

Rousseau, J. S., J. D. Alexander, and M. G. Betts. 2020. Using continental-scale bird banding data to estimate demographic migratory patterns for Rufous Hummingbird (*Selasphorus rufus*). *Avian Conservation and Ecology* 15(2):2. <https://doi.org/10.5751/ACE-01612-150202>
Copyright © 2020 by the author(s). Published here under license by the Resilience Alliance.

Research Paper

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

Josée S. Rousseau^{1,2} , John D. Alexander²  and Matthew G. Betts¹ 

¹Forest Biodiversity Research Network, Forest Ecosystems and Society, Oregon State University, ²Klamath Bird Observatory

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 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.

Utilisation de données de baguage à l'échelle continentale pour évaluer les tendances démographiques migratoires du Colibri roux (*Selasphorus rufus*)

RÉSUMÉ. La conservation efficace des oiseaux repose sur la connaissance des dynamiques de population propres aux espèces. Toutefois, ces dynamiques au moment de la migration et pour les différentes cohortes d'âges et de sexes sont mal connues chez les petits oiseaux. L'objectif de la présente étude était d'évaluer les tendances de migration automnale à grande échelle chez le Colibri roux (*Selasphorus rufus*). Parce que les cohortes d'âges et de sexes de cette espèce quittent les sites de nidification, migrent et arrivent sur leur lieu d'hivernage à des semaines différentes, nous avons prédit que chacune de ces cohortes utiliseraient des routes migratoires différentes, auraient des vitesses de migration différentes et varieraient dans leur répartition hebdomadaire. Le Colibri roux est parmi les quelques espèces en diminution pour lesquelles il existe une grande quantité de données de baguage durant la migration, et celles-ci sont réparties le long du corridor de migration. Nous avons assemblé un imposant jeu de données de captures de colibris (28 948 captures, 459 positions uniques, migrations automnales de 1998 à 2013) et avons utilisé le centre de la position de chaque groupe âge-sexe-année-semaine afin de calculer les corridors, le moment et la vitesse de migration. Les femelles adultes ont eu tendance à utiliser un corridor de migration vers le sud parallèle et entre ceux empruntés par les jeunes et les mâles adultes. De plus, davantage de jeunes ont migré vers le sud par la Californie comparativement aux femelles et aux mâles adultes. Nos résultats indiquent que la migration de chaque cohorte âge-sexe est séparée de deux semaines environ, les mâles adultes arrivant en premier, suivis des femelles adultes, puis des jeunes des deux sexes; cependant, les vitesses de migration n'était pas statistiquement différentes. Enfin, les mâles adultes ont été capturés à l'intérieur d'une répartition géographique plus restreinte, c.-à-d. l'aire durant n'importe quelle semaine de migration, comparativement aux femelles adultes et aux jeunes. Nous concluons que les différentes cohortes âge-sexe de Colibris roux utilisent des routes distinctes et se distinguent sur le plan migratoire, tant en matière de phénologie que de répartition. Nos résultats laissent entrevoir que les cohortes âge-sexe pourraient être affectées différemment par la perte d'habitat, les changements phénologiques et le climat durant les migrations. La prise en compte de ces dynamiques démographiques migratoires pourrait améliorer les résultats en matière de conservation.

Key Words: *conservation; demography; distribution; hummingbird; migration; population dynamics*

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 (Sillert 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 1, Fig. A1.1). 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 \times year and sex \times 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 \times year or sex \times 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 \times year $F_{(15,283)} = 0.97$, $p = 0.49$; sex \times year $F_{(15,283)} = 0.52$, $p = 0.93$; Appendix 1, Fig. A1.1), 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 \times 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 \times 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 \times 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 \times 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.

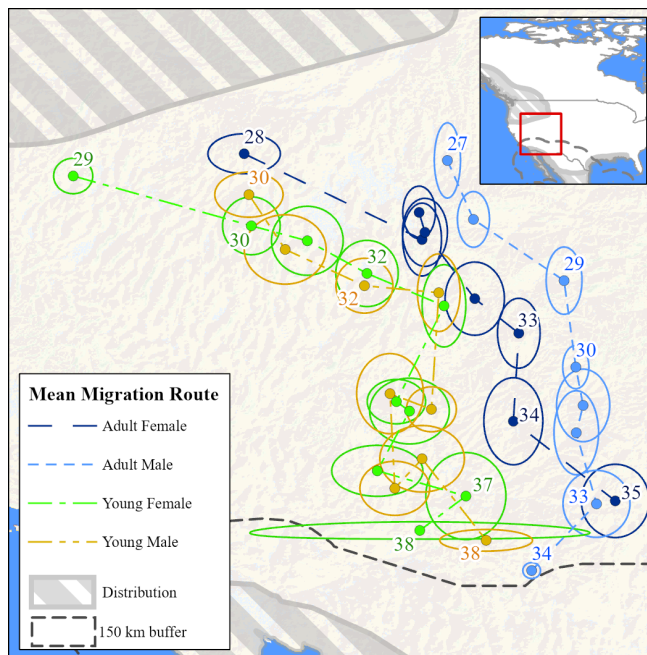
We defined the migration distribution as the total area occupied by captures in a particular week. We calculated this separately for each age-sex, year, and subsample. Here, a large area would represent a protracted migration with individuals spread over large distances between the migration front and 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 \times 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

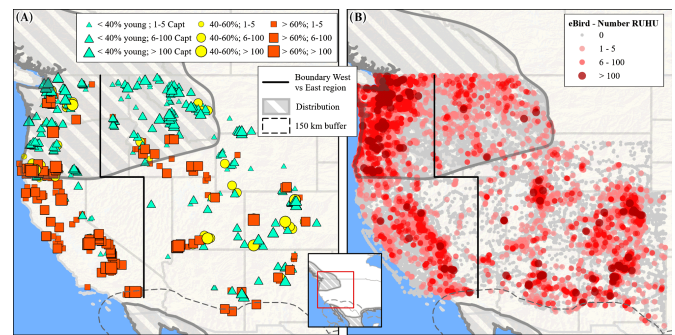
Southbound (fall) migration routes of Rufous Hummingbirds depended strongly on age and sex (Fig. 1). There were three main migration routes (Fig. 1). On average, adult females migrated east of the young of both sexes and west of the adult males. The migration routes of young males and young females were 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 (Fig. 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.

Fig. 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.



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% ; Fig. 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.

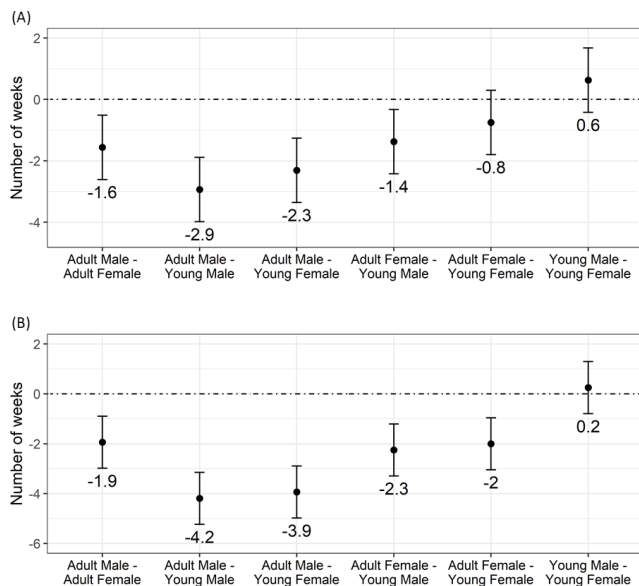
Fig. 2. Locations of Rufous Hummingbird (*Selasphorus rufus*) captures (A) and eBird observations (B) occurring in a western and an eastern region (delimited by the black line) during two different time periods. The symbols overlapping the breeding distribution (Oregon, Washington, Idaho, and Montana; 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 U.S.-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. Although 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 where > 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.



The start and end of migration differed significantly among age and sex categories (age \times 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 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 \pm 0.39 [SE]; $t_{(45)} = 5.16$, $p < 0.0001$). See Figure 3B for a comparison of migration end for each age and sex categories.

Fig. 3. Estimated differences in (A) mean start and (B) mean end 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 on average 1.6 weeks earlier than females. Note, 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.



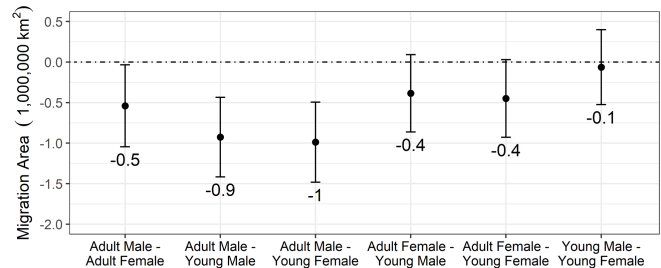
Results from analysis of migration speed differed from migration timing. We did not detect a difference in migration speed among age-sex categories (age: $F_{(1,44)} = 0.91$, $p = 0.34$; sex: $F_{(1,44)} = 0.84$, $p = 0.36$; age \times sex: $F_{(1,44)} = 0.65$, $p = 0.42$). Rufous Hummingbirds migrated 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 2 (Fig. A2.1).

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 \times sex ($F_{(1,312)} = 3.27$, $p = 0.071$). Adults of both sexes tended to migrate using a relatively smaller distribution area than young (mean for adults = 2,963,906 km² \pm 196,062 [SE]; 95% CI = 2,546,009 to 3,381,803; mean for young = 3,650,676 km² \pm 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 km² \pm 194,490 [SE]; 95% CI = 2,742,058 to 3,571,152; mean for females = 3,457,977 km² \pm 194,588 [SE]; 95% CI = 3,043,223 to 3,872,730). Figure 4 includes a comparison of migration area for each age and sex categories.

Fig. 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.



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 (Fig. 1). Moreover, capture data show hummingbirds migrating south through the Rocky Mountains and California (Fig. 2A and B). 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 1, Fig. A1), 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 re-nest 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 2, Fig. A2.1) 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 ($38.5 \text{ km/day} \pm 15.5 \text{ SD}$) includes yearly values comparable to those of Supp et al. (2015; $33.41 \text{ km/day} \pm \text{SD } 11.6$) 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 (Fig. 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 (Partners in Flight 2019, Rosenberg et al. 2019), high mortality rates during migration (Sillert 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>

Acknowledgments:

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.

Funding: The author JSR was supported by a Natural Sciences and Engineering Research Council (NSERC) Postgraduate Scholarship and Oregon State University Richardson Family Graduate Fellowship. This research was supported in part by US National Science Foundation grants (DEB-1050954 and DEB-1457837) to MGB. We also thank the Western Hummingbird Partnership and USDA Forest Service Redwood Sciences Laboratory for providing funding for this study.

Data and scripts are available at https://data.pointblue.org/apps/data_catalog/dataset/laknw-2020-002.

LITERATURE CITED

- Alexander, J. D., E. J. Williams, C. R. Gillespie, S. Contreras-Martínez, and D. M. Finch. 2020. *Effects of restoration and fire on habitats and populations of western hummingbirds: a literature review*. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Amrhein, V., B. Scaar, M. Baumann, N. Minéry, J.-P. Binnert, and F. Korner-Nievergelt. 2012. Estimating adult sex ratios from bird mist netting data. *Methods in Ecology and Evolution* 3:713-720. <https://doi.org/10.1111/j.2041-210X.2012.00207.x>
- Bertin, R. I. 1982. The Ruby-throated Hummingbird and its major food plants: ranges, flowering phenology, and migration. *Canadian Journal of Zoology* 60:210-219. <https://doi.org/10.1139/z82-029>
- Betts, M. G., J. C. Hagar, J. W. Rivers, J. D. Alexander, K. McGarigal, and B. C. McComb. 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20:2116-2130. <https://doi.org/10.1890/09-1305.1>
- Betts, M. G., J. Verschuyf, J. Giovanini, T. Stokely, and A. J. Kroll. 2013. Initial experimental effects of intensive forest management on avian abundance. *Forest Ecology and Management* 310:1036-1044. <https://doi.org/10.1016/j.foreco.2013.06.022>
- BirdLife International and Handbook of the Birds of the World. 2016. *Bird species distribution maps of the world. Version 6.0*. BirdLife International, Cambridge, UK.
- Bivand, R., T. Keitt, and B. Rowlingson. 2019. *rgdal: Bindings for the "Geospatial" data abstraction library*.
- Bivand, R., and C. Rundel. 2019. *rgeos: Interface to Geometry Engine - Open Source ('GEOS')*.
- Branick, M. L. 1997. A climatology of significant winter-type weather events in the contiguous United States, 1982-94. *Weather and Forecasting* 12:193-207. [https://doi.org/10.1175/1520-0434\(1997\)012<0193:ACOSWT>2.0.CO;2](https://doi.org/10.1175/1520-0434(1997)012<0193:ACOSWT>2.0.CO;2)
- Briedis, M., B. Silke, P. Adamík, J. A. Alves, J. S. Costa, T. Emmenegger, L. Gustafsson, J. Koleček, F. Liechti, C. M. Meier, P. Procházka, and S. Hahn. 2019. A full annual perspective on sex-biased migration timing in long-distance migratory birds. *Proceedings of the Royal Society B: Biological Sciences* 286:20182821. <https://doi.org/10.1098/rspb.2018.2821>
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516-519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Calenge, C., and S. Fortmann-Roe. 2017. *adehabitatHR: Home range estimation*.
- Carlisle, J. D., G. S. Kaltenecker, and D. L. Swanson. 2005. Molt strategies and age differences in migration timing among autumn landbird migrants in southwestern Idaho. *Auk* 122:1070-1085. <https://doi.org/10.1093/auk/122.4.1070>
- Carpenter, F. L., M. A. Hixon, E. J. Temeles, R. W. Russell, and D. C. Paton. 1993. Exploitative compensation by subordinate age-sex classes of migrant Rufous Hummingbirds. *Behavioral Ecology and Sociobiology* 33:305-312. <https://doi.org/10.1007/bf00172928>
- Clout, M. N., G. P. Elliott, and B. C. Robertson. 2002. Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biological Conservation* 107:13-18. [https://doi.org/10.1016/S0006-3207\(01\)00267-1](https://doi.org/10.1016/S0006-3207(01)00267-1)
- Cooper, N. W., M. T. Hallworth, and P. P. Marra. 2017. Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. *Journal of Avian Biology* 48:209-219. <https://doi.org/10.1111/jav.01096>
- Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2011. Onset of summer flowering in a 'Sky Island' is driven by monsoon moisture. *New Phytologist* 191:468-479. <https://doi.org/10.1111/j.1469-8137.2011.03705.x>
- DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. R. Norris. 2015. Transoceanic migration by a 12 g songbird. *Biology Letters* 11:20141045. <https://doi.org/10.1098/rsbl.2014.1045>
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, et al. 2010. Conserving migratory land birds

- in the New World: do we know enough? *Ecological Applications* 20:398-418. <https://doi.org/10.1890/09-0397.1>
- Gass, C. L. 1979. Territory regulation, tenure, and migration in Rufous Hummingbirds. *Canadian Journal of Zoology* 57:914-923. <https://doi.org/10.1139/z79-112>
- Healy, S., and W. A. Calder. 2020. Rufous Hummingbird (*Selasphorus rufus*), version 1.0. In A. F. Poole, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.rufhum.01>
- Hedenstrom, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:287-299. <https://doi.org/10.1098/rstb.2007.2140>
- Henshaw, H. W. 1886. List of birds observed in summer and fall on the upper Pecos River, New Mexico. *Auk* 3:73-80.
- Hijmans, R. J. 2019. *geosphere: Spherical trigonometry*.
- Holmes, R. T. 2007. Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis* 149:2-13. <https://doi.org/10.1111/j.1474-919X.2007.00685.x>
- Johnsgard, P. A. 2016. *The hummingbirds of North America. Second edition*. Smithsonian Institution, Washington, D.C., USA.
- Kennedy, R. S. H., and T. A. Spies. 2005. Dynamics of hardwood patches in a conifer matrix: 54 years of change in a forested landscape in Coastal Oregon, USA. *Biological Conservation* 122:363-374. <https://doi.org/10.1016/j.biocon.2004.07.022>
- Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Alerstam. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology* 83:176-184. <https://doi.org/10.1111/1365-2656.12135>
- Kodric-Brown, A., and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285-296. <https://doi.org/10.2307/1936374>
- La Sorte, F. A., D. Fink, W. M. Hochachka, J. P. DeLong, and S. Kelling. 2014. Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proceedings of the Royal Society of London B: Biological Sciences* 281:20140984. <https://doi.org/10.1098/rspb.2014.0984>
- La Sorte, F. A., D. Fink, W. M. Hochachka, and S. Kelling. 2016. Convergence of broad-scale migration strategies in terrestrial birds. *Proceedings of the Royal Society B: Biological Sciences* 283:20152588. <https://doi.org/10.1098/rspb.2015.2588>
- La Sorte, F. A., D. Fink, and A. Johnston. 2018. Seasonal associations with novel climates for North American migratory bird populations. *Ecology Letters* 21:845-856. <https://doi.org/10.1111/ele.12951>
- Lenth, R. 2019. *emmeans: Estimated marginal means, aka least-squares means*.
- McGarigal, K., W. H. Romme, M. Crist, and E. Roworth. 2001. Cumulative effects of roads and logging on landscape structure in the San Juan Mountains, Colorado (USA). *Landscape Ecology* 16:327-349. <https://doi.org/10.1023/A:1011185409347>
- McGuire, J. A., C. C. Witt, J. V. Remsen, A. Corl, D. L. Rabosky, D. L. Altshuler, and R. Dudley. 2014. Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* 24:910-916. <https://doi.org/10.1016/j.cub.2014.03.016>
- McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130:211-222. <https://doi.org/10.1525/auk.2013.12226>
- Miller, E. A., and C. B. Halpern. 2009. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science* 9:265-282. <https://doi.org/10.2307/3237126>
- Mock, C. J. 1996. Climatic controls and spatial variations of precipitation in the Western United States. *Journal of Climate* 9:1111-1125. [https://doi.org/10.1175/1520-0442\(1996\)009<1111:CCASVO>2.0.CO;2](https://doi.org/10.1175/1520-0442(1996)009<1111:CCASVO>2.0.CO;2)
- Moran, J. A., L. I. Wassenaar, J. C. Finlay, C. Hutcheson, L. A. Isaac, and S. M. Wethington. 2013. An exploration of migratory connectivity of the Rufous Hummingbird (*Selasphorus rufus*), using feather deuterium. *Journal of Ornithology* 154:423-430. <https://doi.org/10.1007/s10336-012-0906-3>
- Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4:663-673. <https://doi.org/10.1046/j.1461-0248.2001.00265.x>
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147:146-166. <https://doi.org/10.1007/s10336-006-0058-4>
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* 271:59-64. <https://doi.org/10.1098/rspb.2003.2569>
- North American Bird Conservation Initiative. 2014. *The state of the birds 2014 report*. U.S. Department of Interior, Washington, D.C., USA.
- North American Bird Conservation Initiative, U.S. Committee. 2010. *The state of the birds 2010 report on climate change, United States of America*. U.S. Department of the Interior, Washington, D.C., USA.
- Northrup, J. M., J. W. Rivers, Z. Yang, and M. G. Betts. 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Global Change Biology* 25:1561-1575. <https://doi.org/10.1111/gcb.14571>
- Ortiz-Crespo, F. I. 1972. A new method to separate immature and adult hummingbirds. *Auk* 89:851-857. <https://doi.org/10.2307/4084114>
- Partners in Flight. 2019. Avian conservation assessment database, version 2019. [online] URL: <http://pif.birdconservancy.org/ACAD>
- Paxton, E. H., S. L. Durst, M. K. Sogge, T. J. Koronkiewicz, and K. L. Paxton. 2017. Survivorship across the annual cycle of a migratory passerine, the Willow Flycatcher. *Journal of Avian Biology* 48(8):1126-1131. <https://doi.org/10.1111/jav.01371>

- Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. *R Journal* 10:439-446. <https://doi.org/10.32614/RJ-2018-009>
- Petry, W. K., J. D. Soule, A. M. Iler, A. Chicas-Mosier, D. W. Inouye, T. E. X. Miller, and K. A. Mooney. 2016. Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science* 353:69-71. <https://doi.org/10.1126/science.aaf2588>
- Phalan, B. T., J. M. Northrup, Z. Yang, R. L. Deal, J. S. Rousseau, T. A. Spies, and M. G. Betts. 2019. Impacts of the Northwest Forest Plan on forest composition and bird populations. *Proceedings of the National Academy of Sciences* 116(8):3322-3327. <https://doi.org/10.1073/pnas.1813072116>
- Phillips, A. R. 1975. The migrations of Allen's and other hummingbirds. *Condor* 77:196-205. <https://doi.org/10.2307/1365790>
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R-core Team. 2019. *nlme: Linear and nonlinear mixed effects models*.
- Pyle, P. 1997. *Identification guide to North American birds, part I: Columbidae to Ploceidae*. State Creek Press, Bolinas, California, USA.
- R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ralph, C. J. 1971. An age differential of migrants in coastal California. *Condor* 73:243-246. <https://doi.org/10.2307/1365846>
- Robinson, W. D., M. S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R. H. Diehl, T. H. Kunz, S. Mabey, and D. W. Winkler. 2010. Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment* 8(7):354-361. <https://doi.org/10.1890/080179>
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. *Science* 366:120-124. <https://doi.org/10.1126/science.aaw1313>
- Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, A. Couturier, D. W. Demarest, W. E. Easton, J. J. Giocomo, R. H. Keller, A. E. Mini, A. O. Panjabi, D. N. Pashley, T. D. Rich, J. M. Ruth, H. Stabins, J. Stanton, and T. Will. 2016. Partners In Flight Landbird Conservation Plan: 2016 revision for Canada and Continental United States. *Partners in Flight Science Committee*.
- Saino, N., D. Rubolini, L. Serra, M. Caprioli, M. Morganti, R. Ambrosini, and F. Spina. 2010. Sex-related variation in migration phenology in relation to sexual dimorphism: a test of competing hypotheses for the evolution of protandry. *Journal of Evolutionary Biology* 23:2054-2065. <https://doi.org/10.1111/j.1420-9101.2010.02068.x>
- Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. *The North American Breeding Bird Survey, results and analysis 1996-2015. Version 2.07.2017*. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Schondube, J. E., S. Contreras-Martinez, I. Ruan-Tejeda, W. A. Calder, and E. Santana. 2004. Migratory patterns of the Rufous Hummingbird in western Mexico. Pages 80-95 in G. P. Nabhan, editor. *Conserving migratory pollinators and nectar corridors in Western North America*. University of Arizona Press, Tucson, Arizona, USA.
- Shankar, A., C. H. Graham, J. R. Canepa, S. M. Wethington, and D. R. Powers. 2019. Hummingbirds budget energy flexibly in response to changing resources. *Functional Ecology* 33:1904-1916. <https://doi.org/10.1111/1365-2435.13404>
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296-308. <https://doi.org/10.1046/j.1365-2656.2002.00599.x>
- Stiles, F. G. 1972. Age and sex determination in Rufous and Allen Hummingbirds. *Condor* 74:25-32. <https://doi.org/10.2307/1366446>
- Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896. <https://doi.org/10.1126/science.1166664>
- Sullivan, B. L., J. L. Aycrigg, J. H. Barry, R. E. Bonney, N. Bruns, C. B. Cooper, T. Damoulas, A. A. Dhondt, T. Dietterich, A. Farnsworth, D. Fink, J. W. Fitzpatrick, T. Fredericks, J. Gerbracht, C. Gomes, W. M. Hochachka, M. J. Iliff, C. Lagoze, F. A. La Sorte, M. Merrifield, W. Morris, T. B. Phillips, M. Reynolds, A. D. Rodewald, K. V. Rosenberg, N. M. Trautmann, A. Wiggins, D. W. Winkler, W.-K. Wong, C. L. Wood, J. Yu, and S. Kelling. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation* 169:31-40. <https://doi.org/10.1016/j.biocon.2013.11.003>
- Supp, S. R., F. A. L. Sorte, T. A. Cormier, M. C. W. Lim, D. R. Powers, S. M. Wethington, S. Goetz, and C. H. Graham. 2015. Citizen-science data provides new insight into annual and seasonal variation in migration patterns. *Ecosphere* 6:1-19. <https://doi.org/10.1890/ES14-00290.1>
- Swarth, H. S. 1904. Birds of the Huachuca Mountains, Arizona. Pages 1-70 *Pacific Coast Avifauna* No. 4. Cooper Ornithological Club of California, Los Angeles, California, USA. <https://doi.org/10.5962/bhl.title.30674>
- Takaoka, S., and F. J. Swanson. 2008. Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. *Professional Geographer* 60:527-540. <https://doi.org/10.1080/00330120802212099>
- Thorup, K., F. Korner-Nievergelt, E. B. Cohen, and S. R. Baillie. 2014. Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: a review including methodological perspectives. *Methods in Ecology and Evolution* 5:1337-1350. <https://doi.org/10.1111/2041-210X.12258>
- Warnes, G. R., B. Bolker, T. Lumley, and R. C. Johnson. 2018. *gmodels: Various R programming tools for model fitting*. R package version 2.18.1. Contributions from Randall C. Johnson are Copyright (2005) SAIC-Frederick, Inc. Funded by the Intramural Research Program, of the NIH, National Cancer Institute, Center for Cancer Research under NCI Contract NO1-CO-12400. [online] URL: <https://CRAN.R-project.org/package=gmodels>

Waser, N. M. 1976. Food supply and nest timing of Broad-Tailed Hummingbirds in the Rocky Mountains. *Condor* 78:133-135. <https://doi.org/10.2307/1366943>

Weatherhead, P. J. 2005. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of Red-Winged Blackbirds. *Oecologia* 144:168-175. <https://doi.org/10.1007/s00442-005-0009-4>

Wethington, S. M., and S. M. Russell. 2003. The seasonal distribution and abundance of hummingbirds in oak woodland and riparian communities in southeastern Arizona. *Condor* 105:484-495. <https://doi.org/10.1093/condor/105.3.484>

Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York, New York, USA.

Williamson, S. L. 2001. *Hummingbirds of North America*. Houghton Mifflin Company, New York, New York, USA.

Woodworth, B. K., A. E. M. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright, and D. R. Norris. 2016. Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia* 181:413-422. <https://doi.org/10.1007/s00442-015-3527-8>

Zenzal, T. J., and F. R. Moore. 2016. Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration. *Auk* 133:237-250. <https://doi.org/10.1642/AUK-15-160.1>



Appendix 1.

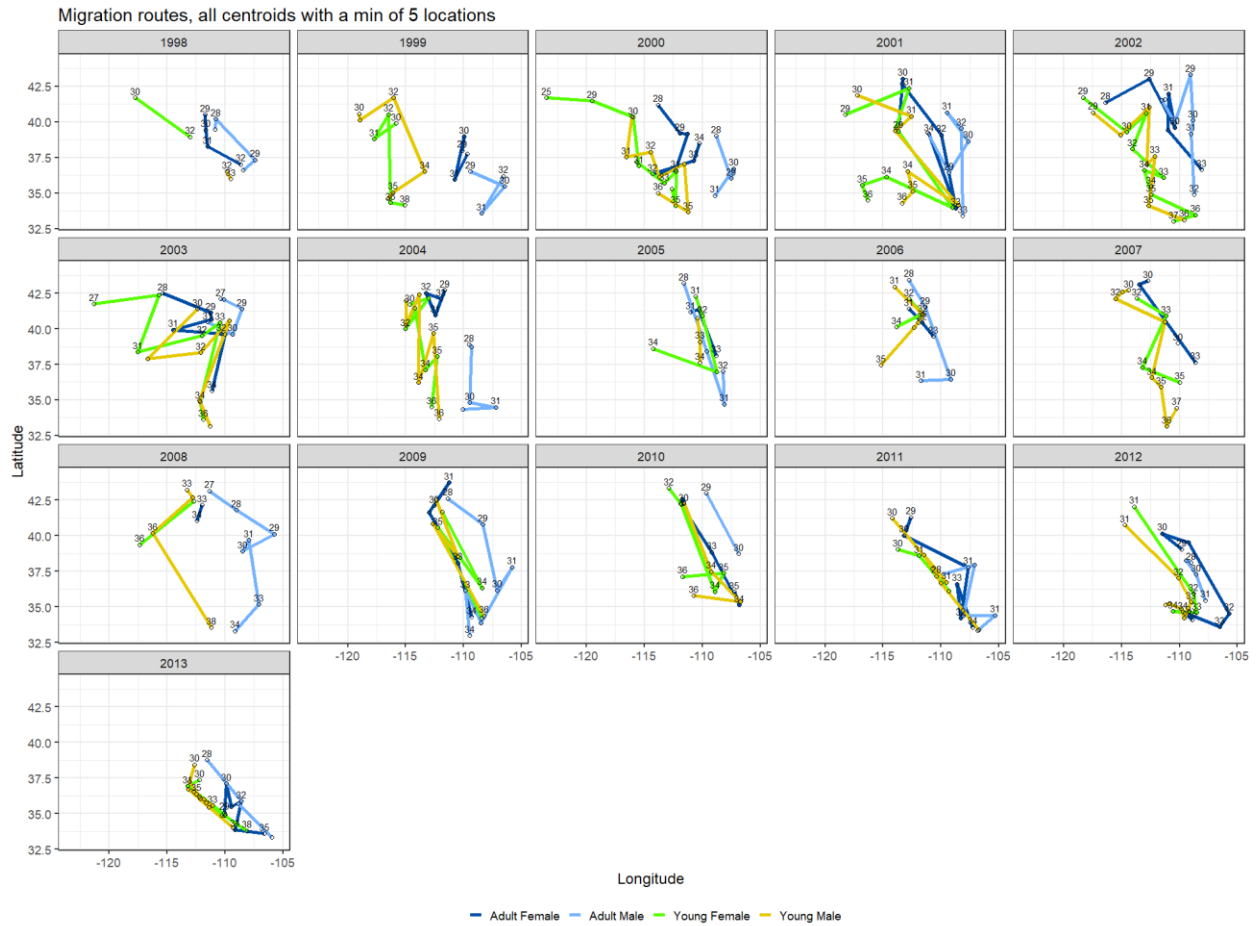


Fig. A1.1. Yearly migration routes for each age and sex category. Dots represent the weekly mean location per age-sex and lines are the mean migration routes. Adult males are in light blue, adult females in dark blue, young males in yellow, and young females in green. Numbers in each graph represent the week within a year.

Appendix 2.

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

Fig. A2.1. Yearly migration speed, all age-sex categories combined.

* Year 2007 does not include data from the adult male category.