations in eastern Oregon, eastern Washington, Idaho, and Montana (for breeding), and in the Rockies south of the breeding distribution and at least 150 km north of Mexico (for migration). The western regions included western Washington and western Oregon (for breeding), and California and western Nevada (for migration).

Migration timing for each age-sex and year was calculated using the weeks when the centroids lay in the migration corridor. Migration start was defined as the first week per age-sex-year where the centroid moved outside of the breeding range, while migration end was defined as the last week within the migration corridor. We used a linear mixed model to determine if migration start and end were significantly different across age and sex categories. We used minimum (or maximum) week as response variables, age, sex, and the age × sex interaction as independent variables, and year as a random effect. To reduce the chance of Type I error, we used Bonferroni-adjusted multiple comparisons to assess the differences in timing among age-sex categories. We also tested if migration timing progressed with years because this could reflect an effect of climate change. We used linear models with week (start and end) as response, and age, sex, age × sex interaction and year as independent variables. We looked at the residuals of the model in relation with year. The residuals did not follow a pattern across years.

We defined migration as the period including both flight and fueling stops (Hedenstrom 2008), and migration speed as the average speed throughout this migration period. We did not account for any specific migration patterns (such as leapfrog) because this would require a much larger number of re-encounters than were available. We first calculated the distance between consecutive weekly centroids to obtain one migration distance per age-sex and year category. This distance was then divided by the number of weeks represented by the centroids within the migration corridor, to obtain a migration speed per age-sex and year. To test if migration speed was statistically different among age-sex categories during fall migration, we used a linear mixed model with migration speed as the response variable, age, sex, and the interaction of age × sex as independent fixed variables and year as a random effect. To allow comparison with other studies, we report the migration speed as the number of kilometers per day.

Based on the results from the migration timing and speed, we did a post-hoc analysis examining mean migration distance among age-sex categories. We used a linear mixed model with distance as the response variable and age, sex, the interaction of age × sex, and the number of weeks included in the distance as independent fixed variables and year as a random effect. We included the number of weeks as a fixed effect so that any difference among age and sex categories would account for differences in migration duration.

We defined the migration distribution as the total area occupied by captures in a particular week. We calculated this separately for each age-sex, year, and subsample. Here, a large area would represent a protracted migration with individuals spread over large distances between the migration front and tail. We used a 50%, 80%, and 95% probability utilization distribution kernel (Calenge and Fortmann-Roe 2017), using the default ad hoc method available in the R package "adehabitatHR" version 0.4.16 (Calenge 2006) as smoothing parameter, to calculate the distribution of each age-sex-year-week and subsample. Each of the 100 subsamples had similar numbers of Rufous Hummingbirds per age-sex category. For each core area probability, we then combined the subsamples to obtain a mean area per age-sex-year-week. We used a linear mixed model to assess whether the age-sex categories used different migration distributions. We used area (km²) as the response variable, age, sex, and the age × sex interaction as the fixed effect, and year as a random effect. Again, we assessed differences in distribution area among age-sex categories using Bonferroni-adjusted multiple comparisons. We only present results from analysis of the 50% probability utilization distribution because all three core areas considered (50, 80, and 95%) yielded similar results for both main effects and interactions.

We used R version 3.6.0 (R Core Team 2019) for our analysis, with the packages 'emmeans' version 1.3.4 (Lenth 2019), 'geosphere' 1.5-10 (Hijmans 2019), 'ggplot2' 3.1.1 (Wickham 2016), 'gmodels' 2.18.1 (Warnes et al. 2018), 'nlme' 3.1-140 (Pinheiro et al. 2019),'rgdal' 1.4-6 (Bivand et al. 2019), 'rgeos' 0.5-2 (Bivand and Rundel 2019), and 'sf' 0.8-0 (Pebesma 2018).

RESULTS

Southbound (fall) migration routes of Rufous Hummingbirds depended strongly on age and sex (Figure 2.1). There were three main migration routes (Figure 2.1). On average, adult females migrated east of the young of both sexes and west of the adult males. The migration routes of young males and young females were similar. The westerly migration routes of young were likely due to a substantial proportion of birds migrating south through California as compared to adults, who migrated largely through the Rocky Mountains region (Figure 2.2A). Although the total number of Rufous Hummingbirds captured (banding data) and observed (eBird data) was much larger in the Rockies ($n = 10,403$ and 26,678, respectively) as compared with California ($n = 2818$ and 9139, respectively), the percentage of young birds (males and females) captured in California was much higher than through the Rockies. Indeed, the mean percentage of young per location in California was 76.7%, compared with 40.0% in the Rockies.

The percent of young and total number of captures on the breeding grounds showed a slightly different pattern from those observed during fall migration. Although the percentage of young being captured during breeding was also higher for the western region (29.9%) as compared with eastern region (15.1%; Figure 2.2A), the total number of captures and eBird observations was actually higher in the western region ($n = 10,034$ captures and 49,896 observations) as compared with eastern region (7870 captures and 3644 observations). This higher number of hummingbirds and higher percentage of young in the western breeding region could suggest higher productivity in the western region.

The start and end of migration differed significantly among age and sex categories (age × sex interactions: $F(1,45) = 15.75$, $p = 0.0003$ and $F(1,45) = 15.93$, $p = 0.0002$, respectively). Adult males started migration earlier than adult females (mean = 1.56 weeks ± 0.39 [SE]; $t(45) = 4.01$, $p = 0.0009$). Adult males started migration, on average, at week 27.94 (95% CI = 27.15 to 28.72) whereas females started migration around week 29.5 (95% CI = 28.71 to 30.29). Adult males also started migration earlier than the young of both sexes (mean = 2.94 weeks ± 0.39 [SE]; $t(45) = 7.54$, $p < 0.0001$). See Figure 2.3A for a comparison of migration start for all ages and sexes. Migration end followed a slightly different pattern, with adult males still ending migration earlier than adult females (mean = 1.94 weeks ± 0.39 [SE]; $t(45) = 5.00$, $p < 0.0001$;

adult males ended migration, on average, at week 31.69 [95% CI = 30.97 to 32.40] and females at week 33.62 [95% CI = 32.91 to 34.34]). Adult males also ended migration significantly earlier than the young of both sexes (mean = 4.19 weeks ± 0.39 [SE]; t(45) = 10.80, $p < 0.0001$), but although adult females did not start migration significantly earlier than the young, they ended migration earlier (mean = 2.0 weeks ± 0.39 [SE]; t(45) = 5.16, $p < 0.0001$). See Figure 2.3B for a comparison of migration end for each age and sex categories.

Results from analysis of migration speed differed from migration timing. We did not detect a difference in migration speed among age-sex categories (age: F(1,44) = 0.91, p = 0.34; sex: F(1,44) = 0.84, p = 0.36; age × sex: F(1,44) = 0.65, p = 0.42). Rufous Hummingbirds migrated an average of 38.48 km per day (SD = 15.46) during their southbound migration. Yearly migration speeds, all age-sex combined, are presented in Appendix B (Table B.1).

The yearly mean migration distance traveled by Rufous Hummingbirds differed between age groups (F(1,43) = 18.10, $p < 0.0001$). Adult hummingbirds traveled shorter distances (mean = 1176.09 km, 95% CI = 979.44 to 1372.74) than young hummingbirds (mean = 1279.03, 95% CI = 1084.05 to 1474.02).

The difference in mean 50% utilization distribution area was statistically different as a function of age (F(1,312) = 25.63, $p < 0.0001$) and sex (F(1,312) = 4.52, p = 0.034) but not by age × sex (F(1,312) = 3.27, p = 0.071). Adults of both sexes tended to migrate using a relatively smaller distribution than young (mean for adults = 2,963,906 km^2 ± 196,062 [SE]; 95% CI = 2,546,009 to 3,381,803; mean for young = 3,650,676 km^2 ± 193,151 [SE]; 95% CI = 3,238,984 to 4,062,368). Males also tended to use a smaller distribution than females (mean for males = 3,156,605 km^2 ± 194,490 [SE]; 95% CI = 2,742,058 to 3,571,152; mean for females = 3,457,977 km^2 ± 194,588 [SE]; 95% CI = 3043,223 to 3,872,730). Figure 2.4 includes a comparison of migration area for each age and sex categories.

DISCUSSION

To our knowledge, our study is the first to document the spatial and temporal patterns of southbound Rufous Hummingbirds during migration and how these patterns vary among age and sex categories. Our results suggest that adult females follow a fall migration route parallel to adult males, but it is, on average, more westerly. The adult female route also lies farther east than the routes taken by young (Figure 2.1). Moreover, capture data show hummingbirds migrating south through the Rocky Mountains and California (Figure 2.2A and 2.2B). Few studies have documented this Californian migration route (Stiles 1972, Williamson 2001, Schondube et al. 2004, Healy and Calder 2020). The use of this westerly route is more prominent in some years than others (Appendix B, Table B.1), which could have caused the high variance in fall migration longitude observed by Supp et al. (2015). These mean differences in migration routes may be caused by the age-sex categories migrating at different times.

As with site-level studies of Rufous Hummingbirds (Stiles 1972, Phillips 1975, Kodric-Brown and Brown 1978), our findings suggest that adult males migrate before adult females during fall migration, and adult females before young hummingbirds of both sexes (Wethington and Russell 2003). However, this pattern is not consistent with the migration timing observed in adult Ruby-throated Hummingbirds (*Archilochus colubris*) where adult males and females have similar fall migration timing (Zenzal and Moore 2016). In Rufous Hummingbirds, as with most other species of hummingbirds, only females build nests and assume parental care (Johnsgard 2016). This allows adult males to start fall migration earlier than adult females and young. This adaptation in migration timing likely decreases competition for quality food resources during migration (Gass 1979, Newton 2006). The age-specific pattern of young birds beginning their fall migration later, and having a more westerly route, raises several questions. The higher percentage of young in the western region during fall migration (July to September) could be due to higher productivity in the western region on the breeding grounds during the months of April to July. Another possibility is that the southward route through California may be more favorable than the Rocky Mountains later in the season. It could be hypothesized that colder conditions later in the season hinder eastward crossing of the Rockies, requiring young hummingbirds to migrate directly south. Another hypothesis is that differences in plant phenology between California and the Rockies favor using a California route later in the season. Indeed, La Sorte et al. (2014) found that for western flyway migrants, although migrating south through California is a longer route, it is associated with higher greenness, than through the more easterly (and typical) southbound migration route. Our results suggest that young males and females had significantly longer migration routes compared with adults. Young hummingbirds may be selecting a route with more resources to increase their chances of survival in lieu of the more direct but drier eastern migration route favored by adults.

Hummingbirds are known to follow peak plant phenology during fall migration (Bertin 1982). Because flowering phenology varies with plant species and location, and because the different demographic categories of hummingbirds migrate at different times, it is likely that they need to use slightly different routes, or use different plant species, if they are to take advantage of peak flowering phenology. Although we have little information about the use of different plant species across demographic categories during migration (Kodric-Brown and Brown 1978), the difference in routes among demographic categories observed in this study suggests that hummingbirds may be adapting to spatiotemporal differences in plant phenology by following different routes.

Habitat quality and rates of habitat change likely differ among migratory routes and therefore may have differential demographic impacts. Rufous Hummingbirds are associated with broadleaf early seral forests (Betts et al. 2010) and upland meadows (Kodric-Brown and Brown 1978, Carpenter et al. 1993). Yet these habitats are changing at varying rates across western USA (McGarigal et al. 2001, Kennedy and Spies 2005, Takaoka and Swanson 2008, Miller and Halpern 2009, Phalan et al. 2019). Some of the factors affecting the amount, quality, and location of these habitats include fire regimes and suppression, forest management practices, land ownership, topography, and elevation (McGarigal et al. 2001, Kennedy and Spies 2005, Miller and Halpern 2009). For example, forest management practices such as clear cutting may temporarily increase the amount of early seral habitat, however, depending on land ownership, the practice is often associated with the application of broadleaf herbicides (Kennedy and Spies 2005), which negatively impact the abundance of Rufous Hummingbirds (Betts et al. 2013). As such, there is a need to assess Rufous Hummingbird habitat availability across their migration distribution and whether they adjust their migration routes based on changes in habitat.

On average, adult males end migration three to five weeks before young hummingbirds. The observed difference in migration timing among age-sex categories could mean that they are exposed to both different plant phenologies and climatic conditions. It is unknown if the different environmental conditions faced by the age-sex categories during migration result in differential survival. For example, the timing of monsoon and its associated impacts on vegetation and flower phenology (Mock 1996, Crimmins et al. 2011) may favor different age-sex categories. Moreover, more extreme weather events tend to occur later during the fall season in the contiguous United States (Branick 1997). Thus, early migration may offer an advantage for males considering that their higher wing disc loading makes them more susceptible than females to bad weather (Saino et al. 2010). As such, climate change and associated extreme events may affect sex ratios across the migratory range (see Petry et al. (2016) for a plant example). This may contribute to the biased sex ratio observed in the number of captured adult males to adult females (1:1.8). Yet an additional reason for males to depart first from the breeding grounds is to arrive first on the wintering grounds. Males and females, depending on their breeding location, may be segregated on their wintering grounds based on altitude (Moran et al. 2013).

Fall migration of Rufous Hummingbirds spans several weeks over a large area (Phillips 1975, Supp et al. 2015). Yet within this time frame, adult males migrated using a smaller weekly distribution, i.e., area, compared to adult females and young of both sexes. A more protracted migration by young Ruby-throated Hummingbirds was also observed by Zenzal and Moore (2016). Our data show that adult males were captured at a smaller number of locations than adult females and young, but at these locations, they were often found in higher numbers. This is consistent with the finding of Kodric-Brown and Brown (1978) who observed that adult males tend to defend smaller territories with higher flower densities than adult females and young. Adult males thus rely on peak phenology during migration and are found in higher numbers wherever flower resources are denser. Another consideration is that adult males defend their migration territories more aggressively than the other age-sex categories (Kodric-Brown and Brown 1978), thus relying on the high density of flowers to fulfill their energetic needs during migration. This higher energetic need may result in lower survival rates in some years, which could lead to the reduced numbers of captured adult males observed in this study. However, the lower number of captured males could have been caused by insufficient sampling at locations where they migrate. The larger distribution covered by adult females and young could also be caused by nesting asynchrony. Although Rufous Hummingbirds may nest synchronously, like their close relative Broad-tailed Hummingbirds (*Selasphorus platycercus*; Waser 1976, McGuire et al. 2014), the egg laying dates span over a month within various regions and vary among regions (Healy and Calder 2020). They may also renest if their first nesting attempt failed (Healy and Calder 2020). Because females build the nest, incubate, and provide parental care alone (Healy and Calder 2020), they are more likely to have a wider range of migration departure after the breeding period.

Migration speed includes both the time flying and at stop-over locations (Hedenstrom 2008). In this case, low recapture rates did not allow us to measure individual migration speeds. Our results reflect an average migration speed for the species. The high variation in average migration speed from year to year (Appendix B, Table B.1) and among age-sex categories precluded detection of differences in migration speed among age-sex categories. This may suggest that Rufous Hummingbirds have high phenotypic plasticity in migration speed, which may be determined by weather and resource availability. Indeed, Shankar et al. (2019) observed a rapid response in daily energy expenditures in relation to resource availability for Broad-billed Hummingbirds (*Cynanthus latirostris*). Our overall mean migration speed (38.5 km/day ± 15.5 SD) includes yearly values comparable to those of Supp et al. (2015; 33.41 km/day ± SD 11.6) for the fall migration of Rufous Hummingbird.

Study limitations

Our analysis assumed that the large sample (n = 28,948) was representative of the true spatial and demographic distribution patterns of Rufous Hummingbirds during fall migration. Still, the lack of metadata in the form of capture effort from many banding stations makes it impossible to infer the results to all individuals of the species. Our scope of inference is thus limited to the hummingbird records used in this study. It is likely that several biases are present. First, the data set available did not allow determination of whether sampling was adequate to capture the full range of locations and conditions used by Rufous Hummingbirds on migration. Thus, our data may misrepresent the true distributions of an age or sex category during migration. Although Rufous Hummingbirds use a wide range of elevations (C. Bishop, personal communication, 1 June 2020), there is likely less monitoring done at higher elevations. Only 11.5% of the fall migration records represent captures at elevations between 2438 and 2743 meters (8000 to 9000 feet), yet these elevations have been associated with the highest abundance of Rufous Hummingbirds in the fall (Henshaw 1886, Swarth 1904). This spatial misrepresentation problem is exacerbated by the low number of records in Mexico. As such, the results close to Mexico should be interpreted with caution because it is unknown what proportion of the population had already migrated south of the United States. Second, as noted above, the lack of metadata also means that we were not able to assess whether the absence of Rufous Hummingbirds was associated with a true absence or a lack of sampling. For example, very few captures were from the state of Nevada. eBird observations for Nevada (Figure 2.2B) also show reduced effort in general, likely due to topography, yet Rufous Hummingbirds were detected within those efforts, i.e., they are present in Nevada. This potential sampling effect is likely the reason for the absence of captures in Nevada. Third, the protocol used to capture hummingbirds at each station is also unknown. Capturing and studying hummingbirds often involves techniques not commonly used with other species. As such, most hummingbirds represented in this study were likely captured at feeders. More studies are needed to investigate and account for capture probability across demographic categories (Amrhein et al. 2012) and re-encounter probabilities across large-scales (Thorup et al. 2014).

Although these limitations are important, they do not necessarily preclude the study of the relative differences among ages and sexes during migration. Males and females may use different habitats (elevation, or level of urbanization) or food sources (flowers vs feeders) during migration, and males certainly defend sources of food more aggressively than females (Kodric-Brown and Brown 1978), which may cause biases in the capture rate of each age and sex category. However, we assume that these biases are consistent throughout migration. Despite these limitations, the complete lack of information in the literature on age and sex structure at broad spatial scales in hummingbird migration renders our analysis a useful and conservation-relevant first attempt at estimating these parameters.

CONCLUSION

Effective conservation of migratory birds requires a better understanding of their distribution, movement, and demographics. This becomes even more important as we consider bird population declines (Rosenberg et al. 2019, Partners in Flight 2020), high mortality rates during migration (Sillett and Holmes 2002, Klaassen et al. 2014), and the impact of climate change on bird populations (North American Bird Conservation Initiative, U.S. Committee 2010, Northrup et al. 2019). Although most conservation actions rightly prioritize management decisions benefiting “all” individuals of a species, some evidence suggests that different age and sex categories are differentially affected by habitat and climate (Clout et al. 2002, Norris et al. 2004, Weatherhead 2005). In our study, adult males, adult females, and young Rufous Hummingbirds migrated using different timing and migration routes. Therefore, each age-sex category likely encounters different habitats, climate, and phenology. A next step will be to assess if these varying conditions among age-sex categories cause differences in survival rates and breeding success. Whenever a demographic category suffers from a lower survival rate, management actions could more efficiently address population declines through localized actions, e.g., habitat protection, benefiting the specific and most at-risk category. There is thus a need to address information gaps regarding hummingbird biology and life history (Alexander et al. 2020). Finally, we recommend documenting sampling effort (a minimum of date and location) and adding the information to all archival systems of capture and banding data (Alexander et al. 2020). This would allow inference of future results to the population or species and would increase the accuracy and usefulness of species distribution models (Elith et al. 2006). Large-scale programs should also aim to systematically monitor different habitats and elevations, to allow better inference of results to the broader population. Minimizing biases (or at least being informed of the biases) would allow more accurate prioritization of conservation efforts.

Responses to this article can be read online at: http://www.ace-eco.org/issues/responses.php/1612

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The safe capture and banding of birds and the collection of quality data require training and skills. This, combined with costly banding equipment make capture data especially valuable. One impact, however, is lower sample size compared with many field monitoring methodologies. The balance between the value of each detailed banding record versus sample size highlights the importance of partnership and large-scale banding data repositories. This study would not have been possible without the existence of such efforts. This study is also possible because thousands of banders shared and submitted their data to such organizations (thank you!). We would like to thank all of the bird banders who have shared data with the Avian Knowledge Network (AKN), Institute for Bird Populations (IBP), Bird Banding Laboratory (BBL), and Bird Banding Office (BBO). We thank Danielle Kaschube and Phil Nott for providing and giving permission to use IBP data, CJ Ralph and Kim Hollinger for helping to make data available through the AKN, and Danny Bystrack from BBL and Louise Laurin from BBO for making the Rufous Hummingbird data available. We thank an anonymous BBL bander for giving us permission to use their data, which consisted of more than 5% of the recent data provided by BBL (as of 2015). Thanks to Carol Wilson for sharing old literature on hummingbirds, and to Ariel Muldoon for the statistical guidance and review of R scripts. Thank you to the following reviewers for their helpful comments on previous versions: Bruce Peterjohn, Susan Wethington, Urs Kormann, Hankyu Kim, and Diego Zarrate. Lastly, thanks to all eBirders and to the Cornell Lab of Ornithology for sharing bird observation data.

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TABLES AND FIGURES

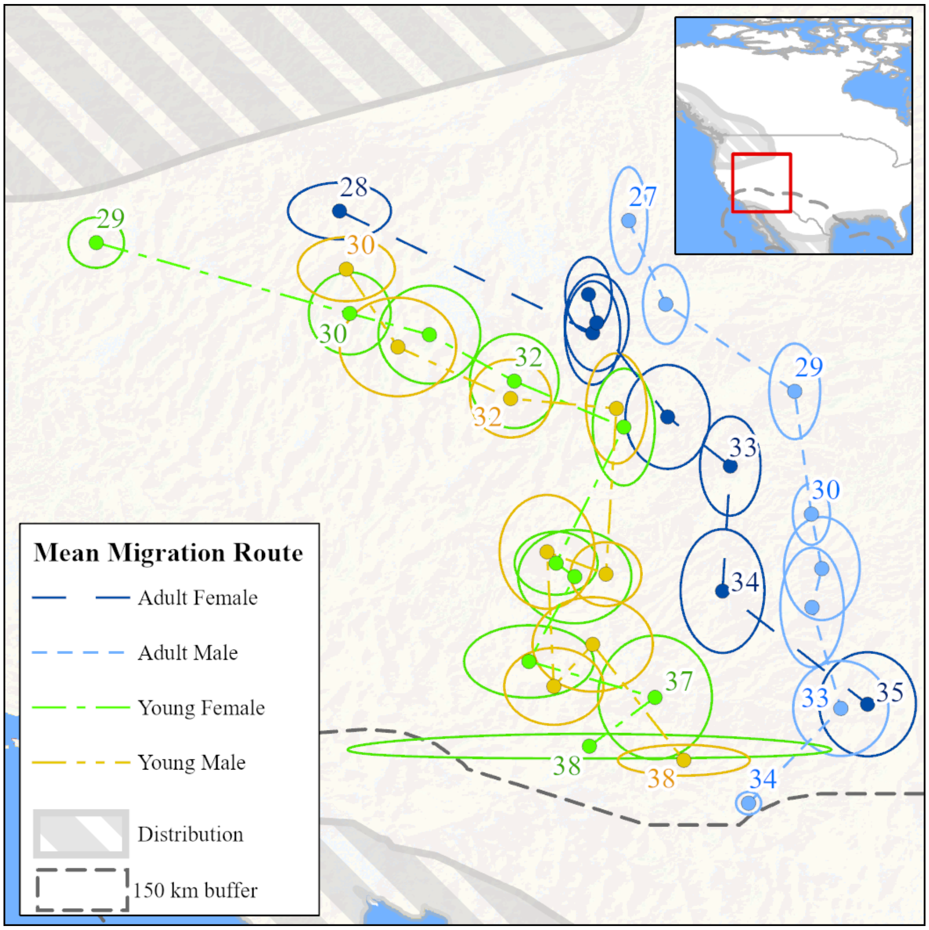

Figure 2.1. Estimated fall migration routes for each age and sex category of Rufous Hummingbird (*Selasphorus rufus*). Dots represent the weekly mean locations per age-sex, ellipses represent the standard errors, and lines connecting the centroids represent mean migration routes. Numbers represent the week within a calendar year.

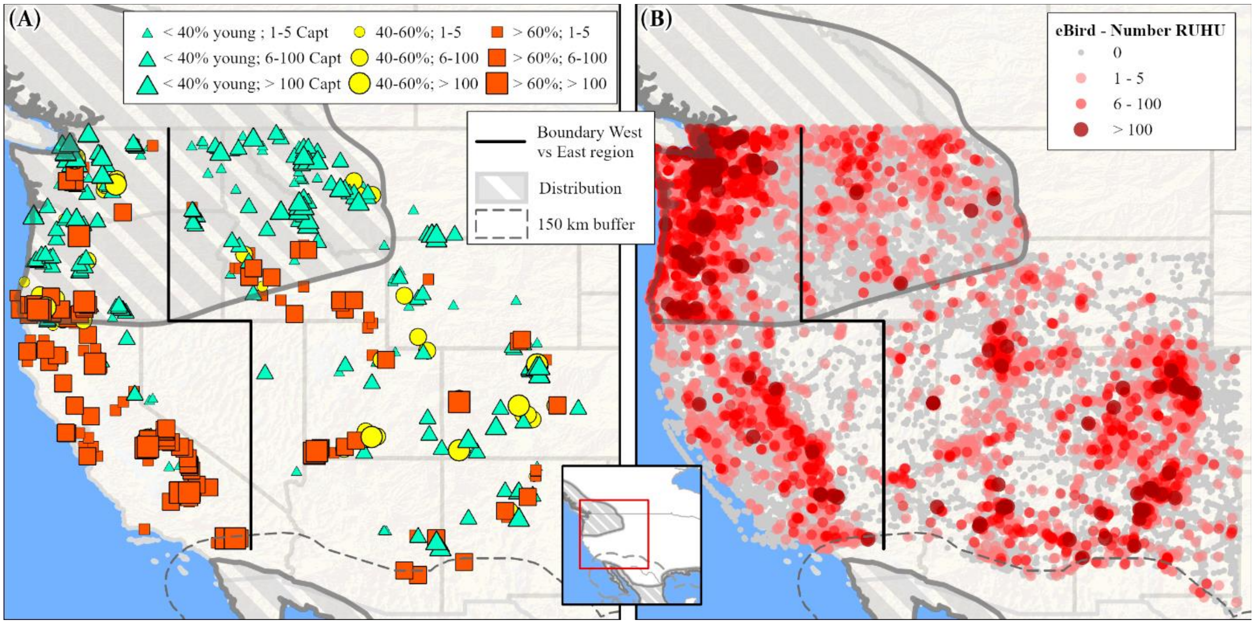

Figure 2.2. Locations of hummingbird captures (A) and eBird observations (B) occurring in a western and an eastern region (delimited by the black line) during two different time periods. The symbols overlapping the breeding distribution (Oregon, Washington, Idaho, and Montana; BirdLife International and Handbook of the Birds of the World, 2016) represent captures and observations made during the months of April to July that are inclusive of the breeding season. The symbols south of the breeding distribution and north of the buffer line drawn 150 km north of US-Mexico border represent fall migration records compiled from July to September. Map (A) represents the percentage of young vs. adult hummingbirds captured at each sampling location. The larger symbols reflect locations with larger number of captures (the largest are locations where >100 individuals were captured). The orange squares represent locations where >60% of the captures were young and the turquoise triangles are locations where the adults represented >60% of the captures; the yellow circles represent locations with relatively similar percentages of young and adult captures. While more individuals (of both ages) migrated using the Rocky Mountains region (east of the black line), a higher percentage of young is observed along a California region (west of the black line). On Map (B) darker red circles represent locations were >100 individuals were observed. More Rufous Hummingbirds were observed in the western region during the earlier time period and in the eastern region during migration.

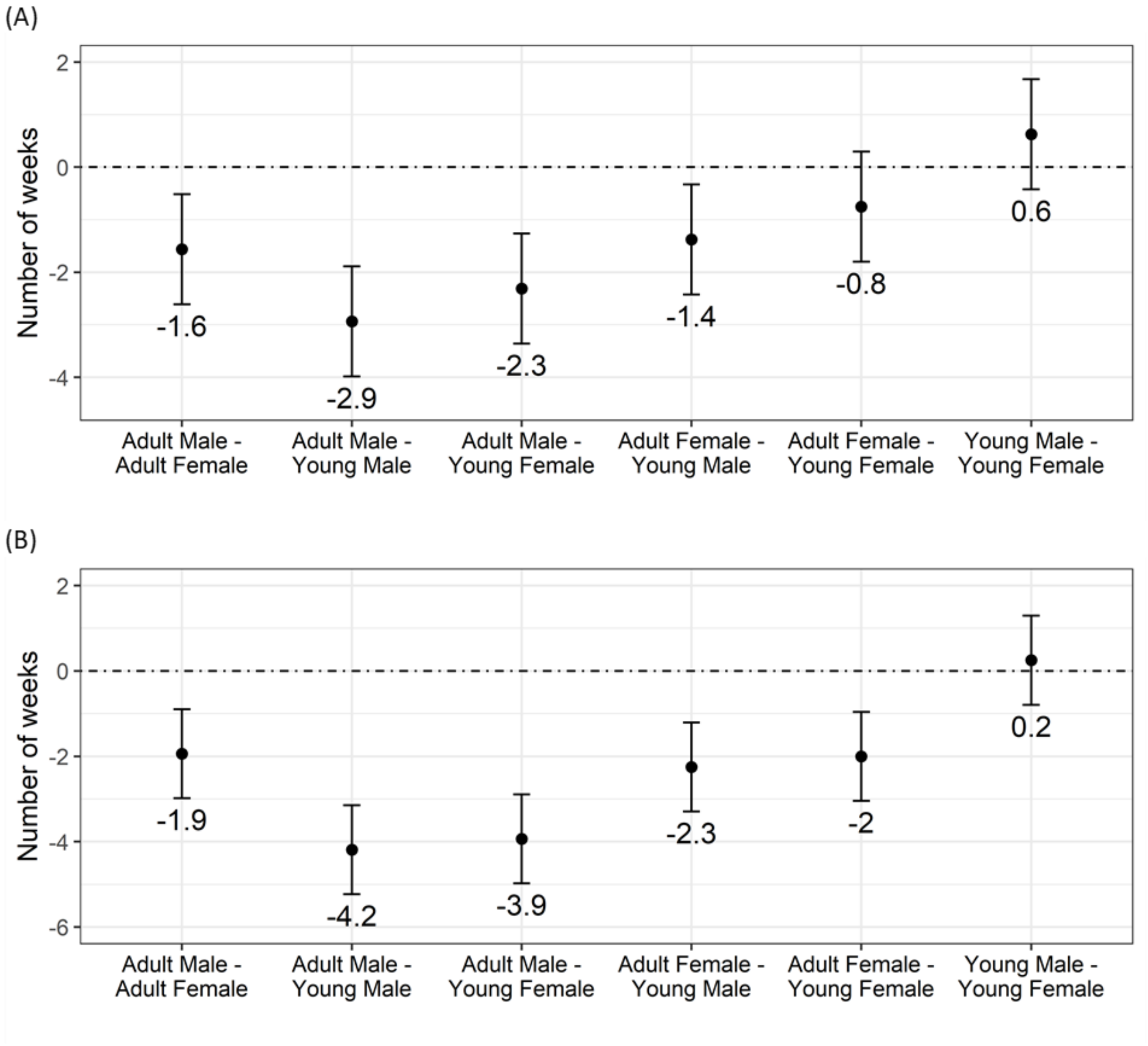

Figure 2.3. Estimated differences in mean start (A) and mean end (B) of migration between age-sex categories, using Bonferroni-adjusted 95% confidence intervals. Error bars that do not cross the zero-dash line represent statistically significant differences between age-sex categories. For instance, the first comparison [i.e., the first dot and interval on panel (A)] suggests that adult males migrate in average 1.6 weeks earlier than females. Adult males start and end fall migration significantly earlier than adult females and young, and adult females end migration earlier than young of both sexes

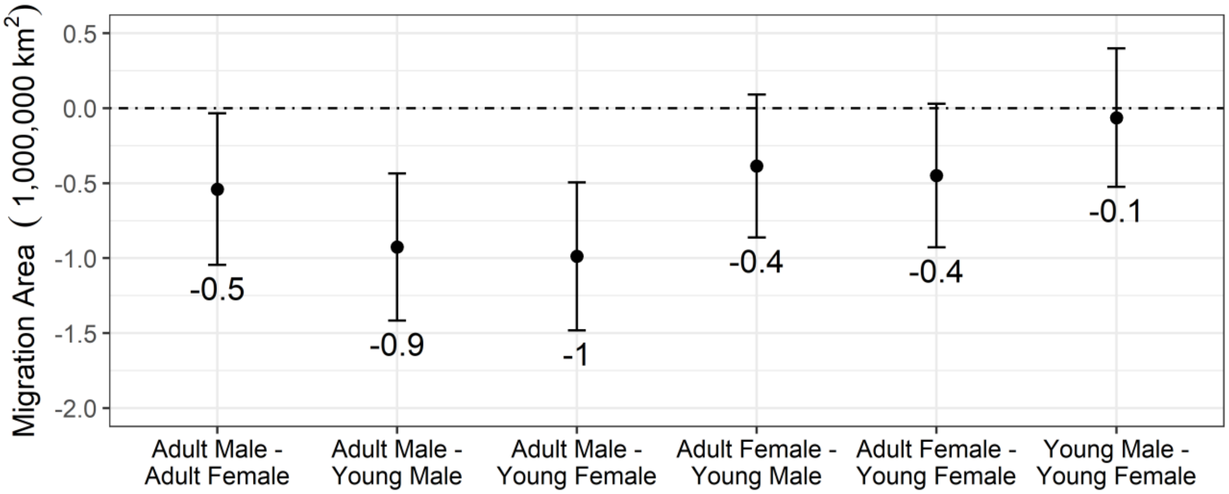

Figure 2.4. Estimated differences in mean distribution area, using a 50% core kernel, during fall migration between age-sex categories, using Bonferroni-adjusted 95% confidence intervals. Error bars that do not cross the zero-dash line represent statistically significant differences between age-sex categories. Note -- adult males use a significantly smaller distribution area compared with adult females, young males, and young females.

CHAPTER 3 – Species distribution models and the stationarity assumption

ABSTRACT

Species distribution models (SDMs) provide insights into species' ecology and distributions and are frequently used to guide conservation priorities. However, most SDMs assume stationarity, which refers to a model or process for which the parameters are fixed through space. If a species has a stationary distribution, the relationship between abundance and predictor variables should be constant across a breeding distribution. We used Breeding Bird Surveys, climate and remote sensing data, and a novel model transferability methodology to test whether 131 species of North American birds show consistency in their habitat relationships across their range. We also assessed whether species' traits were correlated with stationarity. Lastly, we tested the hypotheses that prediction accuracy between modeled regions should decrease with 1) geographical distances, 2) degree of extrapolation, and 3) were affected by a 'core-boundary' effect, which assesses distances to the boundary of a distribution. Our results suggest that very few species exhibit spatial stationarity. Species with large distributions, with distributions located in areas with low topographic relief, and with a short lifespans are more likely exhibit non-stationarity. Transferability between modeled regions also decreased with geographical distances and level of extrapolation. We expect that low transferability in SDMs potentially resulted from both ecological non-stationarity (i.e., biological differences within a species across its range) and statistical non-stationarity (i.e., over-extrapolation). Accounting for non-stationarity in SDMs should increase our ability to predict the presence and abundance of species in space and time, and thus increase the success of conservation efforts.

INTRODUCTION

The accuracy of species distribution models (SDMs) is essential for sound conservation decision making. By predicting the presence of a species through time and space, biologists and managers can use SDMs to forecast biological invasions, identify critical habitats, prioritize the locations of reserves, and appropriately translocate endangered species (Guisan et al. 2013). While SDMs are a ubiquitous tool, they have several assumptions that may not be realistic in the real world, decreasing prediction accuracy (Guisan and Thuiller 2005, Pearman et al. 2008, Elith and Leathwick 2009).

The ecological niche has often been defined as the environmental conditions under which a species can survive and reproduce (Hutchinson 1957). While this concept is highly relevant to distribution models (Guisan and Thuiller 2005), it is also often assumed that species have consistent niches throughout their distributions. In other words, a species is associated with the same abiotic and biotic factors over time and at all locations (Pearman et al. 2008). However, theory and empirical evidence suggest otherwise. Spatial variation in species' niches may occur if there are genetic differences among populations (Pearman et al. 2008) or if a species is facing different degrees and types of competition, predation, and diseases across their range (Araújo and Luoto 2007, Daskin and Alford 2012, Chamberlain et al. 2014, Vergnon et al. 2017).

The assumption that species have spatially and temporally consistent niches is related to the concept of stationarity, defined here as a model or process for which the parameters are fixed in space and time (Miller 2012, Dale and Fortin 2014). There are some indications that the assumption of stationarity may not always hold true (Whittingham et al. 2007, Fink et al. 2010, Schmidt et al. 2014, Shirk et al. 2014, Howard et al. 2015, Laube et al. 2015, Gómez et al. 2016, Zuckerberg et al. 2016, Wan et al. 2017). However, little information is available about which species, and more specifically which species traits, may be associated with stationary, or non-stationary, processes. For example, life history traits, such as clutch size, number of broods, and longevity may correlate with stationarity. Other traits such as the size and topography of a distribution, as well as primary habitat used, may result in some species being more stationary than others. Understanding such correlates of non-stationarity will provide advance knowledge about the likely reliability of species distribution model predictions.

Within a species' geographic range, it is also likely that geographical, ecological, and environmental features impact prediction accuracies. Under the stationarity assumption, a regional model should predict equally well within and between regions of a distribution. However, at least three mechanisms may promote non-stationarity and decrease prediction accuracy.

First, it is widely known that ecological similarity decreases with increasing distance – a phenomenon known as Tobler's law in geography (Tobler 1970). Therefore, under this *geographic distance hypothesis* (Figure 3.1a), we would expect species distribution model predictions to become less accurate with increasing physical distances between where a model has been built (i.e., trained) and where it is applied (i.e., tested; Yates et al., 2018). Second, prediction accuracies may decrease between models that are located at different distances from a distribution's core. Under this *core-boundary hypothesis* (Figure 3.1b), prediction accuracies may increase if a model is transferred between core or boundary regions. This hypothesis is built on the premise that species may have different levels of fitness, competition, gene flow, and abundance across their ranges, following a gradient along the range's core to boundary (Sexton et al. 2009, Orme et al. 2019). This hypothesis is different from the *geographical distance hypothesis* because two regions may both be located at the boundary of a distribution yet be very geographically distant from each other. Lastly, models transferred between regions with overlapping ranges of environmental values (termed "interpolation") should have higher predictive accuracy than models transferred between regions where the environments are not analogous (i.e., termed "extrapolation"; Elith and Leathwick 2009, Bahn and McGill 2013, Qiao et al. 2019). We refer to this hypothesis as the *analogue environment hypothesis* (Figure 3.1c). While the concept of extrapolation is different from the assumption of stationarity, the two may be related through the concept of spatial autocorrelation (Fotheringham 2009, Bahn and McGill 2013, Wolkovich et al. 2014). For example, a species could have a quadratic relationship between abundance and temperature across a distribution, where temperature has a gradient from warm in the south to cold in the north (i.e., temperature is spatially autocorrelated across large distances). If a model is trained in a colder northern region of the distribution, the relationship between abundance and temperature would be positive. But if that same model is used to predict abundance in a warmer southern region, the model would not yield accurate predictions because the relationship between abundance and temperature in the second region is negative. These three hypotheses have some commonalities. Regions further apart geographically are more likely to have different climate and habitats, thus increasing the level of extrapolation.

While the predictive pattern of each species' unique distribution may fit best with a specific hypothesis, we expect that support for some hypotheses may be more common across species than others. Moreover, while these hypotheses relate to prediction accuracies across space, the results are relevant to predictions over time. For example, prediction accuracies would decrease when predicting across longer time periods, as they would with increasing geographical distances (Likens 1989, Damgaard 2019). In light of global climate change, our capacity to predict across time has already been challenged by non-stationarity issues (Harris et al. 2006, Milly et al. 2008, Wiens 2012, Betts et al. 2019). As such, poor stationarity across space could yield similar conservation challenges as a lack of stationarity over time and impact large-scale land management practices (Thomas et al. 2006, Millar et al. 2007), ecological restoration success (Harris et al. 2006, Wiens 2012), our predictions of animal communities (Williams and Jackson 2007, La Sorte et al. 2009), and our capacity to predict relationships between reproductive success and climate (Schmidt et al. 2014).

Here, we used 131 species of North American birds to address three main questions: (1) Can we assume model stationarity across bird’s SDMs? Because we expected variation across species, and to clarify when and why SDMs failed to predict species abundance, we aimed at answering two additional questions. (2) What geographic and life history predictors can explain variation in species-level stationarity? Here, our results would provide guidance as to which species, based on their traits, are more likely to exhibit non-stationary SDMs. (3) For non-stationary SDMs, what causes the decrease in model prediction across space? To answer this question, we tested three hypotheses associated with features of a distribution – the *geographical distance hypothesis,* the *core-boundary hypothesis,* and the *analogue environment hypothesis* (Figure 3.1). We addressed these questions using 131 avian species observed over 5 years across the coterminous US and Canada.

MATERIALS AND METHODS

Data – Bird species and abundance

We used data from the USGS Breeding Bird Survey (BBS) to extract abundances of bird species in Canada and USA. BBS consists of routes surveyed once a year during the breeding season (typically June). A BBS route includes 50 three-minute point counts, separated by a distance of at least 0.5 miles (Sauer et al. 2003). The points remain at approximately the same locations and are often conducted by the same observer from year to year to maintain consistency. The location and associated data for over 5,000 routes, spanning Canada and the continental USA, are available on the BBS website (Pardieck et al. 2019); www.pwrc.usgs.gov/bbs/).

We selected bird species (n = 138) based on three main criteria. First, a species had to be detected in at least 30 different routes per year. This provided for a minimum sample size in the number of routes where a species is present and helped ensure our models would predict reasonably well (Stockwell and Peterson 2002, Hernandez et al. 2006, Wisz et al. 2008). Second, we selected species with a prevalence, defined as the percentage of routes within the distribution where the species was present, of at least 20%. We also excluded highly common species (prevalence >75%). These prevalence values are recommended to improve the fit of SDMs (McPherson et al. 2004). Third, a minimum of 80% of the breeding distribution of each species had to be within the area covered by the BBS routes. We used breeding bird distributions from BirdLife International (2018). The area covered by the BBS routes was determined using a minimum convex polygon surrounding all BBS routes.

For each BBS route and species, we used the mean abundance for the years of 2013 to 2017 (inclusively; Howard et al., 2014). This range of years represents the latest five years available at the time of download. Using the mean abundance across a short time frame enabled us to account for metapopulation dynamics and reduce the noise caused by yearly changes in detections, while limiting the impact caused by long-term changes in habitat and climate on bird abundance (Gutiérrez-Illán et al. 2014, Betts et al. 2019).

Data – Environmental covariates

We used climatic and land cover covariates known to be correlated with bird abundance (Austin 2002, Shirley et al. 2013, Gutiérrez-Illán et al. 2014, Howard et al. 2015, Betts et al. 2019). Data were obtained from Google Earth Engine (Gorelick et al. 2017) and were summarized for each BBS route and year (2013 to 2017), using a 400 m buffer (Bahn and McGill 2013). Datasets were selected based on their availability across North America. Climatic covariates were obtained from Daymet V3 (Thornton et al. 2017) and included summer precipitation (prcpSummer), winter precipitation (prcpWinter), maximum summer temperature (tMax), and minimum winter temperature (tMin). We used the equivalent of the band 3 (B3) and 4 (B4) of Landsat 7, from Landsat 5, 7, and 8 as land cover variables. These land cover data were summarized using the LandTrendr tools (Kennedy et al. 2018). LandTrendr includes several preprocessings of the images such as geometric rectification and cloud and shadow screening. It creates a yearly surface reflectance composite which we used to summarize the data for each BBS route. We used B3 to discriminate between built-up environments and vegetation, and B4 to compare rates of chlorophyll absorption which is useful to distinguish between conifer and broadleaf as well as young versus senescent vegetation. The climatic and land cover covariates used in the analysis are summarized in Table 3.1. To be consistent with bird data and to increase model transferability (Tuanmu et al. 2011), covariates for each BBS route were then averaged over the period from 2013 to 2017. The number of BBS routes used for each species was dependent on the size of its breeding distribution (mean number of BBS routes per species: 1568.5 ± 1061.4 SD).

Model transferability analysis

We divided the distribution of each species into equal-sized hexagons of 106,088 km^2 (apothem of 175 km; we refer to these as ‘regions’; Figure 3.2). We established a hexagon size that jointly maximized both the within-hexagon number of BBS routes, and number of hexagons within each distribution. We determined this optimum via sensitivity analysis, in which we used different sizes of hexagons and species to assess the greatest number of hexagons containing at least 30 BBS routes. Out of 138 species, 131 had at least one pair of hexagons with a minimum of 30 BBS routes per hexagon.

We trained a Random Forest regression model (Breiman 2001, Liaw and Wiener 2002) on each hexagon, using mean abundance of each bird species per BBS route as response variables and the BBS route environmental variables (Table 3.1) as explanatory variables. Because we considered both the BBS routes where a species was present and those where a species was absent, i.e., what each species used versus what was available, these models likely reflect the habitat selected by each species. For the Random Forest models, we used an ensemble of 1,000 trees. To avoid overfitting, each tree was split using two randomly selected variables and a randomly selected (with replacement) subset of the records. We zero-centered and scaled by the standard deviations all predictors to avoid bias in the variable selection process (Boulesteix et al. 2012). The remainder (out-of-bag) records from each tree were used to predict abundance within the same hexagon (referred to 'within-region predictions'). The within-region prediction accuracy, the relationship between observed and predicted within the same hexagon, was calculated using a Spearman coefficient of correlation (ρ_i) (Yates et al. 2018, Qiao et al. 2019). We used Random Forest because this machine-learning algorithm has previously been shown to provide satisfactory, in-sample, predictive performances (Wenger and Olden 2012) and it has the advantage of modeling multiple interactions and relationships between variables (Evans et al. 2011, Boulesteix et al. 2012). While model transferability performance is less desirable in some cases (Elith and Graham 2009, Heikkinen et al. 2012, Wenger and Olden 2012, but see Mi et al., 2017), it is unlikely that our choice of model affected the direction of our results because our interest lay in the relative difference in prediction accuracies between regions, rather than absolute prediction accuracies.

We paired all hexagons, keeping track of the directionality of each pair (i.e., keeping the pairs for hexagon 1 to 2 and hexagon 2 to 1). For each pair of hexagons, we used the training model from one hexagon to predict abundance in the second hexagon (referred to 'between-regions prediction'). We also assessed between-regions prediction accuracy using a Spearman coefficient of correlation (Qiao et al. 2019). Each species had a different number of Spearman coefficients based on the number of pairs of prediction (i.e., number of pair of hexagons) within their distribution.

Stationarity analysis

We used the within-region predictions per species to calculate a mean within-region Spearman ($\overline{\rho_\iota}$). Species with a high $\overline{\rho_\iota}$ were species for which models generally predicted well within the same hexagon. We selected species with a $\overline{\rho_\iota} > 0.2$ for the remainder analyses. This value is associated with models that have a small positive predictive strength of association between predicted and observed values (Cohen 1992, Møller and Jennions 2002, Betts et al. 2019). We also completed a sensitivity analysis to assess if different cutoffs for $\overline{\rho_\iota}$ would yield different results. The direction of the results did not qualitatively change with different cutoff values.

We created a Stationarity Index (*S*) per species. This index represents the mean change in predictive value between the within-region and between-regions, such that:

$$\text{Stationarity } (S) = 1 - \left(\frac{1}{i*j}\sum_{i*j}^{1} |\rho_i - \rho_{ij}|\right)$$

where ρ_i is the within-region Spearman coefficient of correlation for region i of each species, ρ_{ij} is the between-regions Spearman for a model trained in region i and tested in region j, and i*j represent the total number of pairs of regions. If a species has a stationary process regulating abundance, then a model trained in one region should predict abundance in another region with similar accuracy, and thus yield a small difference in Spearman coefficients between the within-region and between-regions. The stationarity index ranges from 0 to 1, with mean differences closer to 1 representing stationary processes. This index represents a gradient of stationarity and one would need to consider sample size (number of independent pairs) to assess the level of significance in *S* for each species (Cohen 1992). For the purposes of this analysis, we suggest that species with non-stationary models are likely to have an index value lower than 0.85.

Geographical and life history traits associated with stationarity

We expected that degree of stationarity (*S*) would be predictable based on the geographical and life-history traits of species. For example, shorter lived species, and species with a greater number of broods and higher clutch size may have more rapid evolution and greater potential for adaptation to their environment (Vedder et al. 2013) as a result of quick turnover between generations; this could result in reduced stationarity across their ranges. Alternatively, long-lived species, which tend to have bigger brains (Minias et al. 2017), have a higher capacity for behavioral adaptation and would thus be less stationary in their distributions. The geographic range size of a species and its topographic heterogeneity may also impact stationarity. Larger geographic ranges should have more varied populations across space (Phillimore et al. 2007) and would likely cross a more diverse set of habitats and climatic conditions. Further, in North America, western regions tend to have more topographic relief, which also offers greater diversity of habitats and climatic conditions than in the mid-west region of North America. Spatial autocorrelation in biophysical features should be shorter in the west and habitat heterogeneity larger, and both of which are known to impact stationarity (Miller 2012). We also expected that the maximum summer temperature tolerated by a species within their ranges, i.e., the 10% warmest locations where the species is present (referred to as maximum temperature tolerance), could be correlated with stationarity. Jiguet et al. (2010) showed that bird species with higher thermal maximum are more likely to have positive population trends. These species may also be better adapted to a range of environmental conditions and have non-stationary distributions. Lastly other species traits such as migration status and primary habitat have been correlated with species' abilities to adapt to new environments (Pulido and Widmer 2005, Colles et al. 2009) and may be affecting the assumption of stationarity.

We used a phylogenetic linear model and the R package 'phylolm' (Ho and Ané 2014) to assess if the response variable, *S*, was correlated with species traits (explanatory variables). We accounted for differences in within-region model fit of each species by including $\overline{\rho_1}$ as an explanatory variable (Figure 3.2). A total of 117 species had phylogenetic data available and a $\overline{\rho_1} > 0.2$. The phylogenetic data were extracted from Jetz et al. (2012; www.birdtree.org). We used 5,000 trees from Ericson et al. (Ericson et al. 2006, Hackett et al. 2008) and 5,000 trees from Hackett et al. (2008). We used the R package 'ape' (Paradis and Schliep 2019) to calculate one consensus tree from the combined 10,000 trees. This consensus tree was used in the linear model to account for the lack of independence between closely related species.

We included six traits in the phylogenetic linear model. Each corresponds to the hypotheses above: distribution size, topographic variation where the range is located, maximum temperature tolerance, breeding habitat, migration status, and a single combined variable representing a slow-fast continuum in life history traits (Bennett and Owens 2002). We calculated topographic variation by calculating the standard deviation of the elevation pixels overlapping each distribution. We calculated maximum temperature tolerance for each species using the mean temperature of the warmest 10% BBS routes where the species was detected. We extracted breeding habitat information from the Partners In Flight database (Partners in Flight 2020). All species with the word 'forest' within the name of their primary breeding habitat were associated with the category 'forest', all others were associated with the category 'non-forest'. Based on Partners in Flight (2020), birds without the word forest as a primary habitat did not rely on forests during breeding. We visually assessed migration status using the distribution maps in Birds of the World (Billerman et al. 2020). All species with a summer distribution that is estimated to be more than 10% different from their distribution on other seasons were categorized as migrants, the others as residents. Lastly, we combined three life history traits into a Principal Component Analysis (PCA): maximum longevity, number of broods, and maximum clutch size. The life history traits for most species (n = 102) was extracted from Amniote (Myhrvold et al. 2015). Whenever data were absent from Amniote, we used the information from Birds of the World (Billerman et al. 2020). The PCA axis 1 explained 85.8% of the variance, with the 'longevity' responsible for 99.9% of its weight, therefore representing a "slow-to-fast" continuum in avian life-histories (Bennett and Owens 2002). The PCA analysis was completed using the R function prcomp (R Core Team 2019). The axis 1 values were then used as input in the phylogenetic linear model.

Attributes of a distribution

In total, 104 species satisfied our criteria for inclusion in the analysis (between-regions $\overline{\rho}_1 > 0.2$, 30 hexagon pairs). For each species, we tested whether the ρ_{ij} (response) were correlated with three aspects a species distribution, representing our three hypotheses above (*geographic distance hypothesis*, *core-boundary hypothesis,* and *analogue environment hypothesis*; Figure 3.1). We tested whether the ρ_{ij}, for each species, were correlated with geographical distance between hexagons. We used the center point of each hexagon to calculate a great circle distance (as the crow flies) between paired regions.

We tested if the location of the hexagons, whether at the core of a distribution or towards its boundary (i.e., *core-boundary hypothesis*) affected prediction accuracy between regions. We first calculated the distance between a hexagon's center to the closest range boundary line. We then used the absolute difference between the two hexagons' distances to the boundary. Under this hypothesis, hexagons with the greatest distances between core and range edge should have lowest prediction accuracy.

We tested the *analogue environment hypothesis* for each of the covariates used in the training and predicting models: prcpSummer, prcpWinter, tMax, tMin, B3 mean and standard deviation, and B4 mean and standard deviation. We compared the range of each covariate between each pair of hexagons. A range overlap of 100% could either represent a perfectly identical environmental range between paired hexagons, or more likely, that the range of the hexagon used for training included 100% of the values represented in the predicted hexagon. A percentage of overlap lower than 100% is associated with predictions that involved at least some degree of extrapolation. Negative percentages represent ranges that did not overlap.

We tested which of these three hypotheses were associated with each species using a univariate model selection approach (Figure 3.2). This allowed us to include a greater number of species, at the cost of excluding possible interactions between variables. Each univariate model consisted of a linear mixed model with ρ_{ij} as a response, one feature as an explanatory variable, and two random effects, the training hexagon ID and the predicted hexagon ID. The two random effects were needed since each hexagon was used multiple times as the training and as the predicted hexagon, resulting in a lack of independence among predictions. We used a Bayesian information criterion (BIC) approach to select the top model(s) per species. We selected BIC because it controls for differences in sample size in model selection (Burnham and Anderson 2003, Vrieze 2012). While controlling for sample size was not as important within each model selection analysis, i.e., within each species, we wanted to compare the top model(s) between species and each species had different sample sizes. BIC is also more consistent when simple models are considered (Vrieze 2012). We compared 11 univariate models: a null (intercept) model, a model representing geographical distance, one for the core vs boundary difference, and eight models representing the *analogue environment hypothesis*, one per climatic or land cover variable's percent range overlap. For each species, we retained the model(s) that had a delta BIC < 2. If the null model was among the best models, we only retained the null model.

RESULTS

Stationarity

Across 131 species, there was a consistent decrease in model prediction accuracy when testing models within-region ($\overline{\rho_i}$) than when testing between-regions ($\overline{\rho_{ij}}$; Figure 3.3a). A total of 119 species, out of the 131, had a $\overline{\rho_i} > 0.2$. These species had a mean decrease in prediction accuracy of 53.5% ± 28.3 between $\overline{\rho_i}$ and $\overline{\rho_{ij}}$, and a mean stationarity index of 0.70 ± 0.09 (Figure 3.3b; Appendix C).

Species traits

Several species traits were correlated with stationarity. As expected, species with larger geographic ranges tended to have lower stationarity (Table 3.2; Figure 3.4a). Topographic variation within distributions was also important; species inhabiting regions with greater topographic variation are more likely to have stationary SDMs (Table 3.2; Figure 3.4b). Maximum temperature tolerance was marginally significant and was negatively correlated with stationarity (Table 3.2). Finally, we found that SDMs for short-lived species tended to be less stationary.

Attributes of distributions

We found that several attributes of species' geographic ranges were useful predictors of model transferability between-regions. Of the 104 species used in this analysis, 76.9% (80 species) had prediction data fitting at least one of the three hypotheses tested (Figure 3.5; Appendix D). We found strong support for the *geographic distance hypothesis* for 24.0% of species (Figure 3.5; example in Figure 3.6a). As expected, larger distances between regions decreased model transferability. Further, the *analogue environment hypothesis* was supported for 51.0% of species; the greater the amount of extrapolation from the environmental conditions observed in the model training region, the greater the fall-down in prediction success. However, one covariate stands out as being the most impactful; 22.1% of species had model transferability decreased by extrapolation in the amount of vegetation (B3 mean) between regions (Figure 3.5; example in Figure 3.6b). Overall, 30.8% of species were affected by extrapolation in at least one land-cover covariate and 22.1% of species by extrapolation in at least one climate covariate. Unexpectedly, the *core-boundary hypothesis* was supported for only 3.8% of species. Overall, 9.6% of species were affected by both distance and extrapolation, i.e., these species had two hypotheses reflected among the top models (delta BIC < 2), one representing the *geographic distance hypothesis*, one representing the *analogue environment hypothesis*.

DISCUSSION

We used abundance data from 131 bird species breeding in North America to 1) assess model stationarity, 2) identify species traits most likely correlated with non-stationary SDMs, and 3) within each species' SDM, assess if model transferability results were correlated to three hypotheses - the *geographical distance hypothesis*, the *core-boundary hypothesis*, and the *analogue environment hypothesis*. We assumed that if stationary processes govern bird abundance within breeding distributions, then models trained in one region should predict other regions with similar accuracy. However, we found between-regions predictions were 53% poorer than models making predictions within-regions – suggesting poor model transferability and violation of the stationarity assumption. While selection of modeling tool can impact between-region model performance (Osborne et al. 2007, Heikkinen et al. 2012, Bahn and McGill 2013, Bell and Schlaepfer 2016, Qiao et al. 2019), our results support previous studies indicating that an increase in geographical distances (Qiao et al. 2019) and an increase in extrapolation (Torres et al. 2015, Bell and Schlaepfer 2016, Qiao et al. 2019) between model training and testing areas contributes to the reduction in prediction accuracies. Moreover, our results suggest that extrapolating between regions with different amounts of vegetation seems especially problematic for model transferability.

We used a combination of within-region and between-regions prediction accuracies to calculate a stationarity index, *S*, per species. While species fell along a gradient of stationarity, our results suggest that most models violated the stationarity assumption. Species stationarity indices, in this study, were correlated with three ecological and life history traits: size of a distribution, amount of topographic relief within a distribution, and species' longevity. Consistent with the results of McPherson and Jetz (2007), we found that species with large distributions were less likely to have stationary SDMs. Species with distributions containing a lower amount of topographic relief were also less likely to have a stationary SDM. Moreover, short-lived species were more likely to have a non-stationary distribution. We recommend caution when transferring models across space for such species.

As predicted, we found that species with distributions in areas with low topographic relief are less likely to exhibit stationarity in SDMs. If the objective is prediction to new areas, we recommend that model training areas include as broad a range of environmental and land-cover variables as possible. For instance, in mountain landscapes, environmental conditions often reflect those encountered by species across their entire geographic ranges. This limits the risks posed by extrapolation.

It is likely that similar mechanisms drove our findings that species with larger geographical ranges are more likely to have non-stationary SDMs, and that increases in geographic distance reduce stationarity. However, species with large geographical ranges are not always those affected by distance. The cause of this discrepancy could be the presence of different populations or subspecies across space, with each population responding slightly differently to environmental conditions. While an increase in distance increases the likelihood of encountering different populations, populations could be relatively close to each other, if for example, separated by a physical barrier (Pomara et al. 2014, Kopuchian et al. 2020).

Our results emphasize the importance of testing the stationarity assumption in SDMs prior to extrapolating to new geographic locations or into the future (Legendre and Fortin 1989, Betts et al. 2006, Dormann et al. 2007, Hawkins 2012, Ghorbani 2013, Sequeira et al. 2018). We also recommend assessing the level of extrapolation used in model transfer analysis (Broennimann et al. 2012, Zurell et al. 2012, Qiao et al. 2019) and documenting the results in publications. When in doubt, statistical analyses should instead assume spatial non-stationarity and use statistical tools designed to account for non-stationarity. Several options are available to test for stationarity (Hadri 2000, Gelfand et al. 2003, Fuentes 2006, Fuentes et al. 2008, Cressie et al. 2009, Rangel et al. 2010, Ghorbani 2013, Benhamou 2014, Dale and Fortin 2014, Dixon et al. 2016, Fotheringham et al. 2017, Wan et al. 2017), to account for non-stationary processes (Hastie and Tibshirani 1993, Brunsdon et al. 1998, Assunção 2003, Rangel et al. 2010, Fink et al. 2010, Matthiopoulos et al. 2011, Fink et al. 2013, Fletcher and Fortin 2018) and to compare stationary versus non-stationary methodologies and models (Diniz-Filho et al. 2008, Fink et al. 2010, Miller 2012, Montanari and Koutsoyiannis 2014).

Two mechanisms could influence the degree to which the assumption of stationarity is met. First, the actual biological processes governing a species' distribution could vary across geographic space; such factors influence what we term *ecological stationarity*. For instance, new competitors could arise in particular parts of the species range, which could alter relationships between observed predictors and species abundances (Jankowski et al. 2010). Similarly, geographic isolation and different climatic conditions could combine to enable subpopulations within species - each with somewhat different environmental niches (Bush 1994, Peterson and Holt 2003). In short, a lack of ecological stationarity could be caused by the presence of unaccounted differences in biotic interactions or processes such as emergence of sub-population structure across a species' range.

However, even if a species exhibits a high degree of ecological stationarity, a lack of *statistical stationarity* can also impinge severely on model prediction success. This occurs due to non-linear relationships to various environmental variables throughout a species' range.

Model misspecification is yet another mechanism that likely affects model stationarity and transferability (Miller 2012, Dale and Fortin 2014). For instance, SDMs often use predictor variables collected at broad spatial scales, but organisms often respond to the environment at finer scales (Potter et al. 2013, Frey et al. 2016). Adding additional covariates to a model could help, but it involves a cost, both statistically in terms of model complexity, and the economic costs of gathering additional data. Considering limited conservation and management resources, it becomes important to balance the level of accuracy in model prediction with the cost involved in improving the model accuracy (Montanari and Koutsoyiannis 2014).

Management and conservation applications

Our results highlight the difficulty associated with predicting abundance across space for most species of birds breeding in North America. If unaccounted for, non-stationarity could mislead conservation efforts by inaccurately predicting species occurrences and abundances across space and time. The problems associated with extrapolation are well known, and yet many applications of SDMs ignore the consequences. Moreover, rarely are attempts made to directly tests for stationarity in space or time. If handled appropriately, ecological non-stationarity (Legendre and Fortin 1989, Ghorbani 2013, Dale and Fortin 2014) may not be a problem in itself but a source of information to be quantified. It can elucidate potential patterns in habitat use and selection across geographic ranges that could imply population structure (Hawkins 2012).

Regardless of the source of non-stationarity, and as mentioned by Milly et al. (2008, 2015)– "In a nonstationary world, continuity of observations is critical". In order to improve the accuracy of SDMs and to better identify stationary versus non-stationary ecological processes, we need more data, both in terms of responses (e.g., abundance points) and covariates (Montanari and Koutsoyiannis 2014, Pennekamp et al. 2017, Yates et al. 2018). The future of conservation and success of management actions may rely on the notion that many ecological processes are spatially and temporally non-stationary (Wiens 2012, Wolkovich et al. 2014). They thus rely on continual and consistent monitoring of our environment.

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TABLES AND FIGURES

Table 3.1. Summary of the environmental covariates used in the modeling analysis.

Variable	Source	Pixel Size	Cadence – range used	Summary per pixel, per year	Summary per route, per year
Band 3*	Landsat 5, 7 & 8	30 m averaged to 90 m	16 days – May 15 to July 15	Medoid**	Mean and SD
Band 4*	Landsat 5, 7 & 8	30 m averaged to 90 m	16 days – May 15 to July 15	Medoid**	Mean and SD
Precipitation Summer	Daymet V3 - prcp	1,000 m	Daily – May 15 to July 15	Sum	Mean
Precipitation Winter	Daymet V3 - prcp	1,000 m	Daily – Jan. 1 to March 15	Sum	Mean
Maximum Summer Temperature	Daymet V3 - tmax	1,000 m	Daily – May 15 to July 15	Medoid**	Mean
Minimum Winter Temperature	Daymet V3 - tmin	1,000 m	Daily – Jan. 1 to March 15	Medoid**	Mean

* Used LandTrendr to summarize the values.

** The mediod is obtained by selecting the image pixel with the smallest difference between the median from all layers and the observation, per band.

Table 3.2. Results of phylogenetic linear models assessing relationship between stationarity index *S* and species traits. Traits in bold had 95% confidence intervals that did not include zero.

Species Trait	**Estimate**	**95% CI**
(Intercept)	0.803	0.468 to 1.139
Within-region mean Spearman	0.068	-0.062 to 0.199
Distribution size (1,000,000 Km^2)	**-0.013**	**-0.019** to **-0.007**
Topographic variation (km)	**0.091**	**0.021** to **0.160**
Maximum temperature (°C)	-0.005	-0.011 to 0.001
Habitat – Forest vs non-forest	0.014	-0.041 to 0.070
Migration status – Migrants vs Residents	0.001	-0.107 to 0.109
PCA axis 1 (Longevity)	**0.007**	**0.001** to **0.013**

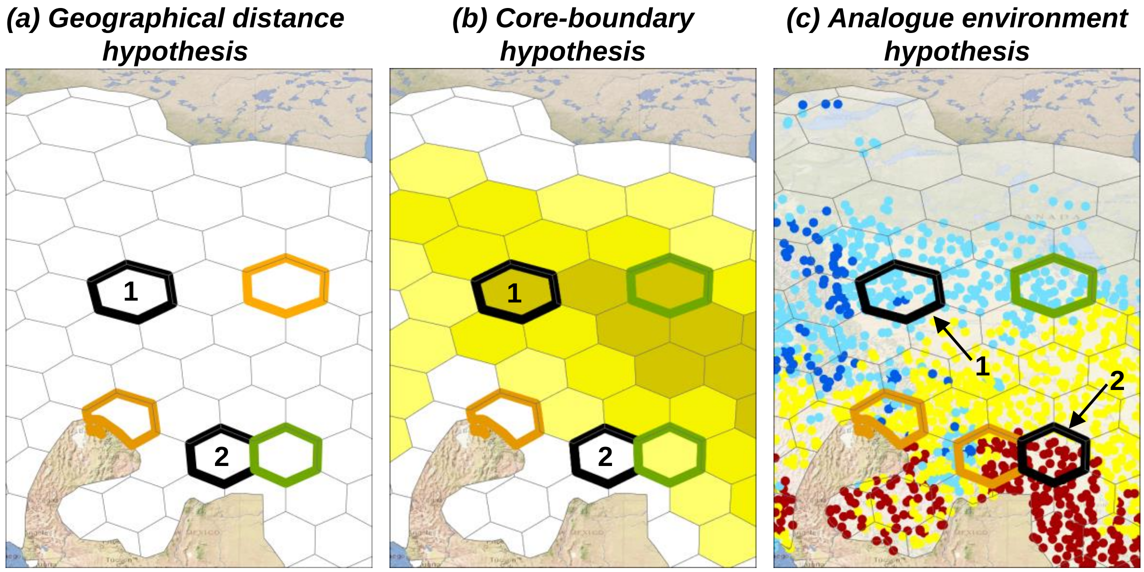

(a) Geographical distance hypothesis
(b) Core-boundary hypothesis
(c) Analogue environment hypothesis

Figure 3.1. Graphical representation of the three hypotheses associated with our model transferability analysis. Black hexagons represent regions where a model was trained. Green hexagons represent regions where we expect good model transferability, and orange hexagons where we expect poor model transferability. (a) Under the *geographical distance hypothesis*, model transferability will be greatest over shorter geographical distances. A model trained in 1 would do poorly in the orange regions and a model trained at 2 would predict well the abundance in the neighboring green region. (b) The *core-boundary hypothesis* is symbolized by a yellow gradient across regions, where core regions are dark yellow and boundary regions are white. Under this hypothesis, a model at the core, such as model 1 would predict well other core regions such as the adjacent green region. The same applies for two boundary regions such as 2 and its neighboring region, but a core region such as 1 would poorly predict the region in orange because it is at the range boundary. (c) Under the *analogue environment hypothesis*, regions with a similar range of environmental conditions should show high transferability. Here the color dots represent temperature, from warm in red to cold in dark blue. Region 1 would predict well the green region because they have the same range of temperature (light blue dots) but poorly the regions in orange. Region 2 would also poorly predict the regions in orange, even if within close proximity.

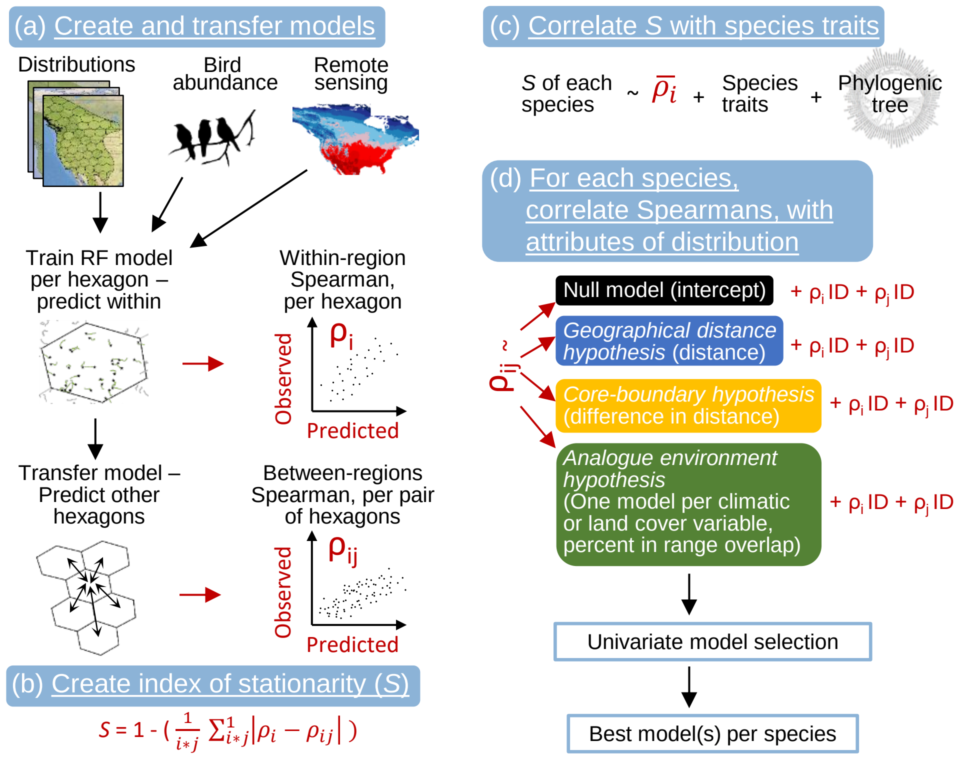


Figure 3.2. Summary of the methodology used in this paper. (a) We used bird distributions, abundance, and remote sensing data to train models within small regions (hexagons) of each distribution. For each model, we calculated a Spearman coefficient of correlation (ρ_i) representing the within-region prediction accuracy. Each trained model was transferred to all other regions of the distribution. We calculated a between-regions prediction accuracy using Spearman (ρ_{ij}). (b) For each species, we calculated a stationarity index (*S*) using the average difference between ρ_i and ρ_{ij}. (c) We assessed whether *S* was correlated with species traits using a phylogenetic linear model. (d) For each species, we completed a univariate model selection analysis, using the between-region predictions (ρ_{ij}) as response variables and variables representing our three hypotheses as explanatory variables. We then compiled the best model(s) from all species to assess which hypothesis best fitted our species.

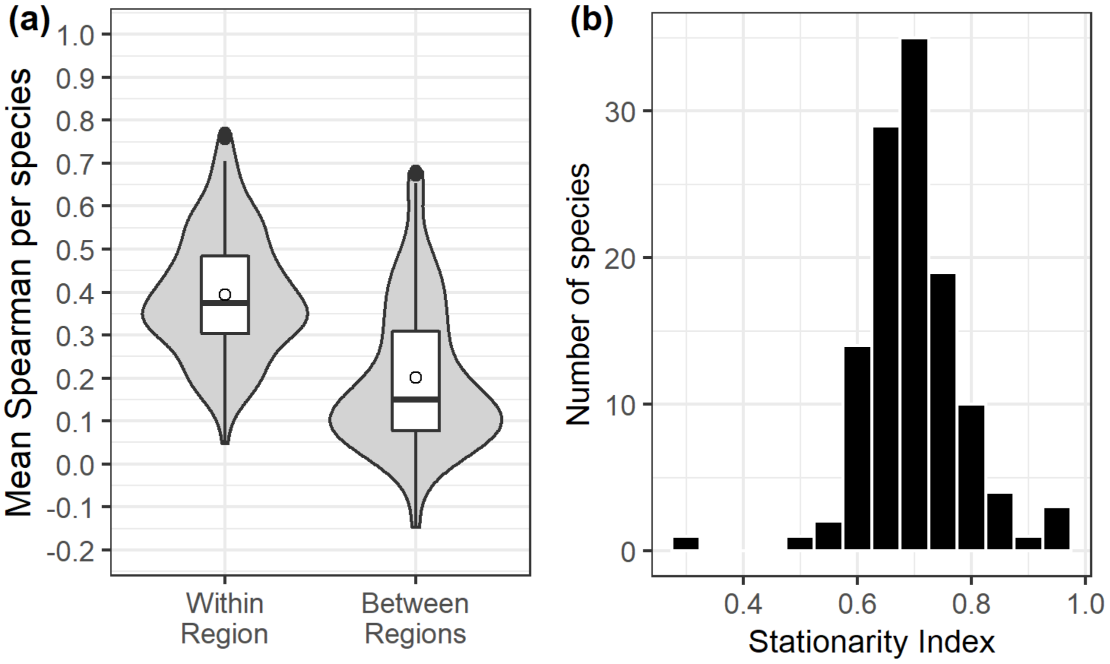


Figure 3.3. (a) Comparisons of the mean within-region Spearman ($\overline{\rho_{\imath}}$) per species and mean between-regions Spearman ($\overline{\rho_{\imath\jmath}};$). The models predicted within the same region had substantially higher prediction accuracy than between regions. The white circles represent the mean per category. The violin plots represent the distribution of means among species and the boxplot shows the quartile spread of the data. (b) Histogram of the stationarity index (*S*) per species, where large values of *S* indicate high model transferability.

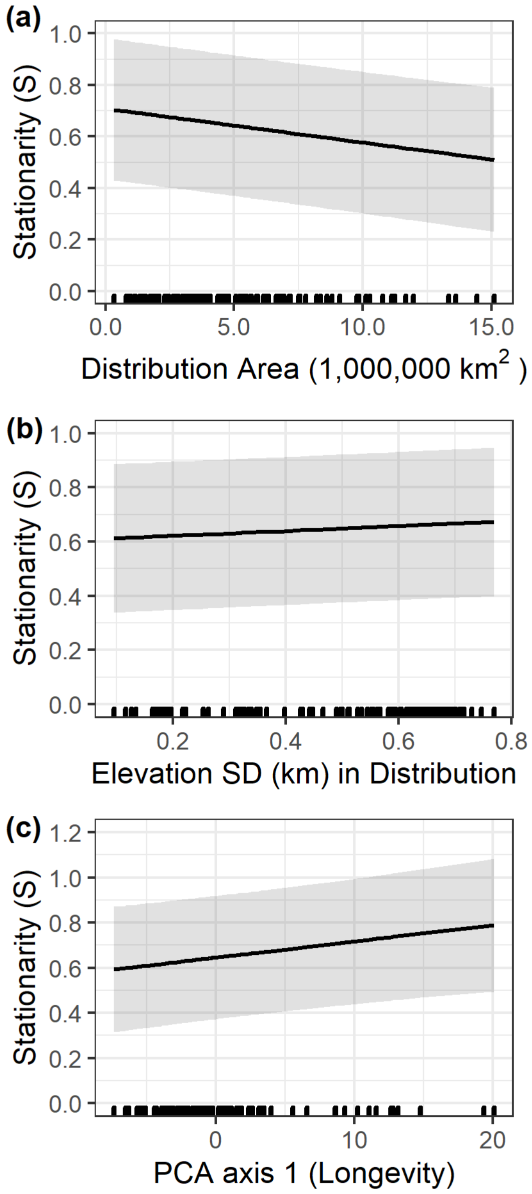


Figure 3.4. Rug plots showing the correlation between the stationary index (*S*) and (a) species breeding distribution size, (b) standard deviation of the elevation where the distribution is located, representing topographic variation, (c) life history PCA axis 1 representing a fast to slow live history strategy (with long-lived species having high values) While the slope of these correlations are significant (their confidence intervals do not cross zero; Table 1), the confidence intervals depicted here are much larger and cover a wide range of intercepts because several species were phylogenetically related to each other.

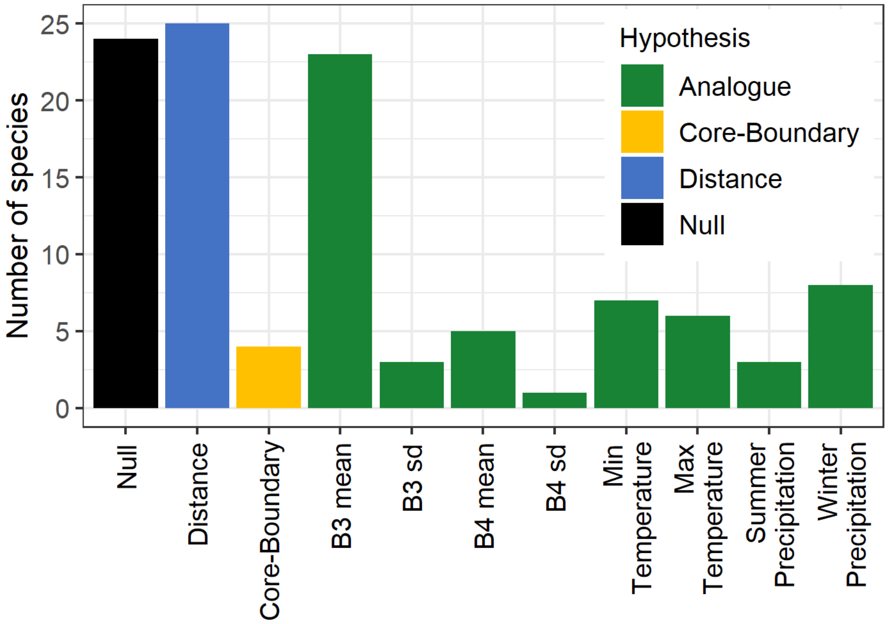
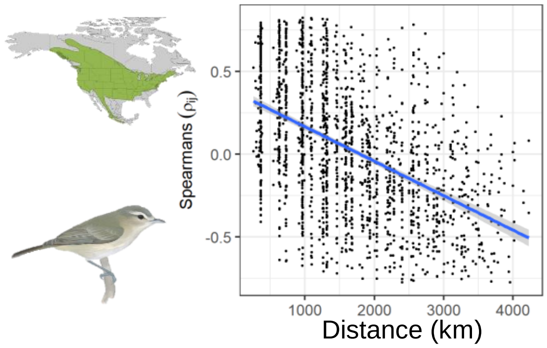


Figure 3.5. For each species, we compared 11 models in a model selection analysis. The top model(s) of each species is represented by a bar in this graph. The colors represent the hypothesis tested by each model. The blue bar represents the *geographic distance hypothesis*, the yellow bar represents the *core-boundary hypothesis*, and the green bars represent each variable tested as part of the *analogue environment hypothesis*. We added a null model (in black) to each species. Out of 104 species, most species (76.9%) had model transferability results that fitted at least one of the three hypotheses. Most species had prediction accuracies correlated with geographical distance between regions and with extrapolation in the amount of vegetation (B3 mean) between regions.

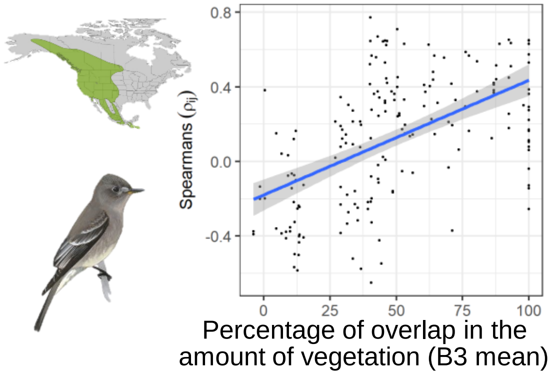
(a) Warbling Vireo

$\overline{\rho_i} = 0.46$; $\overline{\rho_{ij}} = 0.03$, S = 0.51



(b) Western Wood-pewee

$\overline{\rho_i} = 0.42$; $\overline{\rho_{ij}} = 0.13$, S = 0.60



(c) Magnolia Warbler

$\overline{\rho_i} = 0.65$; $\overline{\rho_{ij}} = 0.39$, S = 0.68

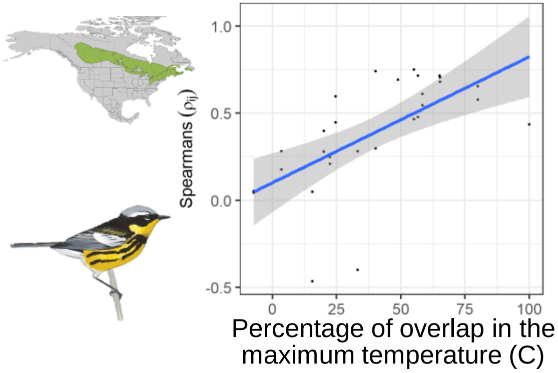


Figure 3.6. Example of results on the attributes of a distribution that influenced model transferability among study regions (hexagons). (a) Increases in geographic distances between training and testing regions decreased model transferability for Warbling Vireo, (b) Model transferability was improved with a decrease in extrapolation (an increase in percentage of overlap) in the amount of vegetation (B3 mean) for the Western Wood-pewee, and (c) model transferability was improved with a decrease in extrapolation in maximum summer temperature for the Magnolia Warbler.

CHAPTER 4 – Avian niche breadth is plastic throughout the annual cycle

ABSTRACT

Migratory species likely encounter different environmental conditions throughout their annual life cycle, yet, our knowledge of their niches across that cycle is limited. A long-held assumption is that each species is associated with one niche, which is conserved year-round. However, it is also possible that migratory species switch niches between seasons because their life events requirements are different. Lastly, an intermediate hypothesis is that the niche of migratory species changes slightly throughout the year, contracting and expanding, depending on the seasons. We used remotely sensed land use and climate data, combined with year-round eBird data for 83 species to challenge these hypotheses. We calculated a niche per species, season and year (2005 to 2020) and compared niches across years (within seasons) and across seasons (within years). As expected, niche overlap is higher over years within seasons, than across seasons. Consistent with our *niche plasticity hypothesis*, the niches of most migratory birds were largely stable across their annual life cycle, but with some small and statistically significant differences among them. Our results suggest that niches are most similar for spring and fall migrations, and most different between breeding and over-wintering grounds. Moreover, migratory birds seem to have smaller niches during their breeding season in relation to other seasons. We believe this is caused by behavioral differences across seasons and that this warrants the conservation of a wider range of habitats across their life cycle.

INTRODUCTION

In ecology, we typically associate each species with a set of preferred environmental conditions, which allows them to survive and reproduce. This idea is often referred as the concept of niche (Hutchinson 1957, 1978). Each species selects their environment based on life history requirements, which are associated with their physiology and behavior. The environmental space occupied by species will be heavily influenced by biotic interactions (e.g., competition, mutualisms, predation; Soberon and Peterson 2005). Such a niche is termed “realized niche”, with each species being defined by one realized niche (Hutchinson 1957).

However, to date, the concept of the niche has been mainly conceptualized and quantified with sedentary, non-migratory species in mind. This is remarkable given that many thousands of species of insects, birds, and mammals are migratory (Robinson et al. 2009, Runge et al. 2014).

While Hutchinson himself briefly considered ‘motile species’ (Hutchinson 1957; p.417), our knowledge of a migratory species’ niches is mainly represented by what we know of their environment on the summer breeding grounds (Partners in Flight 2020). There are practical reasons to this. First, it is often challenging to track individuals of a species across their full life cycle. However, considering species’ environmental requirements year-round may be of critical importance. Each species is likely exposed to different conditions across their annual cycle, which could extend across thousands of kilometers.

Moreover, each season is often associated with different life history events which could constrain habitat selection throughout the year. The breeding season is associated with large energetic investments for reproduction. Migration is also associated with unique physical requirements in which birds may change their physiology (Piersma et al. 1996, Jenni and Jenni-Eiermann 1998, Altshuler and Dudley 2006, Hedenstrom 2008, Weber 2009, Swanson 2010), behavior (Ramenofsky and Wingfield 2006, Hedenstrom 2008, Zúñiga et al. 2016), and diet (MacPherson et al. 2018), in order to survive. Lastly, the over-wintering period may lack the high energetic investment associated with other seasons. However, individual fitness often depends on a migrant’s ability to secure quality habitats on the wintering grounds (Marra et al. 1998, Norris et al. 2004, Drake et al. 2013, but see Akresh et al. 2019). Many species are known to change their niches across seasons (Moore and Aborn 2000, Nakazawa et al. 2004, Chernetsov 2006, Zuckerberg et al. 2016, Ponti et al. 2020, Pagel et al. 2020, Hutto 2020). They are referred as niche switchers.

On the other hand, there are also reasons to expect migratory species to have a single niche across their annual life cycle. Indeed, migration is thought to occur in order for individuals to track resources and avoid harsh environments (Berthold 1999, Alerstam et al. 2003). Even during migration, migrants may modify their en route timing (Marra et al. 2005, Hasselquist et al. 2017, Pedersen et al. 2018) or select different migration routes across years (Mellone et al. 2010, Vardanis et al. 2011, Stanley et al. 2012) to account for changes in yearly conditions (Russell et al. 1994, Branick 1997, Mehlman et al. 2005, Qu et al. 2014). We refer to species known to track their niches as niche trackers (Nakazawa et al. 2004, Zurell et al. 2018, Gómez et al. 2018, Fandos and Tellería 2019)

Knowing if migratory species have a high percentage of niche overlap across seasons is essential for guiding the conservation of bird populations year-round. Indeed, it is important to take into consideration changes in niche between seasons if we are to conserve the right habitat in the right places for each species (Berlanga et al. 2010, Rosenberg et al. 2016). Knowing species' year-round requirements would also help in predicting responses to climate change and understanding the relative role of stressors at different points in their annual cycle.

In this study, we selected 83 species of migratory songbirds to assess whether species have a high percentage of niche overlap across seasons throughout the avian annual cycle. To our knowledge, no other study has compared all seasonal niches – breeding, fall migration, over-wintering, and spring migration across a broad suite of avian species. This was made possible through using bird observations made available through the citizen science program eBird, which contains millions of records covering the full annual life cycle of birds, across the Americas. Because the seasonal environments may change across years, we first tested if niches changed on a yearly basis. We predicted that migrants will have a higher niche overlap across years (within each season; hereafter "yearly comparisons"), than between seasons (within years; hereafter "seasonal comparisons"). Under the *niche tracker hypothesis*, we posit that each species will be defined by one niche, and thus will have similarly high niche overlap across the annual cycle. Alternatively, under the *niche switcher hypothesis*, migrants will have low niche overlap across seasons because they have unique life events during each season, requiring them to change their niches throughout their annual cycle. Lastly, the *niche plasticity hypothesis*, lies between the niche tracker and niche switcher hypotheses. Under this hypothesis, the niche of each species will remain relatively constant but may be accompanied by contractions and expansion across seasons. Moreover, the spring and fall migration niches may overlap more than any other seasons because species' physical requirements are similar.

METHODOLOGY

Species and Environmental Data

We used seasonal range maps unique to each species (Fink et al. 2020a) to represent the breeding, over-wintering, spring migration, and fall migration distributions. Each seasonal range map comes with a unique range of dates (Fink et al. 2020a), representing the time period each species used each seasonal range. This range of dates was defined based on the results from abundance models and were confirmed by expert ornithologists (Fink et al. 2020b, a).

We used observations from the bird monitoring project eBird (Sullivan et al. 2014), more specifically the May 2020 eBird Basic Dataset (EBD; eBird Basic Dataset 2020). Observations contained in the EBD have gone through a robust review process before being made available for scientific purposes (Sullivan et al. 2014, Lagoze 2014), with expert birders providing, on average, 3 to 12 times more checklists than novice birders, depending on the region (Kelling et al. 2015). The observations were grouped by species and year, and were associated with a season based on the date of the observation and its location within the corresponding seasonal range. We used data from spring 2005 to spring 2020.

We selected species based on 5 criteria. We first selected landbird species breeding in North America and belonging to the order Apodiformes, Passeriformes, and Piciformes. Within those, we selected species that are migratory and for which we had range maps representing each of the 4 seasons (Fink et al. 2020a). To ensure a minimum sample size was available, we first selected species that had a minimum breeding population size of 8 million individuals (Partners in Flight 2020). With computational limitations in mind, we selected species with a maximum breeding range size of 7 million km^2. We also used the Partners In Flight ACAD database (2020) to select species associated with a unique primary breeding habitat of either forest, grassland, aridland, or wetland. This resulted in 124 species with varying numbers of checklists per season and year. We further limited our analysis to species that had at least 30 observations during each season and year. This limited our number to 83 species.

We used a combination of land cover and climate data to identify the niche of each species, for each year and season. We selected variables based on prior knowledge that they have strongly predicted bird abundance and distributions (Gutiérrez-Illán et al. 2014, Betts et al.

2019). Land cover data, which has a grain size of 30 meters by 30 meters, were extracted from the equivalent of Landsat 7 band 3 (B3) and band 4 (B4), from Landsat 5, 7, and 8. We selected Landsat bands, instead of NDVI or other similar indices, because raw reflectance bands predict better the occurrence of species (Shirley et al. 2013). Here, B3 is used to discriminate between built-up environments and vegetation, while B4 is used to compare rates of chlorophyll absorption which is useful to distinguish between conifer and broadleaf as well as young versus senescent vegetation. We summarized three climate variables within each season and year: mean minimum daily temperature, mean maximum daily temperature, and mean of daily precipitation. We used weather data from ERA5, which has a grain size of 0.25 degrees (Copernicus Climate Change Service (C3S) 2017).

The land cover and weather data were extracted using Google Earth Engine. We first created two sets of points: one representing the locations of bird observations for each species in each season and year, and the second representing the 'available' environment during each season, year, and distribution (referred to as background). This second set consisted of a grid of points, spaced 10 km apart. We assumed each migratory species had access to their available environment because of their highly mobile nature. The land cover and climate summaries were extracted through a three-step process. First, we selected all the layers corresponding to a specific season (range of days; species dependent) and year. For the Landsat layers, we removed shadows, clouds, snow, and water pixels. We then created a one-kilometer buffer around each point and extracted a temporal summary at each pixel. For each pixel location, we used the median pixel value across time for land cover variables and the mean pixel value for the climate. The median value was used to remove bias caused by outliers in the Landsat satellite layers. We used mean values instead from the climate layers because these were the results of models created by ERA5 and less likely to have outliers. A buffered point thus has approximately 3,490 temporally summarized Landsat pixels and up to 4 temporarily summarized weather pixels. Lastly, we did a spatial summary to extract a mean (and standard deviation in the case of Landsat) value for each buffer. Thus, a total of four land cover variables and three climate variables were available for each species observation and background point, each representing a season and year: B3 mean, B3 sd, B4 mean, B4 sd, mean maximum temperature, mean minimum temperature, and mean precipitation. A high B3 mean represents buffers with a high amount of built-up environment, while a high B3 standard deviation represent buffers with a high level of heterogeneity between built-up environment and vegetation (i.e., high fragmentation). A high B4 mean is associated with buffers having a high vegetative productivity and a high standard deviation would be associated with a high level of heterogeneity between conifer and broadleaf or a location with different vegetation stages.

Niche Comparisons

We used land cover and climate variables associated with bird presence and background points to describe a niche for each combination of species, season, and year. The number of observations available to calculate each niche increased across the years and differed among seasons. In general, the number of records was lower on the over-wintering grounds and highest during spring migration. Within each species, we used a consistent number of records to calculate each niche. The number of records varied among species to take advantage of higher number of records, when available. For each species, we used only seasons and years that had at least 100 observations. Once those were excluded (if applicable) we used the lowest number of records available for a season and year to calculate each niche. This number of records varied from 100 to 10,200, depending on the species (median sample size = 202, mean = 592.59 ± SD 1,245.34.

To identify each niche, we first combined the predictors associated with the background points into two axes of a principal component analysis (PCA). This PCA represents the environment space available to each species in each season and year. We divided the first two axes of the PCA into a grid of 100 by 100 cells, where each cell corresponds to a unique combination of the predictors available in environmental space (after Broennimann et al. 2012). We then used the presence points and their associated predictors to calculate a density of occurrence of each species in the environmental space. This density of occurrence was smoothed with a kernel density function to better estimate the entire range of suitable environments (Broennimann et al. 2012, Cola et al. 2017). This resulted in a grid with values ranging from 0 to 1 representing environmental spaces where the species were not observed to most observed, respectively. The grid was further standardized by the availability of each combination of environmental space in the study area. We used the resulting grid of z_{ij} values to compare niches.

We compared niches within a season across years (hereafter "yearly comparisons") or between seasons, within years (hereafter "seasonal comparisons"; Figure 4.1). For each species, we completed 6 seasonal niche comparisons per year (x 15 years = 90 comparisons per species), and 15 yearly niche comparisons per season (x 4 seasons = 60 per species). Within each year, the seasonal niche comparisons were breeding and fall migration, fall migration and winter, winter and spring migration, breeding and winter seasons, and spring and fall migrations. We randomly selected 60 yearly niche comparisons, out of the 420 possible combinations (105 per season). This number was selected in order to limit computational time but still provide sufficient sample sizes. We first listed all possible yearly comparisons (e.g., breeding 2010 to breeding 2015) and calculated the number of years within each comparison (e.g., 5 years). For each season, we randomly selected five yearly niche comparisons with less than a five years time-span, five comparisons with a six to ten years time-span, and five with more than a 10 years span. This selection of time-spans thus covered the temporal range of yearly niche comparisons. For each niche comparison, we calculated a percent niche overlap using the Schoener's D index (Schoener 1968, Warren et al. 2008, Broennimann et al. 2012). This index uses the z_{ij} grid values from each niche as such:

$$D = 1 - \frac{1}{2}\left(\sum_{ij} | z_{1ij} - z_{2ij}|\right)$$

where z_{1ij} represents the grid values in the first niche, z_{2ij}, the grid values in the second niche. The resulting D index ranges from 0, for no overlap, to 1 for complete niche overlap (Warren et al. 2008, Broennimann et al. 2012).

We expected that most species should have a higher percentage niche overlap across years (within seasons), than between seasons. For each species, we first summarized a mean yearly niche overlap per season and a mean seasonal niche overlap from the yearly seasonal comparisons. We compared each pair of means using a two-sided paired t-test.

We assessed the possible drivers of niche dynamics within each pair of niches, through calculating three metrics: proportion of *niche unfilling*, *stability*, and *expansion* (Petitpierre et al. 2012, Guisan et al. 2014, Cola et al. 2017; Equations 1; Figure 4.2). *Niche unfilling* is the proportion of the first niche that is not overlapping, i.e., not used, in the second niche (Guisan et al. 2014). *Niche stability* is the proportion of the second niche overlapping the first, i.e., it is the proportion that is common to both. Lastly, *niche expansion* is the proportion of the second niche that was not used in the first (Guisan et al. 2014).

Equations 1. Proportion Niche Unfilling (NU_p) = $N_1 - (N_1 \cap N_2) / (N_1)$
Proportion Niche Stability (NS_p) = $(N_1 \cap N_2) / (N_2)$
Proportion Niche Expansion (NE_p) = $N_2 - (N_1 \cap N_2) / (N_2)$

where N_1 and N_2 are the two niches being compared. Obviously, the order of the niches within each comparison impacts the results. We ordered the niches chronologically, i.e., in the order a species would encounter them. For example, a species would go through a breeding season before undertaking fall migration season. To calculate these drivers of niche dynamics, we first needed to delineate the boundary of each niche within the environmental space. Our goal was to remove the environmental space less likely to belong to a niche. As such, we calculated results using the 50th and 80th percentile of the environmental space with the highest density of occurrence, for each niche. While the results of both analyses are similar, we are including the 50th percentile because they represent the core of the niche, a concept frequently used when calculating core home ranges with similar tools (Lichti and Swihart 2011, Fleming and Calabrese 2017). The results obtained using the 80th percentile are available in Appendix E. Once a niche was delineated, its region on the PCA grid took a Boolean value representing the presence or absence of the species in the available environmental space. The area covered by these Boolean values was used to calculate proportions (Equations 1). We used a generalized additive mixed model to determine if some drivers of niche dynamics were associated with seasonal niche comparisons (Figure 4.1c). We used the proportion of each niche dynamic metric as response, and three fixed effects: niche driver (unfilling, expansion, stability), seasonal niche comparisons (6 comparisons), and the interaction of the two. We used species nested within family as random effect to account for lack of independence due to multiple comparisons within a species, and phylogenetic non-independence. Lastly, we modeled these relationships using a beta-zero and one-inflated distribution, to reflect the fact that our data were proportions, with several zeros and ones. We confirmed model fit by examining whether residuals were normally distributed. To reduce the chance of Type I error, we used Tukey-adjusted multiple comparisons to assess the differences between seasonal comparisons.

RESULTS

We compared yearly and seasonal niches of 83 species of migratory songbirds, known to specialize on a breeding habitat such as forest, grassland, aridland, and wetland. As expected, species exhibited significantly higher niche overlap across years than across seasons (Figure 4.3; t(80) = -40.21, $p < 0.001$). The mean percent niche overlap for the yearly niche comparisons was 45.04 % ± SD 6.20 and for the seasonal comparisons, the mean was 24.03 % ± SD 5.70.

We assessed the drivers of seasonal niche dynamics to determine if niches changed and in what directions across seasons. Consistent with our *niche plasticity* hypothesis, the proportion of stability across seasons was high (Figure 4.4), with a mean stability proportion across species and seasons ranging from 0.769 to 0.921 (Table 4.1). Also consistent with the *niche plasticity hypothesis*, this range of stability had notable differences across seasons. For example, niches were significantly more stable between spring and fall migrations (mean stability = 0.921, 95% CI = 0.90 to 0.93), compared with all other seasonal niche comparisons (although not significantly so compared with spring migration to breeding; Table 4.2). Outside of spring to fall migrations, the range of stability proportion varied from 0.769 to 0.892 (Table 4.1). Niches across seasons sometimes had a low, but significant proportion of contraction (referred to as unfilling) or expansion. The niches were significantly less stable from breeding to winter (mean stability = 0.769, 95% CI = 0.74 to 0.80; Table 4.1) compared to most other niche comparisons. This was mainly due by an unfilling of the breeding niche (mean unfilling = 0.15, 95 CI = 0.12 to 0.17; Table 4.1) combined with a larger expansion into the winter niche (mean expansion = 0.23, 95 CI = 0.20 to 0.26; Table 4.1; Figure 4.4). Lastly, species are significantly more likely to contract their niche when going from spring migration to breeding (mean unfilling = 0.29, 95% CI = 0.25 to 0.32; Table 4.1), than with any other seasonal niche comparisons, yielding a smaller niche during breeding.

Overall, the transitions across seasons were accompanied by a series of niche expansions, then unfilling (Figure 4.4). If we consider seasons in chronological order, winter to spring migration was accompanied by greater niche expansion. Spring migration to breeding had a much higher proportion of niche unfilling, followed by breeding to fall migration which goes back to having a much higher proportion of niche expansion. To close the loop, fall migration and winter have similar levels of unfilling and expansion.

We report results of two exemplar species that represent niche trackers versus those with more plastic niches (Figure 4.5). These examples demonstrate that even though the mean stability proportion among species is relatively high, we have a range of niche dynamics among species with some having minor changes across seasons while others tended to contract and expand their niches throughout their annual cycle.

DISCUSSION

We used land cover and climate data to calculate and compare niches over 15 years and across four seasons of the avian annual cycle. As expected, migratory birds had greater niche overlap across years (within seasons), then across seasons (within years). This is not surprising considering that many species have high site fidelity on the breeding and over-wintering grounds, returning to the same location year after year (Elgood et al. 1966, Sherry and Holmes 1996, Faaborg et al. 2007, Schlossberg 2009). The percentage of niche overlap, which considers both the density of occurrence and density of available conditions within the environmental space, was 21% lower across seasons than over years.

We assessed drivers of niche dynamics across seasons through calculating the proportion of niches that remained unchanged (referred as “stability”) and that changed (“unfilling” and “expansion”) for each seasonal comparison (Figure 4.4). The results indicate that overall, a large proportion of each niche remains stable across seasons (Table 4.1). However, this proportion was not constant across all seasons. Our results thus support the *niche plasticity hypothesis*, where niches had a relatively high proportion of stability across seasons but also significant differences in niche dynamics throughout the annual life cycle.

Also consistent with the *niche plasticity hypothesis*, the two migration periods were more stable in comparison to each other, compared with all other niche comparisons (Table 4.2). The two migration periods are characterized by similar behavioral processes, where birds fly across large distances to reach their breeding and over-wintering grounds. During migration, birds rely on a high abundance of quality food at stop-over sites to survive. While birds may be selecting slightly different conditions between migrations (La Sorte et al. 2014), these environments may still be more similar to each other than to niches on the breeding or wintering grounds.

Consistent with previous findings, our results suggest that the breeding niche of migrants may be more restricted than any other seasonal niche; migration and over-wintering niches tend to be more expansive (Zuckerberg et al. 2016, Fink et al. 2020b, Hutto 2020). This result could be an artefact of the way that we summarized environmental variables in this study. During migration, birds rely on specific locations for shorter periods of time than during the breeding or wintering periods. For instance, stop-over sites are typically used for only several days or weeks (Tietz and Johnson 2007, Kristensen et al. 2013, Bayly et al. 2017) but our summaries of environmental conditions reflect the whole range of possible dates for each migration, not the more limited period when birds actually used each location. In other words, it could be that birds are tracking their niches on migration, but at finer temporal resolutions than we were able to detect. However, even considering the discrepancy in temporal scale, our results are comparable to findings from others that used completely different methodologies (Zuckerberg et al. 2016, Fink et al. 2020b, Hutto 2020). Moreover, this would not explain why we found wintering niches (where birds spend substantial amounts of time) to be larger than breeding niches.

We hypothesize that the most likely reason for a wider niche during migrations and on the over-wintering grounds (Hutto 2020) is caused by the behavior of each species during those periods. On the breeding grounds, all age and sex demographic categories share the same territories and thus the same habitat, but this is not the case during migration and over-wintering grounds. During fall migration, birds often depart asynchronously, where young or adults, and sometimes males or females depending on the species, may depart first (McCloskey and Thompson 2000, Carlisle et al. 2005, Crysler et al. 2016, Rousseau et al. 2020, but see Murray 1966). During spring migration, males may also tend to depart before females and young (Kissner et al. 2003, Németh and Moore 2012, Briedis et al. 2019) and may use different routes (Ralph 1971, Crysler et al. 2016, Rousseau et al. 2020). This behavior may result in differential habitat selection across different ages and sexes. The story is slightly different on the over-wintering grounds. Contrary to the breeding grounds, males and females, because of habitat segregation, may be associated with different environmental conditions (Lynch et al. 1985, Ornat and Greenberg 1990, Sherry and Holmes 1996, McCloskey and Thompson 2000, Marra 2000).

In summary, birds may use wider niches during migration and on the over-wintering grounds because of differences in behavior among demographic categories.

Conservation implications

Our results suggest that migratory birds have small but potentially important differences in niches across seasons. We argue that it is imperative to determine species' environmental requirements on a seasonal basis and not as a single niche – which is usually quantified as the breeding niche (Laube et al. 2015, Li et al. 2017, Eyres et al. 2017, MacPherson et al. 2018, Ponti et al. 2020). Knowing species' seasonal requirements will help accurately predict bird occurrence and abundance throughout the annual cycle. It will also ensure protection of appropriate habitat at the right times and locations. Lastly, it will help guide decision management efforts as we tackle changes in habitats and climate.

Our results also suggest that migratory birds use a wider niche outside of the breeding season. As such, one could be tempted to think that these species are less specific about their habitat requirements. This could be true and needs further assessment. However, it is also possible that niches outside of the breeding season are wider because migratory birds rely on a wider range of habitats. For example, a wider niche on the over-wintering grounds could represent the use of a limited amount of available optimal habitat, in combination with some amounts of suboptimal habitats (Ornat and Greenberg 1990, Sherry and Holmes 1996, Marra et al. 1998). Yet, these suboptimal habitats may be essential to the species' survival. As such, it would be prudent to conserve a wide range of habitats to make sure each species as a whole is protected (Sherry and Holmes 1996, Faaborg et al. 2010, La Sorte et al. 2017). Lastly, a wider niche during other seasons, such as migration, could be associated with extreme weather pushing a species into using conditions at the edge, or outside of their niche. This is likely the case for migration given that they have the greatest avian mortality (Sillett and Holmes 2002). In both cases – optimal versus suboptimal habitats on over-wintering grounds and weather extremes during migrations – it would be important to test for carry-over effects across seasons (Norris 2005, Finch et al. 2014) and assess the role of each seasonal niche on population trends and survival.

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TABLES AND FIGURES

Table 4.1. Summary of the drivers of niche dynamics for each seasonal comparison. The unfilling proportion is the proportion of the niche used in the first season that was not used in the second. The stability proportion is the proportion of the niche used in the second season that was also used in the first season. Lastly, expansion proportion refers to the proportion of the second niche that was not used in the first. We used a 95% confidence interval to determine the low and upper boundaries of the mean.

Seasonal comparison	**Unfilling proportion**		**Stability proportion**		**Expansion proportion**	
	Mean ± SE	**Low - Upper**	**Mean ± SE**	**Low - Upper**	**Mean ± SE**	**Low - Upper**
Breeding to fall migration	0.086 ± 0.008	0.071 - 0.104	0.828 ± 0.013	0.800 - 0.853	0.172 ± 0.013	0.147 - 0.200
Fall migration to winter	0.119 ± 0.011	0.100 - 0.142	0.875 ± 0.011	0.852 - 0.895	0.125 ± 0.011	0.105 - 0.148
Winter to spring migration	0.109 ± 0.010	0.090 - 0.130	0.847 ± 0.012	0.821 - 0.870	0.153 ± 0.012	0.130 - 0.179
Spring migration to breeding	0.286 ± 0.017	0.253 -0.320	0.892 ± 0.010	0.871 - 0.910	0.108 ± 0.010	0.090 - 0.129
Breeding to winter	0.148 ± 0.013	0.125 - 0.174	0.769 ± 0.016	0.737 - 0.798	0.231 ± 0.016	0.202 - 0.263
Spring migration to fall migration	0.157 ± 0.013	0.134 - 0.183	0.921 ± 0.008	0.904 - 0.935	0.079 ± 0.008	0.065 - 0.096

Table 4.2. Multiple comparisons of the drivers affecting each pair of seasonal comparisons. The contrasts and their associated odds ratio are between the first niche comparison and second niche comparison. Here, an odds ratio > 1 means the first niche comparison has a higher proportion than the second. For example, in the first row, the expansion proportion is higher for the breeding to winter comparison then for the breeding to fall migration comparison, but this measure of association is not significant (p-value > 0.05).

Driver	Contrast – First niche comparison to second niche comparison	Odds ratio	SE	Z ratio	p-value
Unfilling	**Breeding to fall migration / Breeding to winter**	**0.54**	**0.08**	**-4.31**	**0.0002**
	Breeding to fall migration / Fall migration to winter	0.69	0.10	-2.53	0.1144
	Breeding to fall migration / Spring migration to breeding	**0.23**	**0.03**	**-10.74**	**< 0.001**
	Breeding to fall migration / Spring migration to fall migration	**0.50**	**0.07**	**-4.85**	**< 0.001**
	Breeding to fall migration / Winter to spring migration	0.77	0.11	-1.80	0.4668
	Breeding to winter / Fall migration to winter	1.29	0.18	1.80	0.4665
	Breeding to winter / Spring migration to breeding	**0.44**	**0.06**	**-6.43**	**< 0.001**
	Breeding to winter / Spring migration to fall migration	0.93	0.13	-0.49	0.9964
	Breeding to winter / Winter to spring migration	1.43	0.20	2.49	0.1283
	Fall migration to winter / Spring migration to breeding	**0.34**	**0.04**	**-8.27**	**< 0.001**
	Fall migration to winter / Spring migration to fall migration	0.73	0.10	-2.32	0.1865
	Fall migration to winter / Winter to spring migration	1.11	0.16	0.71	0.9806
	Spring migration to breeding / Spring migration to fall migration	**2.15**	**0.27**	**6.03**	**< 0.001**
	Spring migration to breeding / Winter to spring migration	**3.27**	**0.44**	**8.87**	**< 0.001**
	Spring migration to fall migration / Winter to spring migration	**1.52**	**0.21**	**3.01**	**0.0316**

Table 4.2. (Continued)

Driver	Contrast – First niche comparison to second niche comparison	Odds ratio	SE	Z ratio	p-value
Stability	**Breeding to fall migration / Breeding to winter**	**1.45**	**0.19**	**2.88**	**0.0460**
	Breeding to fall migration / Fall migration to winter	0.69	0.09	-2.75	0.0664
	Breeding to fall migration / Spring migration to breeding	**0.58**	**0.08**	**-3.94**	**0.0011**
	Breeding to fall migration / Spring migration to fall migration	**0.41**	**0.06**	**-6.27**	**< 0.001**
	Breeding to fall migration / Winter to spring migration	0.87	0.12	-1.05	0.9004
	Breeding to winter / Fall migration to winter	**0.48**	**0.06**	**-5.58**	**< 0.001**
	Breeding to winter / Spring migration to breeding	**0.40**	**0.05**	**-6.77**	**< 0.001**
	Breeding to winter / Spring migration to fall migration	**0.29**	**0.04**	**-9.06**	**< 0.001**
	Breeding to winter / Winter to spring migration	**0.60**	**0.08**	**-3.92**	**0.0012**
	Fall migration to winter / Spring migration to breeding	0.84	0.12	-1.18	0.8448
	Fall migration to winter / Spring migration to fall migration	**0.60**	**0.09**	**-3.50**	**0.0061**
	Fall migration to winter / Winter to spring migration	1.27	0.17	1.70	0.5284
	Spring migration to breeding / Spring migration to fall migration	0.71	0.10	-2.33	0.1831
	Spring migration to breeding / Winter to spring migration	**1.50**	**0.21**	**2.90**	**0.0433**
	Spring migration to fall migration / Winter to spring migration	**2.11**	**0.30**	**5.23**	**< 0.001**

Table 4.2. (Continued)

Driver	**Contrast – First niche comparison to second niche comparison**	**Odds ratio**	**SE**	**Z ratio**	**p-value**
Expansion	**Breeding to fall migration / Breeding to winter**	**0.69**	**0.09**	**-2.88**	**0.0460**
	Breeding to fall migration / Fall migration to winter	1.45	0.20	2.75	0.0664
	Breeding to fall migration / Spring migration to breeding	**1.72**	**0.24**	**3.94**	**0.0011**
	Breeding to fall migration / Spring migration to fall migration	**2.42**	**0.34**	**6.27**	**< 0.001**
	Breeding to fall migration / Winter to spring migration	1.15	0.15	1.05	0.9004
	Breeding to winter / Fall migration to winter	**2.10**	**0.28**	**5.58**	**< 0.001**
	Breeding to winter / Spring migration to breeding	**2.49**	**0.34**	**6.77**	**< 0.001**
	Breeding to winter / Spring migration to fall migration	**3.50**	**0.48**	**9.06**	**< 0.001**
	Breeding to winter / Winter to spring migration	**1.66**	**0.22**	**3.92**	**0.0012**
	Fall migration to winter / Spring migration to breeding	1.18	0.17	1.18	0.8448
	Fall migration to winter / Spring migration to fall migration	**1.67**	**0.24**	**3.50**	**0.0061**
	Fall migration to winter / Winter to spring migration	0.79	0.11	-1.70	0.5284
	Spring migration to breeding / Spring migration to fall migration	1.41	0.21	2.33	0.1831
	Spring migration to breeding / Winter to spring migration	**0.67**	**0.09**	**-2.90**	**0.0433**
	Spring migration to fall migration / Winter to spring migration	**0.47**	**0.07**	**-5.23**	**< 0.001**

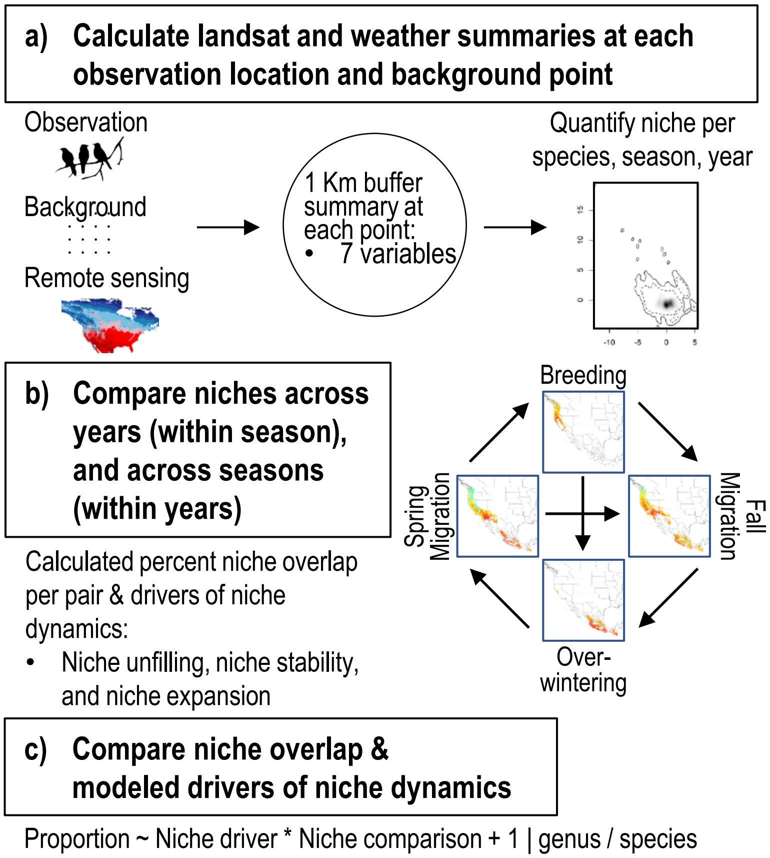

Figure 4.1. Our methodology includes three major steps. In a) we used presence observations, background points, and seven environmental variables to quantify a niche for each species, season, and year. b) We combine the niches in pairs: across years (within season) and across seasons (within years) and calculated, in four metrics per pair. c) We compared niche overlap between yearly and seasonal niche comparisons. We also assessed if the drivers of niche dynamics varied with seasonal niche comparisons

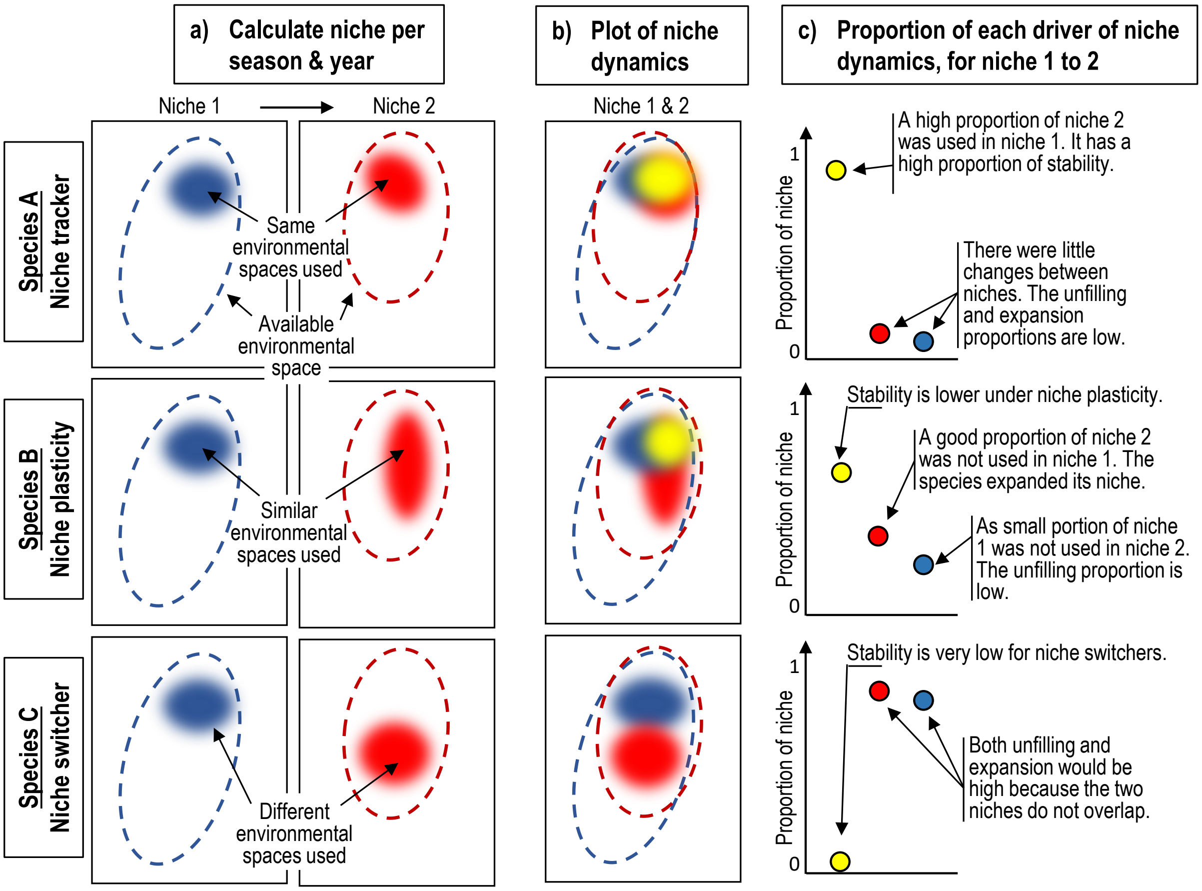

Figure 4.2. Conceptual diagram representing three scenarios of drivers of niche dynamics. The first row represents the *niche tracker hypothesis*, wherein a species uses the same niche across seasons. The second row represents the *niche plasticity hypothesis*. The third row represents the *niche switcher hypothesis*, wherein a species uses different niches across seasons. In column a) each niche is represented by a PCA. The dash lines represent the available environmental space and the filled circles represent the environmental space used by the species. In b) the two niches are combined in the same grid and the proportion of niche unfilling, stability, and expansion are calculated. Niche unfilling is the proportion of grid cells that were used in niche 1 but not in niche 2. Niche stability is the proportion of niche 2 that was also used in niche 1. Niche expansion is the proportion of niche 2 that was not used by niche 1. Lastly, in c) we compared proportions of niche unfilling, stability, and expansion among seasonal comparisons.

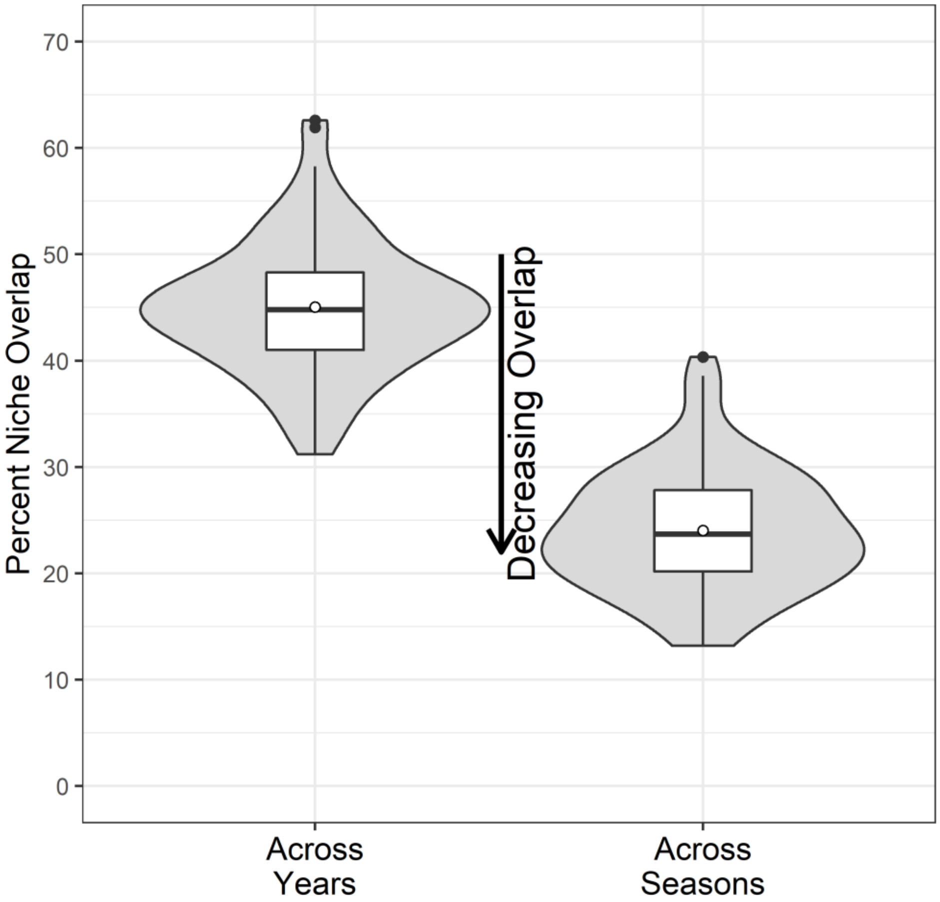

Figure 4.3. Comparison of the yearly and seasonal mean percent niche overlap per species. The violins represent the full distribution of the data. Black line on boxes represent medians and the white dots indicate the mean percent overlap across species.

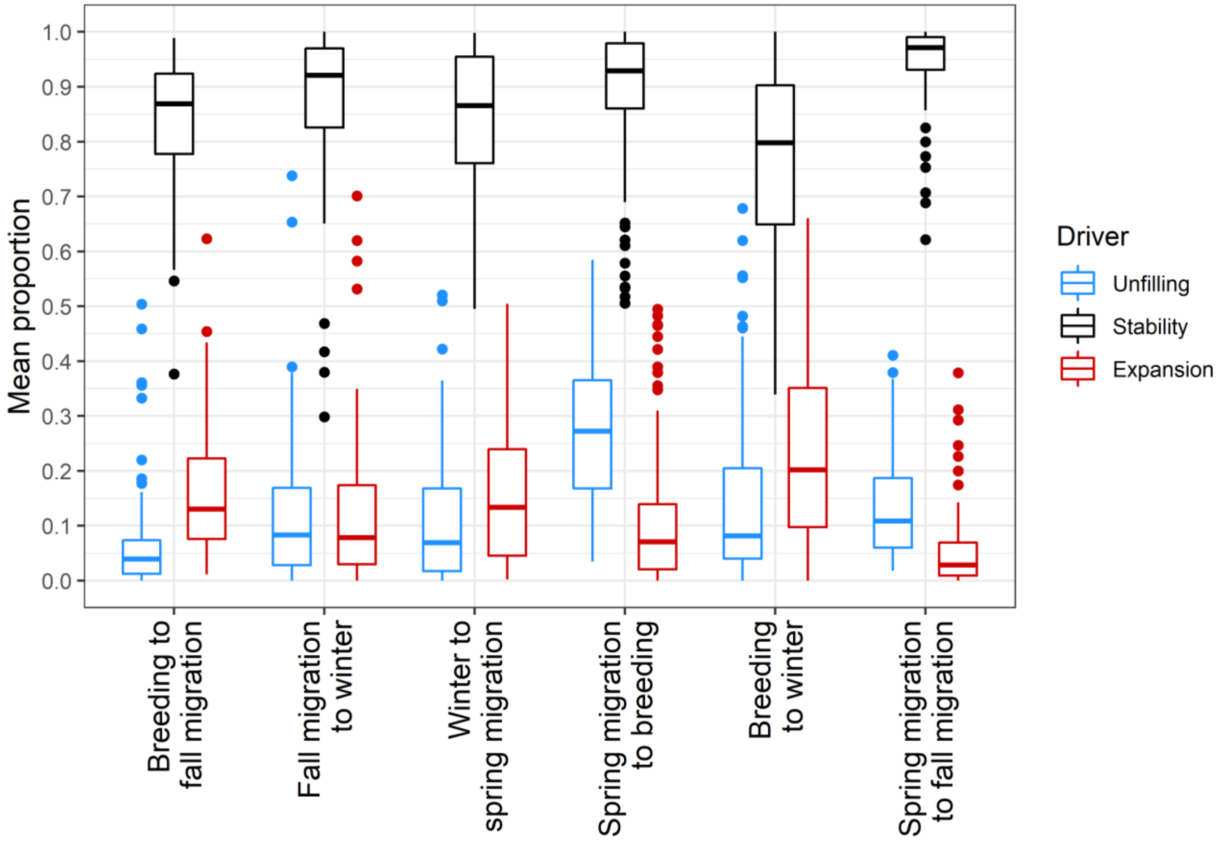

Figure 4.4. Boxplots of the drivers of niche differences across seasonal comparisons for each species. For instance, the first set of three boxplots represent the proportion of unfilling, stability, and expansion going from breeding season to fall migration (the order of the seasons is important). The blue boxplots represent the proportion of a species' first niche that was unfilled (not used) in the second. The black boxplots represent the proportion of the species' second niche that was also used by the first. The red boxplots represent the proportion of species' second niche not used in the first (it expanded in the second season). For example, the breeding to fall migration niches are more likely to be associated with an expansion in niche compared with the spring migration to breeding seasons which are more likely to be associated with an unfilled niche.

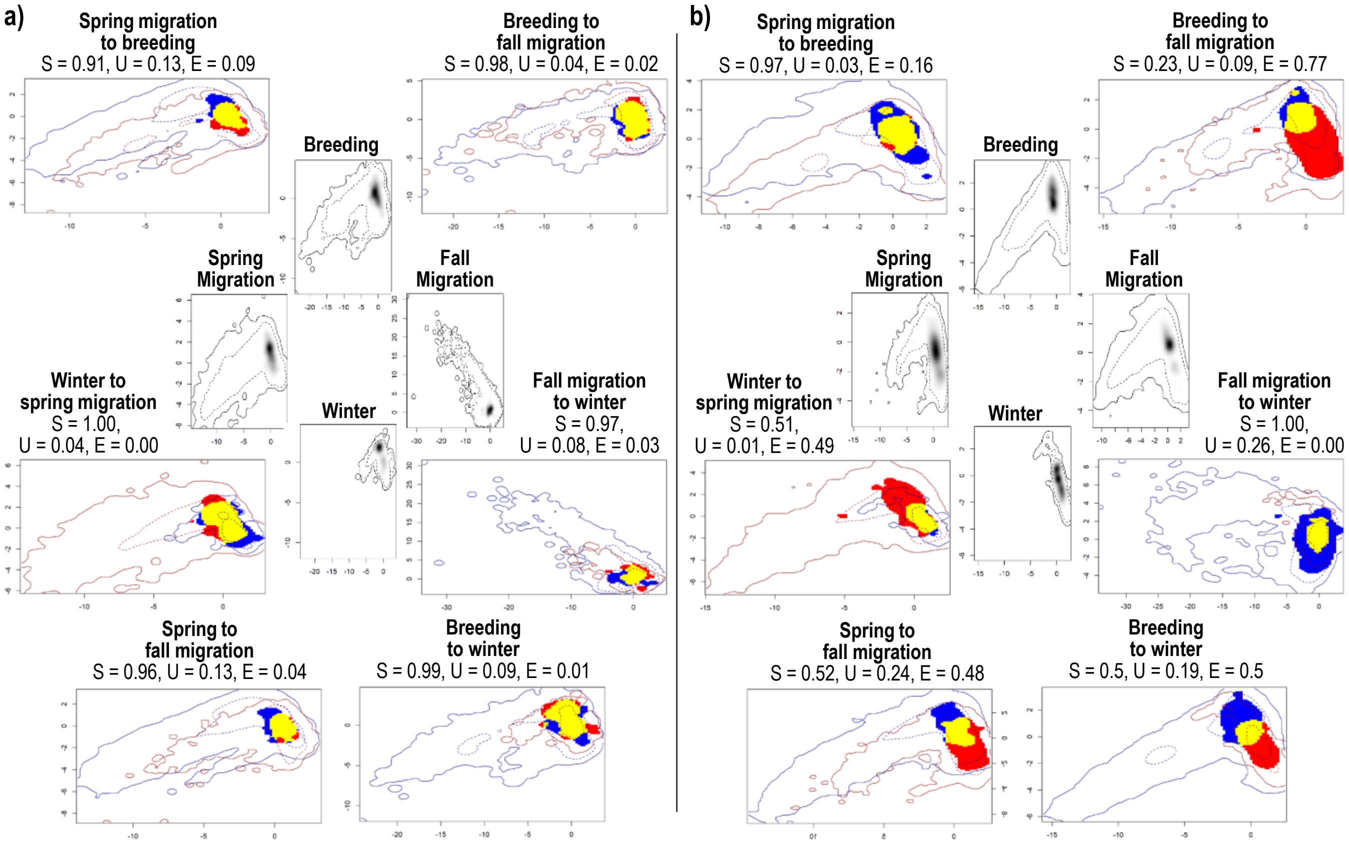

Figure 4.5. Two examples of results from the niche dynamics analysis. The yellow polygons represent proportion of niche stability, blue is the proportion of niche unfilling, and red the proportion of expansion. The associated proportion values are mentioned with each niche comparison, where ‘S’ represent stability, ‘U’ unfilling, and ‘E’, expansion. These results are for the year 2010. a) Violet-green Swallow is an example representing a niche tracker because most niche comparisons had little change across seasons (i.e., a low amount of niche unfilling in blue and expansion in red). b) Rufous Hummingbird is an example of species demonstrating plasticity in its niche because while it has a relatively high proportion of overlap (yellow), it also has relatively large proportions of change (both unfilling and expansion).

CHAPTER 5 – General conclusion

In this dissertation I aimed to assess whether species are defined by one, versus multiple realized niches, within their fundamental niche. In other words, do species use similar sets of environmental conditions across space and time? To do so, I compared migration patterns used by different age and sex categories of hummingbirds. I also compared niches across regions within a species' breeding range, and across seasons throughout the year.

More specifically, in chapter 2, I documented that Rufous Hummingbirds migrate using a wide range of longitudes and week spans, which are not uniform in terms of habitats and weather conditions. As such, my results suggest that each age and sex category could be associated with different environmental conditions during migration. Thus, if we were to represent these sets of conditions as a realized niche per demographic group, I suspect these niches would show some, but not complete, overlap. These results also highlight that if the migration survival of one demographic group is limiting population growth, then localized efforts might more efficiently support this decreasing species. This is especially relevant because migration is associated with the highest mortality rate across the annual cycle (Sillett and Holmes 2002)

The results from chapter 3 suggest that few species have a stationary distribution. To my knowledge, this is the first test of how species traits and geographical factors influence species distribution model performance in new regions (stationarity). This lack of stationarity could, for some species, be caused by changes in ecological processes across their range. This would likely be the case for short-lived species and those with large distributions. These species may consist of different populations, each adapted to their local environments, or perhaps they encounter different biotic interactions across their range. Regardless of the mechanism, these species would likely be represented by more than one realized niche across space during the breeding season. It thus becomes essential to test if distributions are stationary. Not doing so could have large implications on conservation efforts such as the prioritization of land protection, species translocations, and the forecast of invasive species.

In chapter 4, I documented that species had small but significant difference in niches across the annual cycle, with the migration niches being most similar, and breeding niches being most constrained. This suggests that most migratory bird species likely have a core set of habitat requirements which are common across seasons, but that different life events or different available environments throughout the year may cause contraction and expansion across these realized niches. This is important because it suggest that the breeding niche, which we know most about, does not reflect the habitat requirements of most species year-round. This can have serious implications for bird conservation.

Taken altogether, the results from these chapters suggest that, while there is a large amount of overlap across realized niches used by a bird species, there are also some significant differences. The picture that comes to mind is the one of a Venn diagram, with several overlapping circles representing shared and separate regions. In this case, a Venn diagram would represent a species, with each realized niche represented by a circle, and overlapping to different degrees within the boundaries of a fundamental niche. And just like a Venn diagram has regions represented by the union of several overlapping circles, a fundamental niche could have a core set(s) of habitat(s) requirements, needed by all members of a species, at all times, and all places.

CONSERVATION IMPLICATIONS

If each species is best represented by a collection of realized niches within their fundamental niche, it then becomes important to quantify each of these realized niches in order to effectively guide population management and promote species conservation. My research shows that, for many species, these requirements fluctuate across regions, seasons, and among groups of individuals (populations or demographics). On one hand, our goal could be to conserve the environmental conditions associated with a species' 'core' niche (i.e., those conditions that are common across all realized niches within a species). On the other hand, a set of environmental conditions required during perhaps a few weeks, at a stop-over site, by a subset of populations, could still have large impacts on the well-being of the species. It thus becomes imperative not only to identify these niches, but also determine the proportional importance of each environmental component, framed within its own time and place, for the survival and fitness of each species. This could be done, for example, through assessing carry-over effects across locations or seasons, on populations trends and fitness.

This study provides a way to improve conservation outcomes by providing a more flexible view of what defines the niche(s) of a species. It gives room to consider and adapt conservation priorities toward what is needed at a local scale, be it temporal or spatial. And while we still have progress to make in terms of our knowledge of each species, the potential to improve the efficiency and success of conservation efforts is promising, and likely essential to reversing the negative trends observed in our bird populations (Rosenberg et al. 2019).

APPENDICES

APPENDIX A

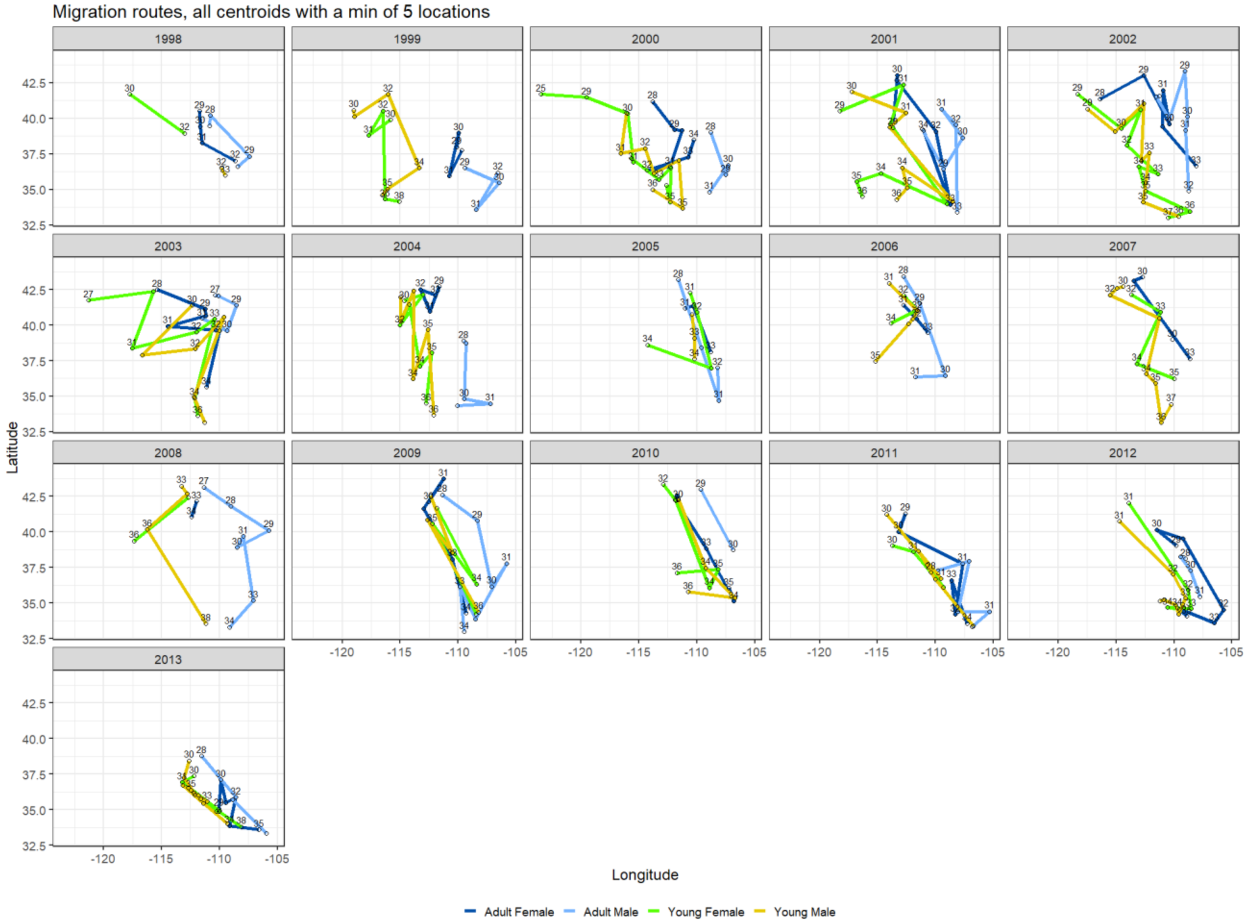

Figure A.1. Yearly migration routes for each age and sex category. Dots represent the weekly mean location per age-sex and lines are the mean migration routes. Adult males are in light blue, adult females in dark blue, young males in yellow, and young females in green. Numbers in each graph represent the week within a year.

APPENDIX B

Table B.1. Yearly migration speed, all age-sex categories combined.

Year	Number age-sex categories	Mean speed	Standard deviation
1998	4	25.3	11.4
1999	4	32.3	8.79
2000	4	31.3	5.61
2001	4	53.1	5.32
2002	4	40.6	5.97
2003	4	36.7	12.4
2004	4	35.8	14.3
2005	4	38.6	13.0
2006	4	31.3	13.5
2007*	3	39.1	8.10
2008	4	29.2	9.23
2009	4	68.5	22.4
2010	4	53.8	18.7
2011	4	43.9	12.2
2012	4	28.5	8.09
2013	4	27.8	7.64

Appendix C

Table C.1. List of species and their scientific name. S is for stationarity index, $\overline{\rho_\iota}$ represent the mean within-region Spearman coefficient of correlation and $\overline{\rho_{\iota\jmath}}$ the mean between-regions Spearman per species. All species used in the species traits analysis have a "x" under column A1. # ρ_{ij} stands for the number of between-regions (pairs of hexagons) predicted. All species with at least 30 ρ_{ij} were used in the attribute of a distribution analysis (A2).

Species	**Scientific name**	**S**	$\overline{\rho_\iota}$	$\overline{\rho_{\iota\jmath}}$	**A1**	**# ρ_{ij}**	**A2**
Acadian Flycatcher	*Empidonax virescens*	0.75	0.35	0.19	x	380	x
American Crow	*Corvus brachyrhynchos*	0.58	0.41	0.06	x	2756	x
American Goldfinch	*Spinus tristis*	0.64	0.34	0.09	x	1640	x
American Redstart	*Setophaga ruticilla*	0.69	0.34	0.17	x	462	x
Baltimore Oriole	*Icterus galbula*	0.67	0.35	0.07	x	650	x
Black-and-white Warbler	*Mniotilta varia*	0.72	0.51	0.33	x	380	x
Black-billed Magpie	*Pica hudsonia*	0.65	0.35	0.10	x	272	x
Black-capped Chickadee	*Poecile atricapillus*	0.67	0.33	0.11	x	812	x
Brown-headed Cowbird	*Molothrus ater*	0.66	0.36	0.13	x	2756	x
Brown-headed Nuthatch	*Sitta pusilla*	0.76	0.22	0.03	x	30	x
Blue-headed Vireo	*Vireo solitarius*	0.80	0.44	0.32	x	72	x
Blackburnian Warbler	*Setophaga fusca*	0.72	0.47	0.26	x	56	x
Blue Jay	*Cyanocitta cristata*	0.66	0.34	0.08	x	1190	x
Bobolink	*Dolichonyx oryzivorus*	0.72	0.26	0.09	x	342	x
Brewer's Blackbird	*Euphagus cyanocephalus*	0.70	0.43	0.22	x	380	x
Brewer's Sparrow	*Spizella breweri*	0.80	0.37	0.26	x	132	x
Brown Thrasher	*Toxostoma rufum*	0.70	0.30	0.05	x	1406	x
Black-throated Blue Warbler	*Setophaga caerulescens*	0.79	0.48	0.40	x	42	x
Black-throated Green Warbler	*Setophaga virens*	0.66	0.56	0.30	x	110	x
Black-throated Gray Warbler	*Setophaga nigrescens*	0.65	0.32	0.12	x	12	.
Bullock's Oriole	*Icterus bullockii*	0.73	0.41	0.22	x	210	x
Carolina Chickadee	*Poecile carolinensis*	0.69	0.26	0.06	x	342	x
Cassin's Finch	*Haemorhous cassinii*	0.68	0.63	0.36	x	12	.
Carolina Wren	*Thryothorus ludovicianus*	0.63	0.42	0.09	x	506	x
Cassin's Vireo	*Vireo cassinii*	0.65	0.45	0.41	x	12	.
Chestnut-backed Chickadee	*Poecile rufescens*	0.90	0.77	0.67	x	2	.
Chestnut-collared Longspur	*Calcarius ornatus*	0.62	0.24	-0.15	x	2	.
Clay-colored Sparrow	*Spizella pallida*	0.61	0.41	0.09	x	30	x
Cedar Waxwing	*Bombycilla cedrorum*	0.72	0.20	0.03	.	702	.
Chipping Sparrow	*Spizella passerina*	0.56	0.39	0.05	x	2256	x
Chimney Swift	*Chaetura pelagica*	0.75	0.18	0.07	.	1056	.
Cliff Swallow	*Petrochelidon pyrrhonota*	0.71	0.21	0.07	x	1560	x

Table C.1. (Continued)

Common Grackle	*Quiscalus quiscula*	0.72	0.50	0.31	x	1806	x
Common Yellowthroat	*Geothlypis trichas*	0.61	0.36	0.04	x	2162	x
Chestnut-sided Warbler	*Setophaga pensylvanica*	0.61	0.57	0.24	x	132	x
Chuck-will's-widow	*Antrostomus carolinensis*	0.75	0.23	0.10	x	90	x
Dickcissel	*Spiza americana*	0.62	0.46	0.14	x	306	x
Downy Woodpecker	*Dryobates pubescens*	0.75	0.20	0.04	.	1482	.
Dusky Flycatcher	*Empidonax oberholseri*	0.82	0.60	0.51	x	42	x
Eastern Bluebird	*Sialia sialis*	0.61	0.41	0.11	x	992	x
Eastern Kingbird	*Tyrannus tyrannus*	0.67	0.33	0.10	x	1722	x
Eastern Phoebe	*Sayornis phoebe*	0.65	0.39	0.12	x	870	x
Eastern Towhee	*Pipilo erythrophthalmus*	0.63	0.36	0.07	x	600	x
Eastern Wood-Pewee	*Contopus virens*	0.70	0.33	0.10	x	930	x
Fish Crow	*Corvus ossifragus*	0.74	0.28	0.07	x	72	x
Field Sparrow	*Spizella pusilla*	0.65	0.46	0.15	x	552	x
Franklin's Gull	*Leucophaeus pipixcan*	0.77	0.05	0.13	.	12	.
Great Blue Heron	*Ardea herodias*	0.66	0.22	0.10	x	2256	x
Great Crested Flycatcher	*Myiarchus crinitus*	0.62	0.35	0.03	x	1190	x
Gray Catbird	*Dumetella carolinensis*	0.63	0.33	0.07	x	1406	x
Gray Flycatcher	*Empidonax wrightii*	0.93	0.14	0.22	.	2	.
Grasshopper Sparrow	*Ammodramus savannarum*	0.69	0.30	0.07	x	462	x
Green-tailed Towhee	*Pipilo chlorurus*	0.80	0.43	0.34	x	56	x
Hammond's Flycatcher	*Empidonax hammondii*	0.83	0.41	0.43	x	56	x
Hairy Woodpecker	*Dryobates villosus*	0.75	0.18	0.10	.	1260	.
Hermit Thrush	*Catharus guttatus*	0.77	0.59	0.46	x	306	x
Hermit Warbler	*Setophaga occidentalis*	0.93	0.69	0.63	x	2	.
House Finch	*Haemorhous mexicanus*	0.69	0.37	0.15	x	1640	x
Hooded Warbler	*Setophaga citrina*	0.74	0.55	0.41	x	182	x
Indigo Bunting	*Passerina cyanea*	0.66	0.32	0.09	x	1056	x
Kentucky Warbler	*Geothlypis formosa*	0.75	0.38	0.22	x	156	x
Killdeer	*Charadrius vociferus*	0.71	0.54	0.37	x	3192	x
Lark Bunting	*Calamospiza melanocorys*	0.71	0.46	0.23	x	30	x
Lark Sparrow	*Chondestes grammacus*	0.70	0.34	0.15	x	342	x
Lazuli Bunting	*Passerina amoena*	0.77	0.30	0.15	x	72	x
Long-billed Curlew	*Numenius americanus*	0.81	0.15	0.02	.	6	.
Least Flycatcher	*Empidonax minimus*	0.69	0.22	0.12	x	156	x
Marbled Godwit	*Limosa fedoa*	0.85	0.25	0.10	x	2	.
Magnolia Warbler	*Setophaga magnolia*	0.68	0.65	0.39	x	30	x
MacGillivray's Warbler	*Geothlypis tolmiei*	0.77	0.54	0.45	x	42	x
Mississippi Kite	*Ictinia mississippiensis*	0.83	0.20	0.16	.	6	.
Mountain Bluebird	*Sialia currucoides*	0.65	0.35	0.13	x	156	x
Mountain Chickadee	*Poecile gambeli*	0.74	0.68	0.45	x	72	x

Table C.1. (Continued)

Mourning Dove	*Zenaida macroura*	0.69	0.48	0.32	x	2652	x
Mountain Quail	*Oreortyx pictus*	0.30	0.55	-0.15	x	2	.
Mourning Warbler	*Geothlypis philadelphia*	0.72	0.39	0.20	x	56	x
Nashville Warbler	*Oreothlypis ruficapilla*	0.79	0.57	0.50	x	42	x
Northern Bobwhite	*Colinus virginianus*	0.63	0.36	0.04	x	552	x
Northern Mockingbird	*Mimus polyglottos*	0.65	0.60	0.30	x	870	x
Northern Parula	*Setophaga americana*	0.66	0.38	0.15	x	506	x
Orchard Oriole	*Icterus spurius*	0.71	0.23	0.00	x	600	x
Ovenbird	*Seiurus aurocapilla*	0.76	0.58	0.43	x	420	x
Pacific Wren	*Troglodytes pacificus*	0.81	0.76	0.65	x	12	.
Pinyon Jay	*Gymnorhinus cyanocephalus*	0.60	0.29	-0.02	x	12	.
Pine Siskin	*Spinus pinus*	0.74	0.56	0.41	x	156	x
Pine Warbler	*Setophaga pinus*	0.69	0.40	0.18	x	272	x
Pileated Woodpecker	*Dryocopus pileatus*	0.79	0.32	0.30	x	756	x
Prairie Warbler	*Setophaga discolor*	0.72	0.35	0.18	x	110	x
Pacific-slope Flycatcher	*Empidonax difficilis*	0.87	0.70	0.64	x	6	.
Purple Finch	*Haemorhous purpureus*	0.71	0.31	0.15	x	90	x
Purple Martin	*Progne subis*	0.71	0.17	0.04	.	702	.
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	0.70	0.31	0.15	x	240	x
Red-breasted Nuthatch	*Sitta canadensis*	0.72	0.53	0.37	x	306	x
Red-breasted Sapsucker	*Sphyrapicus ruber*	0.78	0.17	-0.04	.	2	.
Red-bellied Woodpecker	*Melanerpes carolinus*	0.65	0.35	0.07	x	552	x
Red-headed Woodpecker	*Melanerpes erythrocephalus*	0.66	0.25	0.00	x	702	x
Red-naped Sapsucker	*Sphyrapicus nuchalis*	0.78	0.64	0.43	x	30	x
Red-shouldered Hawk	*Buteo lineatus*	0.73	0.20	0.05	x	306	x
Red-tailed Hawk	*Buteo jamaicensis*	0.74	0.25	0.13	x	2652	x
Ruby-throated Hummingbird	*Archilochus colubris*	0.79	0.12	0.07	.	870	.
Rufous Hummingbird	*Selasphorus rufus*	0.57	0.55	0.16	x	6	.
Red-winged Blackbird	*Agelaius phoeniceus*	0.70	0.48	0.28	x	3080	x
Sagebrush Sparrow	*Artemisiospiza nevadensis*	0.86	0.36	0.37	x	6	.
Say's Phoebe	*Sayornis saya*	0.65	0.34	0.11	x	72	x
Sage Thrasher	*Oreoscoptes montanus*	0.77	0.49	0.44	x	42	x
Scarlet Tanager	*Piranga olivacea*	0.77	0.52	0.34	x	306	x
Song Sparrow	*Melospiza melodia*	0.59	0.39	0.05	x	1640	x
Spotted Towhee	*Pipilo maculatus*	0.62	0.34	0.16	x	132	x
Scissor-tailed Flycatcher	*Tyrannus forficatus*	0.58	0.44	0.11	x	42	x
Swainson's Hawk	*Buteo swainsoni*	0.72	0.32	0.16	x	90	x
Townsend's Warbler	*Setophaga townsendi*	0.97	0.50	0.53	x	2	.
Tree Swallow	*Tachycineta bicolor*	0.64	0.29	0.03	x	1190	x
Tufted Titmouse	*Baeolophus bicolor*	0.68	0.45	0.20	x	462	x
Varied Thrush	*Ixoreus naevius*	0.94	0.69	0.68	x	6	.

Table C.1. (Continued)

Veery	*Catharus fuscescens*	0.70	0.40	0.19	x	210	x
Vesper Sparrow	*Pooecetes gramineus*	0.60	0.45	0.13	x	756	x
Warbling Vireo	*Vireo gilvus*	0.51	0.46	0.03	x	1722	x
White-breasted Nuthatch	*Sitta carolinensis*	0.67	0.33	0.11	x	1056	x
Western Kingbird	*Tyrannus verticalis*	0.70	0.52	0.34	x	420	x
Western Meadowlark	*Sturnella neglecta*	0.67	0.53	0.30	x	420	x
Western Tanager	*Piranga ludoviciana*	0.82	0.60	0.47	x	90	x
White-eyed Vireo	*Vireo griseus*	0.67	0.50	0.26	x	342	x
Western Wood-Pewee	*Contopus sordidulus*	0.60	0.42	0.13	x	182	x
Wild Turkey	*Meleagris gallopavo*	0.72	0.17	-0.01	.	992	.
Winter Wren	*Troglodytes hiemalis*	0.77	0.59	0.53	x	56	x
Wood Thrush	*Hylocichla mustelina*	0.71	0.41	0.21	x	702	x
Yellow-breasted Chat	*Icteria virens*	0.65	0.29	0.08	x	506	x
Yellow-billed Cuckoo	*Coccyzus americanus*	0.71	0.26	0.11	x	756	x
Yellow-bellied Sapsucker	*Sphyrapicus varius*	0.72	0.40	0.27	x	90	x
Yellow-throated Vireo	*Vireo flavifrons*	0.72	0.31	0.15	x	506	x
Yellow-throated Warbler	*Setophaga dominica*	0.74	0.31	0.21	x	182	x

APPENDIX D

Table D.1. List of species and results of the univariate model selection analysis. A species is associated with the null model if the null model is among the models with a delta < 2.

Best model(s)	BIC	Delta	Weight	df	Loglink
Acadian Flycatcher - Null model					
Null model	-141.79	0.00	0.50	4	82.77
B4 mean percent overlap	-139.95	1.84	0.20	5	84.83
American Crow - One best model					
Distance (km)	1,266.99	0.00	1.00	5	-613.69
American Goldfinch - One best model					
B3 mean percent overlap	174.88	0.00	1.00	5	-68.94
American Redstart - Null model					
Min. temperature percent overlap	-112.60	0.00	0.35	5	71.64
Null model	-111.95	0.65	0.25	4	68.25
Core-boundary distance (km)	-110.78	1.82	0.14	5	70.73
Baltimore Oriole - More than one best model					
Distance (km)	5.94	0.00	0.39	5	13.22
Core-boundary distance (km)	6.58	0.64	0.28	5	12.90
Black-and-white Warbler - Null model					
Null model	-192.97	0.00	0.50	4	108.36
Black-billed Magpie - One best model					
Total summer precipitation percent overlap	77.44	0.00	0.49	5	-24.71
Black-capped Chickadee - One best model					
B3 mean percent overlap	15.47	0.00	1.00	5	9.01
Brown-headed Cowbird - One best model					
Core-boundary distance (km)	67.25	0.00	1.00	5	-13.82
Brown-headed Nuthatch - Null model					
B3 mean percent overlap	-0.75	0.00	0.19	5	8.88
Null model	-0.19	0.56	0.14	4	6.89
Total summer precipitation percent overlap	-0.12	0.62	0.14	5	8.56
B4 std percent overlap	0.11	0.85	0.12	5	8.45
B3 std percent overlap	0.19	0.94	0.12	5	8.41
Blue-headed Vireo - One best model					
Total winter precipitation percent overlap	-19.93	0.00	0.68	5	20.66
Blackburnian Warbler - Null model					
Null model	-7.50	0.00	0.36	4	11.80
Blue Jay - One best model					
Total winter precipitation percent overlap	27.77	0.00	0.88	5	3.82

Table D.1. (Continued)

Bobolink - One best model					
Min. temperature percent overlap	12.00	0.00	0.98	5	8.59
Brewer's Blackbird - One best model					
Distance (km)	-34.54	0.00	1.00	5	32.12
Brewer's Sparrow - One best model					
B3 mean percent overlap	-4.75	0.00	0.93	5	14.58
Brown Thrasher - One best model					
Distance (km)	-265.92	0.00	1.00	5	151.08
Black-throated Blue Warbler - Null model					
Null model	6.33	0.00	0.30	4	4.31
Distance (km)	6.61	0.28	0.26	5	6.04
Black-throated Green Warbler - One best model					
B3 std percent overlap	23.36	0.00	0.85	5	0.07
Bullock's Oriole - One best model					
Distance (km)	-32.40	0.00	1.00	5	29.57
Carolina Chickadee - One best model					
Total summer precipitation percent overlap	-43.61	0.00	0.85	5	36.39
Carolina Wren - One best model					
Max. temperature percent overlap	110.58	0.00	1.00	5	-39.72
Clay-colored Sparrow - Null model					
Null model	30.22	0.00	0.27	4	-8.31
B3 mean percent overlap	32.01	1.79	0.11	5	-7.50
Core-boundary distance (km)	32.12	1.90	0.10	5	-7.56
Chipping Sparrow - One best model					
Distance (km)	961.79	0.00	1.00	5	-461.59
Cliff Swallow - Null model					
Distance (km)	30.58	0.00	0.48	5	3.09
Null model	32.04	1.45	0.23	4	-1.31
Common Grackle - One best model					
B3 mean percent overlap	-401.69	0.00	1.00	5	219.59
Common Yellowthroat - One best model					
Distance (km)	245.23	0.00	1.00	5	-103.42
Chestnut-sided Warbler - One best model					
Max. temperature percent overlap	24.24	0.00	0.53	5	0.08
Chuck-will's-widow - One best model					
Core-boundary distance (km)	18.58	0.00	0.73	5	1.96
Dickcissel - More than one best model					
Total winter precipitation percent overlap	75.83	0.00	0.66	5	-23.61
B4 mean percent overlap	77.34	1.51	0.31	5	-24.36

Table D.1. (Continued)

Dusky Flycatcher - Null model					
B3 mean percent overlap	-23.96	0.00	0.25	5	21.32
Max. temperature percent overlap	-23.52	0.44	0.20	5	21.10
Null model	-23.09	0.87	0.16	4	19.02
Distance (km)	-22.28	1.67	0.11	5	20.48
Eastern Bluebird - One best model					
B3 mean percent overlap	121.22	0.00	0.99	5	-43.36
Eastern Kingbird - One best model					
B3 mean percent overlap	32.61	0.00	1.00	5	2.32
Eastern Phoebe - More than one best model					
Total winter precipitation percent overlap	-7.45	0.00	0.61	5	20.64
Distance (km)	-6.51	0.94	0.38	5	20.18
Eastern Towhee - One best model					
B3 mean percent overlap	22.34	0.00	1.00	5	4.82
Eastern Wood-Pewee - One best model					
Distance (km)	-186.50	0.00	1.00	5	110.34
Fish Crow - Null model					
Null model	-14.82	0.00	0.29	4	15.96
Field Sparrow - One best model					
Min. temperature percent overlap	48.65	0.00	0.96	5	-8.54
Great Blue Heron - One best model					
B3 mean percent overlap	-394.83	0.00	0.59	5	216.72
Great Crested Flycatcher - More than one best model					
Distance (km)	89.44	0.00	0.56	5	-27.02
Min. temperature percent overlap	91.37	1.93	0.21	5	-27.98
Gray Catbird - One best model					
Distance (km)	93.19	0.00	1.00	5	-28.47
Grasshopper Sparrow - One best model					
Min. temperature percent overlap	-40.37	0.00	0.99	5	35.52
Green-tailed Towhee - Null model					
Null model	-13.38	0.00	0.30	4	14.74
Max. temperature percent overlap	-11.88	1.50	0.14	5	16.00
Hammond's Flycatcher - One best model					
B4 std percent overlap	-55.51	0.00	1.00	5	37.82
Hermit Thrush - One best model					
Distance (km)	-244.61	0.00	0.98	5	136.61
House Finch - One best model					
Total summer precipitation percent overlap	47.59	0.00	0.59	5	-5.29
Hooded Warbler - One best model					
Distance (km)	-98.92	0.00	0.57	5	62.47

Table D.1. (Continued)

Indigo Bunting - One best model					
Distance (km)	-54.07	0.00	1.00	5	44.44
Kentucky Warbler - Null model					
Min. temperature percent overlap	-49.87	0.00	0.27	5	37.56
Null model	-49.41	0.46	0.22	4	34.81
B3 std percent overlap	-48.52	1.35	0.14	5	36.88
B4 std percent overlap	-48.26	1.61	0.12	5	36.75
Killdeer - One best model					
B3 mean percent overlap	-970.97	0.00	1.00	5	505.65
Lark Bunting - One best model					
Distance (km)	8.98	0.00	0.73	5	4.01
Lark Sparrow - More than one best model					
Max. temperature percent overlap	43.16	0.00	0.33	5	-6.99
Distance (km)	43.19	0.03	0.32	5	-7.01
Total summer precipitation percent overlap	45.02	1.85	0.13	5	-7.92
Lazuli Bunting - Null model					
Core-boundary distance (km)	-7.58	0.00	0.32	5	14.48
Null model	-6.20	1.38	0.16	4	11.65
Max. temperature percent overlap	-5.86	1.72	0.14	5	13.62
Least Flycatcher - Null model					
Total summer precipitation percent overlap	-31.53	0.00	0.39	5	28.39
Null model	-30.73	0.80	0.26	4	25.46
Magnolia Warbler - One best model					
Max. temperature percent overlap	14.56	0.00	0.56	5	1.22
MacGillivray's Warbler - More than one best					
Distance (km)	-7.36	0.00	0.50	5	13.02
Total winter precipitation percent overlap	-6.37	0.99	0.31	5	12.53
Mountain Bluebird - Null model					
Null model	11.21	0.00	0.46	4	4.49
Mountain Chickadee - More than one best model					
Distance (km)	-0.04	0.00	0.58	5	10.71
B3 mean percent overlap	0.86	0.90	0.37	5	10.26
Mourning Dove - One best model					
B3 mean percent overlap	-913.15	0.00	1.00	5	476.29
Mourning Warbler - One best model					
B3 mean percent overlap	10.51	0.00	0.67	5	4.81
Nashville Warbler - Null model					
Null model	-28.76	0.00	0.34	4	21.85
Northern Bobwhite - One best model					
B3 std percent overlap	30.42	0.00	1.00	5	0.57

Table D.1. (Continued)

Northern Mockingbird - One best model					
Core-boundary distance (km)	114.81	0.00	1.00	5	-40.48
Northern Parula - One best model					
B4 mean percent overlap	-83.54	0.00	0.86	5	57.34
Orchard Oriole - One best model					
Distance (km)	-70.08	0.00	1.00	5	51.03
Ovenbird - One best model					
Total winter precipitation percent overlap	-205.62	0.00	0.81	5	117.91
Pine Siskin - One best model					
B3 mean percent overlap	-22.98	0.00	0.92	5	24.12
Pine Warbler - One best model					
B3 mean percent overlap	-39.50	0.00	0.94	5	33.77
Pileated Woodpecker - Null model					
Null model	-573.69	0.00	0.53	4	300.10
Min. temperature percent overlap	-571.76	1.93	0.20	5	302.45
Prairie Warbler - Null model					
Null model	-27.41	0.00	0.43	4	23.11
Purple Finch - Null model					
Null model	-14.07	0.00	0.41	4	16.03
Rose-breasted Grosbeak - More than one best model					
Distance (km)	-35.41	0.00	0.45	5	31.41
B4 mean percent overlap	-34.22	1.20	0.25	5	30.81
Red-breasted Nuthatch - One best model					
B4 mean percent overlap	-46.62	0.00	0.98	5	37.62
Red-bellied Woodpecker - One best model					
Distance (km)	54.96	0.00	0.79	5	-11.70
Red-headed Woodpecker - More than one best model					
Min. temperature percent overlap	-70.90	0.00	0.66	5	51.83
Max. temperature percent overlap	-69.06	1.84	0.26	5	50.91
Red-naped Sapsucker - One best model					
Distance (km)	-14.73	0.00	0.57	5	15.87
Red-shouldered Hawk - Null model					
Null model	-66.66	0.00	0.47	4	44.77
Red-tailed Hawk - One best model					
B3 mean percent overlap	-1,018.74	0.00	1.00	5	529.08
Red-winged Blackbird - One best model					
B3 mean percent overlap	-858.30	0.00	1.00	5	449.23
Say's Phoebe - Null model					
Core-boundary distance (km)	42.10	0.00	0.34	5	-10.36
Total winter precipitation percent overlap	43.20	1.10	0.20	5	-10.91
Null model	43.29	1.19	0.19	4	-13.09

Table D.1. (Continued)

Sage Thrasher - One best model					
B3 mean percent overlap	-41.35	0.00	0.78	5	30.02
Scarlet Tanager - Null model					
Null model	-136.05	0.00	0.34	4	79.47
B4 mean percent overlap	-135.16	0.89	0.22	5	81.89
B3 mean percent overlap	-135.14	0.91	0.21	5	81.88
Song Sparrow - One best model					
Distance (km)	333.94	0.00	1.00	5	-148.46
Spotted Towhee - One best model					
B3 mean percent overlap	17.91	0.00	0.93	5	3.25
Scissor-tailed Flycatcher - Null model					
Null model	14.19	0.00	0.22	4	0.38
Distance (km)	14.28	0.08	0.21	5	2.21
B4 mean percent overlap	15.27	1.07	0.13	5	1.71
Core-boundary distance (km)	15.37	1.18	0.12	5	1.66
Swainson's Hawk - One best model					
B3 mean percent overlap	-13.75	0.00	0.91	5	18.13
Tree Swallow - One best model					
B3 mean percent overlap	166.18	0.00	0.99	5	-65.39
Tufted Titmouse - One best model					
B3 mean percent overlap	-133.70	0.00	1.00	5	82.19
Veery - More than one best model					
Max. temperature percent overlap	56.75	0.00	0.42	5	-15.01
B4 mean percent overlap	57.22	0.48	0.33	5	-15.24
Vesper Sparrow - One best model					
B3 mean percent overlap	190.14	0.00	1.00	5	-78.50
Warbling Vireo - One best model					
Distance (km)	1,027.74	0.00	1.00	5	-495.25
White-breasted Nuthatch - One best model					
Distance (km)	-258.68	0.00	1.00	5	146.74
Western Kingbird - One best model					
Max. temperature percent overlap	-20.34	0.00	0.95	5	25.27
Western Meadowlark - One best model					
Total winter precipitation percent overlap	64.06	0.00	0.68	5	-16.93
Western Tanager - One best model					
Total winter precipitation percent overlap	-38.85	0.00	0.94	5	30.68
White-eyed Vireo - One best model					
B3 mean percent overlap	53.96	0.00	0.80	5	-12.39
Western Wood-Pewee - One best model					
B3 mean percent overlap	78.79	0.00	1.00	5	-26.39

Table D.1. (Continued)

Winter Wren - Null model					
Max. temperature percent overlap	-54.63	0.00	0.32	5	37.38
Total winter precipitation percent overlap	-53.44	1.18	0.18	5	36.78
Null model	-53.41	1.22	0.17	4	34.76
Wood Thrush - One best model					
Distance (km)	-226.91	0.00	0.99	5	129.84
Yellow-breasted Chat - One best model					
Min. temperature percent overlap	0.65	0.00	1.00	5	15.24
Yellow-billed Cuckoo - One best model					
Total winter precipitation percent overlap	-214.62	0.00	0.54	5	123.88
Yellow-bellied Sapsucker - Null model					
Null model	-39.24	0.00	0.32	4	28.62
Total summer precipitation percent overlap	-37.97	1.27	0.17	5	30.23
Yellow-throated Vireo - One best model					
B3 std percent overlap	-190.88	0.00	0.71	5	111.01
Yellow-throated Warbler - Null model					
Null model	-80.64	0.00	0.36	4	50.73
B3 mean percent overlap	-79.62	1.02	0.22	5	52.82

APPENDIX E

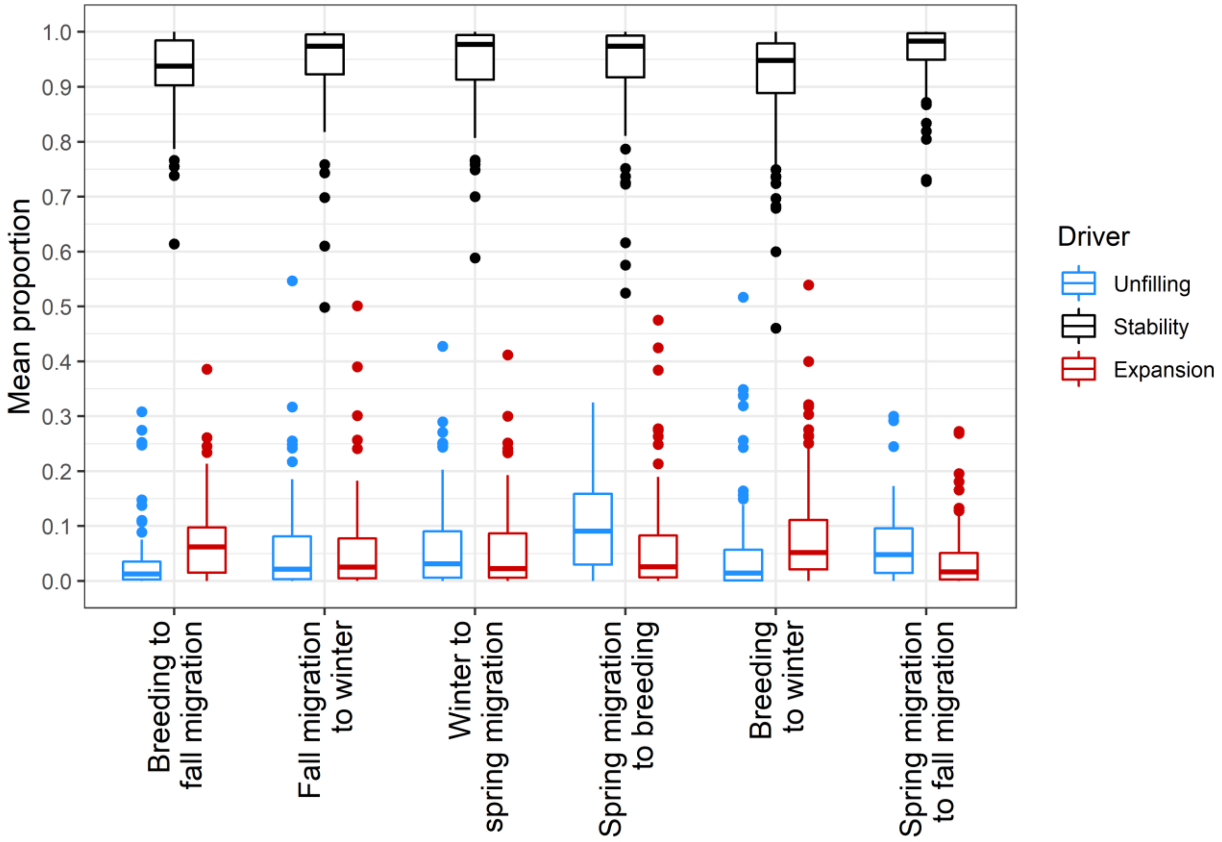

Figure E.1. Boxplots of the drivers of niche differences across seasonal comparisons, using the 80th percentile of the niche used for each species. For instance, the first set of three boxplots represent the proportion of unfilling, stability, and expansion going from breeding season to fall migration (the order of the seasons is important). The blue boxplots represent the proportion of a species' first niche that was unfilled (not used) in the second. The black boxplots represent the proportion of the species' second niche that was also used by the first. The red boxplots represent the proportion of species' second niche not used in the first (it expanded in the second season). For example, the breeding to fall migration niches are more likely to be associated with an expansion in niche compared with the spring migration to breeding seasons which are more likely to be associated with an unfilled niche.

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