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Seasonal Distribution of the Broad-Tailed Hummingbird (*Selasphorus platycercus*): A Climatic Approach

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The seasonal movements of birds are a phenomenon that has historically been of interest in ecology and biogeography. Despite this, information on how environmental conditions influence migratory behavior and its regulation is still scarce. In this work, we study the Broad-Tailed hummingbird *Selasphorus platycercus* from an analysis of its populations through longitudinal and latitudinal gradients. We use the frequencies of monthly presence records throughout the annual cycle to identify the breeding areas (corresponding to the summer months), of winter presence (corresponding to the winter months), and annual residence (presence records throughout the year). Subsequently, we use ecological niche models to reconstruct the potential distribution of the summer and winter niches by correlating the climates of each season with the corresponding records. We evaluate the species' climatic preferences between the breeding and winter seasons by transferring the niches from each season to the opposite and by their capacity to inter-predict records between seasons. In addition, we quantify the overlap between the summer and winter niches using a niche similarity analysis. Geographically, we see a clear seasonal turnover pattern along a north-south gradient and records throughout the year (resident populations) in the south-central region of its distribution. We observed a low inter-prediction of records between seasons. Together with the similarity analysis, we suggest that the species is niche-switching (*i.e.*, has different seasonal niches). We identified three seasonal migration patterns among the species' populations: long-distance migratory, short-distance summer migrant, and resident. Our findings suggest that the different migration patterns in this species' populations all over its distribution can be explained through seasonal climatic variations throughout the year.

Key words: Environmental similarity, Migration, Seasonal climate niche, Seasonal turnover, Temporal ecology.

BACKGROUND

Migration is widely present in diverse animal groups, and it has attracted attention as an important phenomenon in ecology and biogeography (Terborgh 1989; Hagan and Johnston 1995; Chesser and Levey 1998; Webster et al. 2002; Zink 2002; Somveille et al. 2015 2021). Migratory movements in birds present diverse geographic and temporal variants. For example, there are latitudinal migrations (short or long distance), longitudinal migrations (*i.e.*, east-west direction, from extreme climate to warm climate), partial migrations

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(some of the populations migrate and others do not), differential migrations (showing different patterns in the migration of young and adult individuals or between sexes); and altitudinal and intertropical migrations (Rappole 1995; Lincoln et al. 1998; Newton 2008; Jahn et al. 2020). All these migratory behaviors respond directly or indirectly to climatic variations, particularly in regions with marked seasonality that define two well-known periods in the species' life cycle: winter and reproduction seasons (Marra et al. 2005; Newton 2008; Peña-Peniche et al. 2018). However, there are uncertainties in their geographic and temporal distribution patterns for most migratory species. It is unknown whether species follow a particular set of conditions during the migratory cycle, such as the climatic conditions that constitute the species' niche (*e.g.*, Nakazawa et al. 2004; Marra et al. 2005; Battey 2015; Gómez et al. 2016; Pérez-Moreno et al. 2016).

Migratory birds can follow similar climatic conditions even in both seasonal areas (*i.e.*, "niche followers), experience different climatic conditions in each season (*i.e.*, "niche switchers"), or present a combination of both strategies (Nakazawa et al. 2004). Likewise, these strategies may vary among species and populations, probably due to diverse ecological factors (Hedenström 2008). Based on the use of ecological niche models, focused on the macroclimatic analysis of the distribution of species, we have achieved a better definition in the study of the migratory movements of bird species (*e.g.*, Nakazawa et al. 2004; Marra et al. 2005; Newton 2008; Battey 2015; Ruiz-Sánchez et al. 2015; Gómez et al. 2016; Pérez-Moreno et al. 2016; Peña-Peniche et al. 2018). The use of ecological niche models (ENM) and species distribution models (SDM) allows us to analyze the influence of climatic conditions on the seasonal movement patterns of migratory species and predict their migratory cycle based on such climatic conditions (Nakazawa et al. 2004; Papes et al. 2012; Battey 2015; Ruíz-Sánchez et al. 2015; Gómez et al. 2016; Williams et al. 2017). These tools, therefore, allow us to understand the ecology and migratory behavior of the species (Papes et al. 2012; Pérez-Moreno et al. 2016; Toews 2017; Somveille et al. 2021).

To date, the migration patterns of hummingbirds (Trochilidae) have been scarcely studied, and although most of the 350 species included in this group do not possess long-distance migratory movements, those that do reproduce far from the tropics (Schuchmann 1999). Current information on routes and times in hummingbird migration is based primarily on North American species, such as the Rufous Hummingbird (*Selasphorus rufus*), Allen's Hummingbird (*Selasphorus sasin*), Calliope Hummingbird (*Stellula calliope*) (Phillips 1975; Calder 1993; Calder and Calder 1994; Battey 2015), and the Ruby-throated Hummingbird (*Archilochus colubris*) (Németh and Moore 2012; Zenzal Jr. and Moore 2016; Zenzal Jr. et al. 2018). These studies have suggested that various factors influence and regulate the distribution and abundance in migratory hummingbirds, such as morphological and behavioral adaptations (*e.g.*, Calder 2004), the availability of resources (*e.g.*, Arizmendi 2001; Lara 2006), the influence of the biogeographic barriers and the phylogeographic history of the species (González-García et al. 2018), as well as the climatic conditions (*e.g.*, Schondube and Martínez del Rio 2004). This last factor is one of the least studied and understood.

The Broad-tailed Hummingbird (*Selasphorus platycercus*) is a migratory species with two subspecies recently claimed as independent lineages (Malpica and Ornelas 2014): *Selasphorus p. platycercus*, distributed from the northern United States to Oaxaca, Mexico; and *Selasphorus p. guatemalae*, which inhabit the mountains of southern Mexico (Chiapas) and in Guatemala where it resides year-round (Schuchmann 1999; Kaufman 2005; Vuilleumier 2011; Arizmendi and Berlanga 2014). The *Selasphorus p. platycercus* lineage (hereafter *Selasphorus platycercus*) is traditionally recognized as a long-distance seasonal migrant, although it does have some resident populations in central Mexico (Calder 1987; Lara 2006). Malpica and Ornelas (2014) suggested that the divergence between these populations was due to the change in climatic conditions during the last interglacial period when migratory populations began to expand northwards in search of conditions similar to those from the center of Mexico, where the sedentary populations that originate them reside. Likewise, considering the migration systems used by the Birds of the New World (Jahn et al. 2020), it is possible to establish that *Selasphorus platycercus* populations can be categorized as 1) Nearctic-Neotropical migration or long-distance migration, in which birds breed at north-temperate latitudes and overwinter in the Neotropics; 2) Intra-tropical migration, in which birds breed and migrate entirely within the tropics; and 3) permanent residence within the tropics (Calder 1993 2004; Lara 2006). All these types are a product of complex historical and ecological processes that originated the current patterns (Malpica and Ornelas 2014). *Selasphorus platycercus*, as many other currently long-distance North American migrant species, likely lacked suitable breeding habitat in North America at the Last Glacial Maximum (LGM), and it might have reverted to the ancestral state of being tropical sedentary residents (Zink and Gardner 2017). Such complex glacial cycles could also have promoted other migratory systems in the populations of *Selasphorus platycercus* when oscillated between sedentary and migratory strategies with each glacial cycle. Most populations are typically long-distance migrants that breed in North America and migrate south in winter, either toward the eastern United States or toward the center and south of Mexico. However, along the Mexican Volcanic Belt, a region traditionally recognized as a wintering area, several populations describe different seasonal strategies. For example, resident populations (with a continuous presence throughout the year), winter migratory populations (that winter in the region and migrate north to reproduce) as well as reproductive populations (that breed in the area and that during winter move to unknown areas) (Lara 2006; Malpica and Ornelas 2014).

Several studies describe the distribution of *Selasphorus platycercus* (*e.g.*, Calder 1987 1993 2004; Schuchmann 1999; Kaufman 2005; Vuilleumier 2011; Arizmendi and Berlanga 2014). However, seasonal patterns throughout its geographic distribution are not clearly defined. This uncertainty could be explained by the diverse types of seasonal strategies followed by the species' populations, highlighting, in general, the lack of knowledge and delimitation of their seasonal distribution patterns. In this species, the seasonal movements may be influenced by the availability of floral resources and the intra and inter-specific interactions (*e.g.*, Lara 2006). However, the climatic conditions could be defining both the seasonal areas and the migratory movements, as has been described for other species (Battey 2015; Laube et al. 2015; Ruíz-Sánchez et al. 2015; Pérez-Moreno et al. 2016; Peña-Peniche et al. 2018). In this study, we analyze the seasonal geographic distribution of *Selasphorus platycercus* through the latitudinal and longitudinal analysis of occurrence data. Besides, we modeled the species' seasonal distribution and measured the similarity between its summer and winter ecological niches by studying their seasonal climatic associations using ENM and SDM.

MATERIALS AND METHODS

Occurrence records

We obtained specific geographic information on *Selasphorus platycercus* from the Global Biodiversity Information Facility (GBIF 2021) and specialized literature (Lara 2006; Malpica and Ornelas 2014). We remove all duplicate records from the compiled information and those doubtful whose coordinates were not precise or could not be corroborated. To carry out the study of the latitudinal and longitudinal patterns, we obtained 1176 unique presence records. Meanwhile, for the seasonal distribution models, we used 936 occurrences, corresponding to the summer (747 records) and winter (189 records) seasons.

Longitudinal and latitudinal analysis

Using the final database containing unique presence records, we performed a spatio-temporal data analysis of the distribution of *S. platycercus*. For this, we first projected all occurrence records in the geography using the *raster* package v.3.4-5 (Hijmans et al. 2005) in the R programming environment (R Core Team 2017). Once we defined the punctual distribution, the geographic space was divided into two longitudinal segments (between the range -97° and -125°) and into ten latitudinal segments (between the range 47°N and 15°S), which included from the northern United States to southern Mexico. We extracted the number of unique presence records per month from each segment, making it possible to know the longitudinal and latitudinal distribution patterns throughout the annual cycle (Fig. 1).

In addition, based on the temporal correspondence, each segment was identified as associated with the species' presence in summer (or breeding season = June, July, and August), winter (December, January, and February), or both. We want to highlight that we did not consider the spring and autumn seasons since our interest was the areas where the species spend most of the time during their migratory cycle; that is, the zones of actual seasonal residence (summer and winter). In contrast, the records during spring and autumn may correspond only to transitional sites during their migratory cycle.

Ecological niche modeling and species distribution modeling

The estimation of niche limits to species occurrence is named ecological niche modeling (ENM), and when the emphasis is on the species geographical distributions, it is known as species distribution modeling (SDM) (Guisan and Thuiller 2005; Peterson and Soberón 2012; Saupe et al. 2012). We modeled the breeding and winter niches of the *Selasphorus platycercus* populations, using the records by month corresponding to each season (breeding and winter). To characterize the environmental niche seasonally, we created two groups of monthly variables, one for the breeding and one for the winter seasons and corresponding to the same months previously described for the occurrence records. Each group possessed six variables from the WorldClim version 2.1 (Fick and Hijmans 2017): the minimum temperature of the coldest month; the maximum temperature of the warmest month; accumulated precipitation (sum of the three-monthly precipitations); and the average of solar radiation, wind speed and water vapor pressure. These variables were generated by interpolating average monthly climate data from weather stations, ranging from 1970 to 2000 (Fick and Hijmans 2017). These were in raster format with a resolution of 0.0083 decimal degrees (~1 km^2).

We used MaxEnt 3.3.3 algorithm to generate the models (Phillips et al. 2006). This correlative algorithm is based on the principle of maximum entropy used to estimate probability distributions (*i.e.*, uniform distributions) based on the presence records of a species. It is subject to restrictions conferred by environmental information or other variables such as topography (Phillips et al. 2006). MaxEnt is a robust algorithm that provides informative results and requires only presence data (Peterson et al. 2011). We used the kuenm R package (Cobos et al. 2019), which evaluates each candidate model considering: (1) statistical significance, based on the partial ROC area under the curve ratio based on independent random subsets of presence data (we used an omission rate of E = 5%; see Peterson et al. 2008); (2) predictive performance, that considered the omission error derived from independent random subsets of presence data and minimum training presence thresholds adjusted to allow E = 5% among the calibration data (Anderson et al. 2003); and (3)

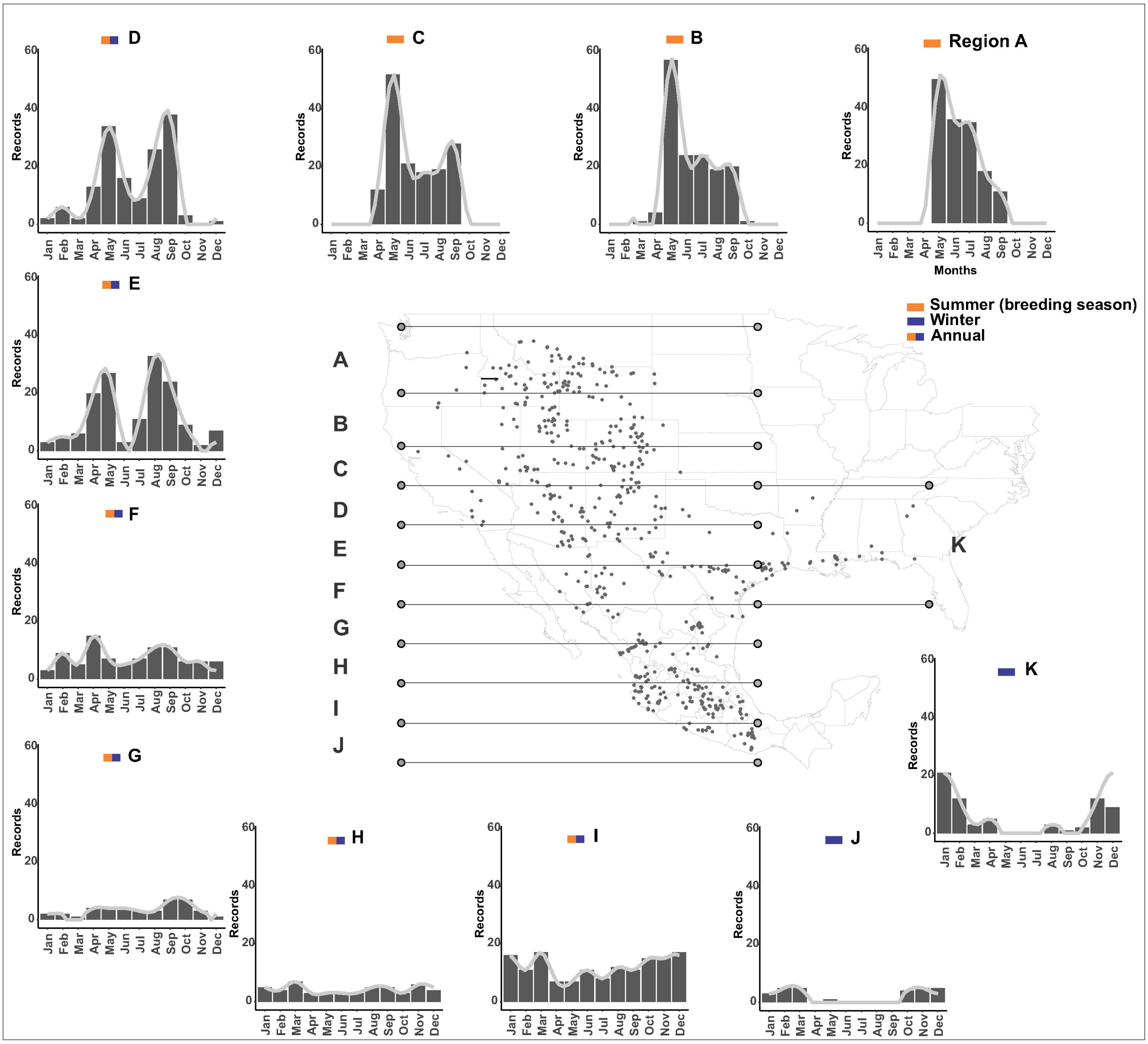

Fig. 1. Geographical space of the records of *Selasphorus platycercus*, showing the 11 segments with letters from A to K. The graphs represent the records by segment along the months of the year.

model fit and simplicity, in terms of the AICc, as adapted and implemented for MaxEnt by Warren and Seifert (2011). We divided the occurrence data into 80% for model calibration and 20% for model evaluation. In kuenm, models are selected as optimal when they are statistically significantly better than random in their predictions of the evaluation subset of occurrence data (*i.e.*, $P \leq 0.05$), present low omission error (*i.e.*, false-negative rate ≤ E) and are within 2 AICc units of the minimum AICc value among the models that are both significant and high-performing (Cobos et al. 2019). We explored two sequences of values of the regularization multiplier: from 0.1 to 1, using 0.1 as the increased unit, and from 2 to 6, using 1 as the increased unit. We allowed six combinations of features ("q", "p", "lq", "lp", "qp", "lqp") and no extrapolation or clamping for transfers (Owens et al. 2013). Once we obtained the ten best models for each model exercise, we used the median of those replicates as a better indicator of the highest frequency in the distribution, rather than the mean, which is affected by extreme values. The final models obtained in MaxEnt are probabilistic maps (cloglog format). We transformed them into binary maps (presence = 1 and absence= 0) using a cut-off threshold at the 10th percentile training presence to generate final distribution maps. Therefore, 10% of the records with the lowest probability values of MaxEnt were excluded (Phillips et al. 2006).

Species distribution modeling follows the BAM reference framework (Soberón and Peterson 2005), which establishes that the geographic distribution area occupied by a species (Go) is the conjunction of the appropriate regions in terms of abiotic conditions (A), biotic factors (B) and areas accessible by dispersion over relevant periods (M). We defined the same factor M using the sum of the historically known distribution, which includes the breeding and the winter ranges. All the climatic variables used were bound to this area.

Ecological similitude

We reconstructed the ecological niche via ENM in each season and identified their distribution area via SDM with optimal environmental conditions. Then, we projected the ecological niches to the other season to evaluate whether during the breeding season the populations follow the same climatic conditions of the winter season and vice versa. However, before the transfers, it is necessary to evaluate whether the environmental conditions between areas are climatically analogous (Owens et al. 2013). Thus, we measure the climatic analogy between breeding and winter conditions using the MESS (Multivariate Environmental Similarity Surface) test implemented in MaxEnt. MESS identifies sites of strict extrapolation and provides an index between the value of each pixel and the median of the most dissimilar variable (Elith et al. 2010).

We also measured the degree of niche similarity between both temporal scenarios (breeding and winter seasons) using the “PCA-env option” from the “ecospat” R package (Bröennimann et al. 2012; Di Cola et al. 2017). A kernel smoother is applied to densities of species occurrence within a gridded environmental space calibrated on the available environmental space. In this case, the observed D metric (Schoener 1970) measures the degree of niche overlap between the niches of these seasons. In each case, the observed D metric is compared with a random subset for 100 iterations generated in the other season and vice versa in the gridded environmental space ($D = 1$: complete overlap; $D = 0$: no overlap). This distribution of overlap is then compared to the observed D metric. Observed D’s greater than the null distribution indicate that the environmental niche models (ENM) are more similar than expected given their geographic ranges, while values significantly less than the null distribution indicate ENMs divergence (*i.e.*, dissimilar). A non-significant result from the similarity test indicates insufficient statistical power to determine either way. Niche similarity analyses were performed using the ecospat package (Di Cola et al. 2017) in R. We tested for niche differentiation, so we used the one-tailed test using the alternative *lower*, *i.e.*, the niche overlap is more dissimilar than would be expected by chance. We used rand.type = 1 since there was no assumption regarding a reference niche.

RESULTS

Latitudinal and longitudinal patterns of presence

As a result of the division of the geographic space, a total of 11 segments possessing unique records of presence were obtained (Fig. 1). The number of records per month for each segment showed that the northernmost segments, A, B, and C, were in the Western United States and were exclusively associated with the summer months. In contrast, the southernmost segment, J (in Southern Mexico), and the easternmost segment, K (on the Gulf Coast in the Southeastern United States), were exclusively associated with the winter months. The intermediate segments D–H (from the north to the center-south of Mexico) were associated with a gradual latitudinal change between the north and the south of the total distribution of the species and coincidentally with a seasonal transition between summer and winter. Finally, and notably, segment I (Central Mexico) presented a more equitable distribution of records during all months of the year (Fig. 2).

Seasonal distribution using ecological niche models and species distribution modeling

The information derived from the models represents the geographic areas with optimal environmental conditions under which different species can potentially be present (Peterson et al. 2011). The summer niche model projected geographically with an extension of 4,759,288 pixels did not predict winter conditions, while the winter model with 3,649,397 pixels predicted 5,508 summer pixels (Table 1, Fig. 3). Analysis using MESS indicated that the extreme northern areas of the United States are areas of strict extrapolation (optimal environmental conditions outside the ranges of values present in the calibration area of this species; Appendix 1).

The niche similarity test between the seasonal models (Fig. 4) showed an observed similarity index $D = 0.004$ (summer versus winter; $p = 0.9604$) and $D = 0.001$ (winter versus summer; $p = 0.9505$); and both were non-significant ($p > 0.05$) considering the similarity index on the basis of null expectations. For both cases, niche overlap falls within the 95% confidence limits of the null distributions; thus, the observed D values can be randomly obtained and therefore there is no significant climatic niche similarity among seasons.

DISCUSSION

The distribution patterns of species are traditionally described using geographical or political features, minimizing the historical and ecological processes responsible for shaping these patterns (Peterson 2001; Peterson et al. 2002). However, the analysis of the longitudinal and latitudinal patterns of the presence records based on the division of the geographic space into segments and considering the registration dates facilitated the recognition of the geographic and seasonal changes in the studied populations. This process made it possible to identify the breeding areas of *Selasphorus platycercus*, located in the northwestern section of the United States in contrast with the eastern region (segment K), as an exclusive winter area. These results suggest an outstanding long-distance longitudinal migration event.

On the other hand, toward the south of the range of the species, populations gradually change seasonally until finding exclusively winter areas in the

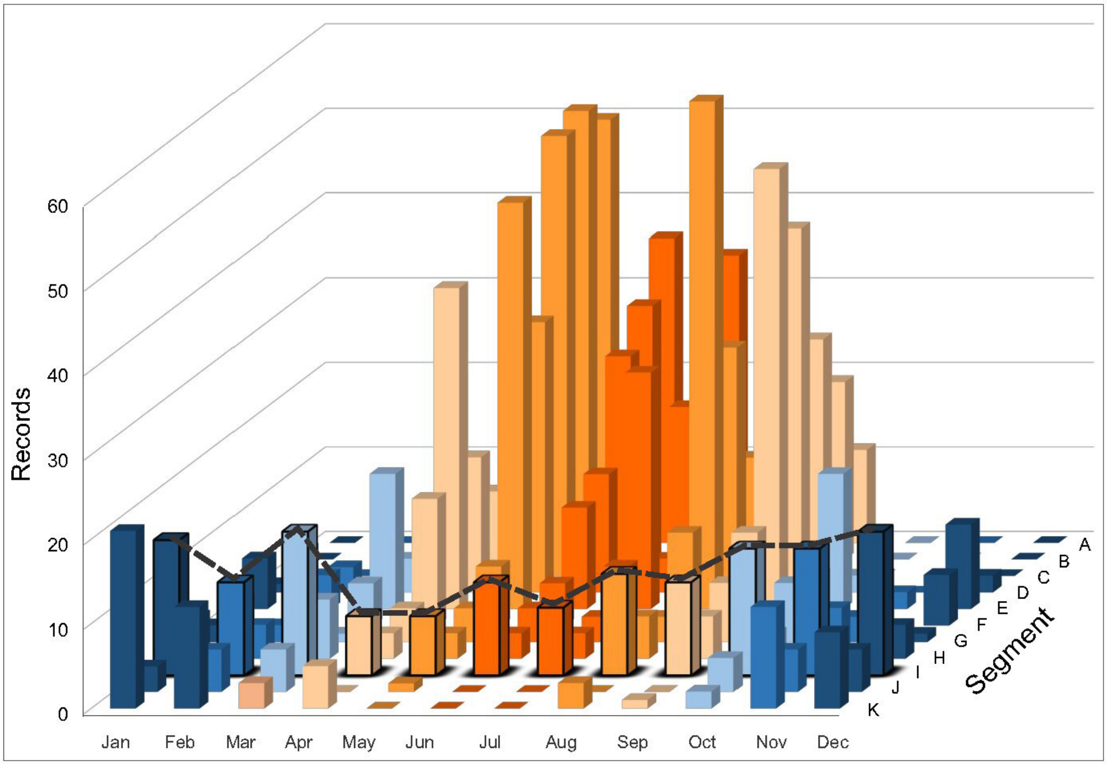

Fig. 2. Frequency of records in the different geographic segments (A-K from north to south) during the year. The dashed line corresponds to segment I.

extreme south, describing the typical long-distance latitudinal migration of *S. platycercus*. In the region corresponding to the Mexican Volcanic Belt (segment I), the presence of the species was recorded throughout the year, a finding that suggests that in this region, both resident (annual presence) and winter migratory populations (winter migratory populations return to the north in summer) can be found. However, in this area, evidence from field studies about populations that reproduce locally (during the summer) and migrate in the winter was obtained (Lara C. unpublished data). These populations possibly present a short distance type of migration in which they breed locally and migrate longitudinally or altitudinally within this same segment or migrate latitudinally toward southern segments in winter. However, the scale of our study did not allow the identification of this type of movement since analysis on a finer scale is required.

The different observed migratory patterns of *S. platycercus* suggest that the movements of its populations are probably differentially influenced by climatic variations (through seasonality) throughout its distribution. For example, previous studies have shown that breeding populations in the U.S. and northern Mexico move south for winter and are usually absent from the northern portions of their range by the end

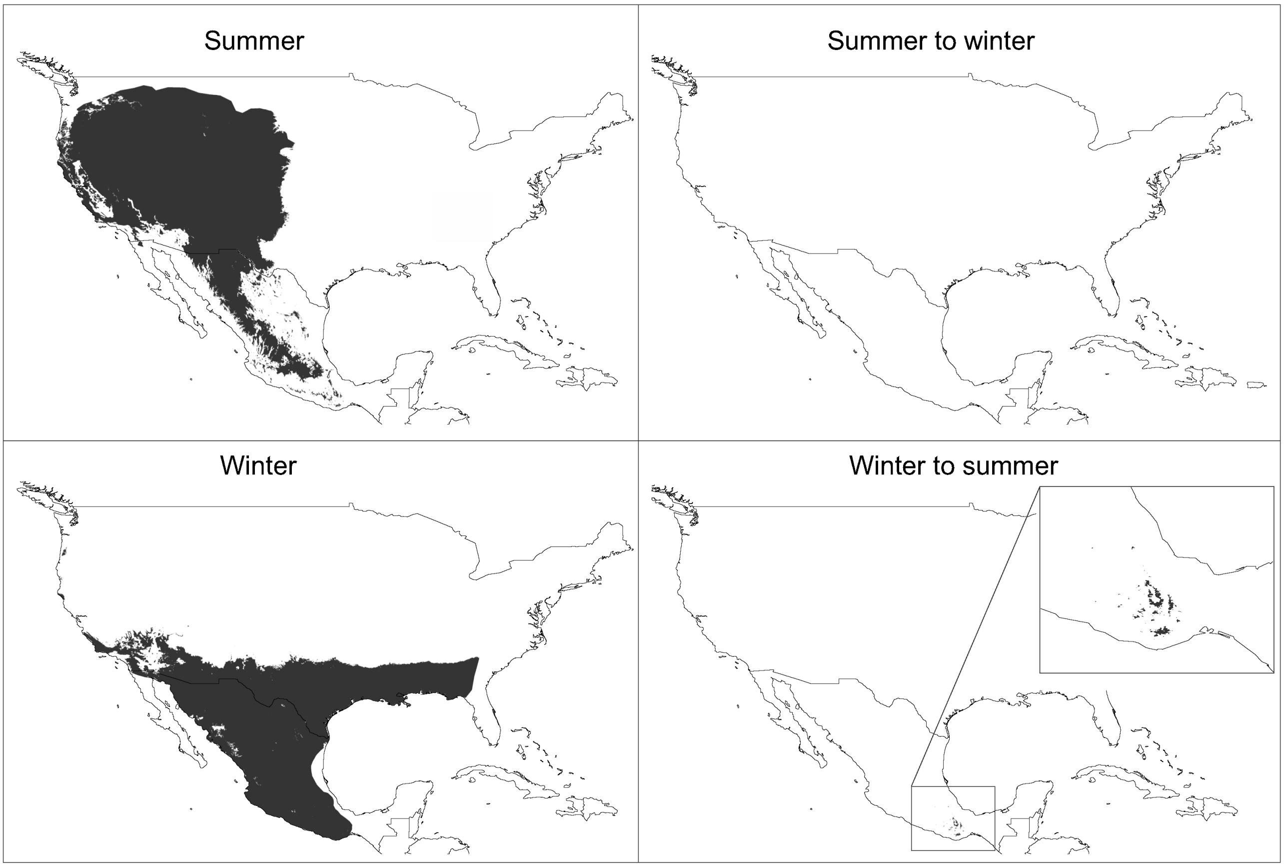

Fig. 3. Ecological niche models (in gray) of the summer seasons and their projection into winter (which result as null projection); from winter with its projection to summer, we show the projected area from winter to summer in an enlarged box.

Table 1. Values obtained from kuenm, pixel number of the binary map (10th percentile threshold), AUC value, AUC radio value, alloprediction (pixel count from one season projected to the opposite season), regularization multiplier and feature (l = linear, q = quadratic)

	Pixel number	AUC	AUC ratio	Allopredicction	Regularization multiplier	Feature
Summer	4,759,288	0.8	1.183	0	0.4	lq
Winter	3,649,397	0.8	1.395	5,508	8	q

of September and from the southern U.S. by October. Conversely, northward migration through the south of the U.S. in the spring occurs during late February to mid-April, allowing for arrival on northern breeding areas around mid-May (Camfield et al. 2013). These movements not only involve facing a wide variety of habitat types, including open woodland, especially pinyon-juniper, pine-oak, and conifer-aspen associations (Camfield et al. 2013), but rather the climatic ranges related to these. Some studies have tried to explain the role of geographic variations in the migratory patterns of different species, finding that these migratory patterns can also significantly affect the variations in reproductive parameters on which the fitness of the populations depends (*e.g.*, Bell 1996; Mérő et al. 2015). In the case of *S. platycercus*, the populations of different geographical areas have been ecologically and differentially established, both in the reproductive

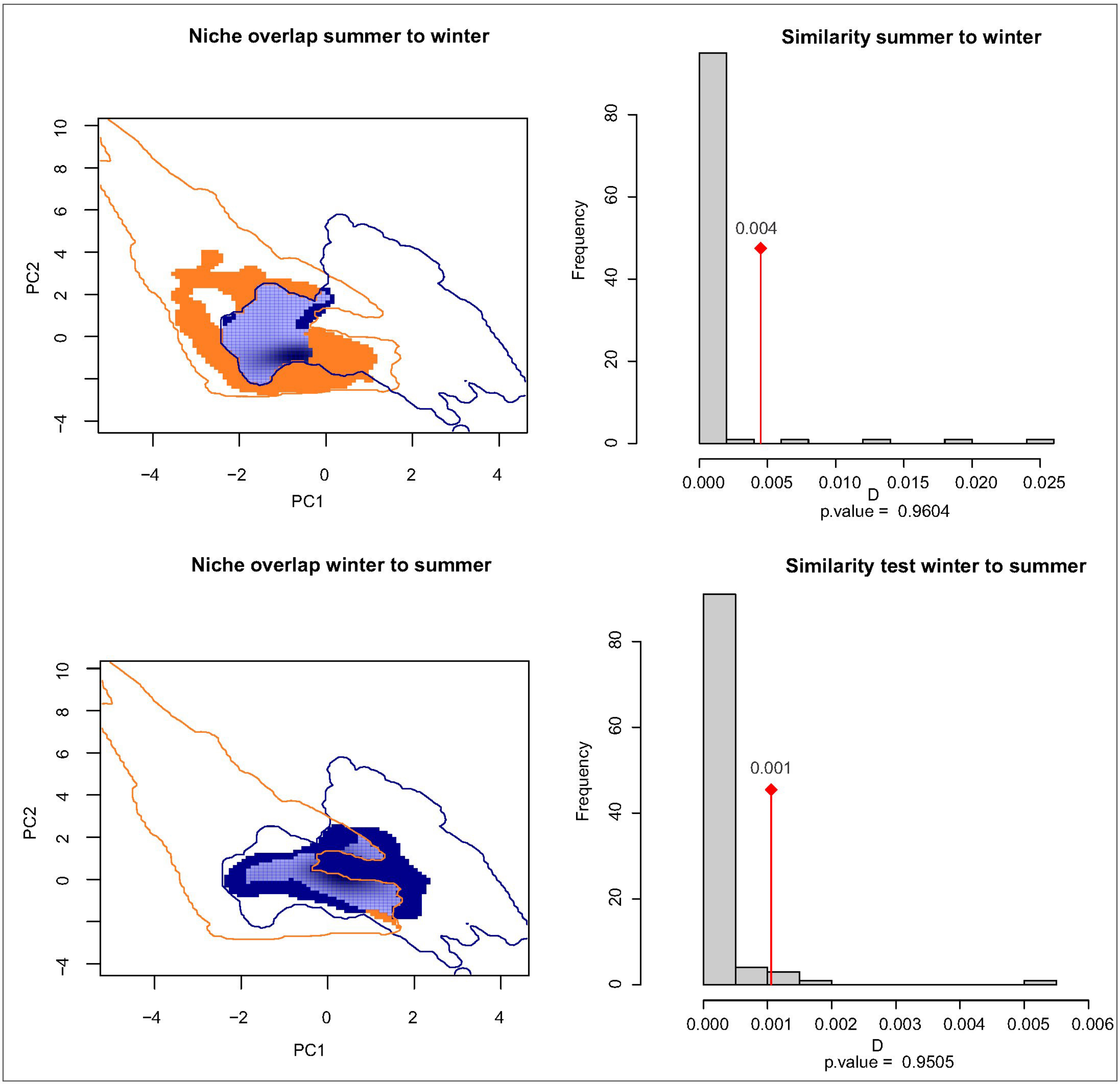

Fig. 4. Niche comparison based on the first two principal components between summer (orange) and winter (blue) seasons. The colored cells indicate the niche area with the highest density presence records, the overlap between the two environments is shown in blue. The polygon represents the availability of the environment for each season. Histograms show the observed overlap between the two environments (red line) and the overlap of simulated niches (gray bars). In both cases, the *p*-value was significant; that is, the null hypothesis that the niches are different in both directions (summer to winter and vice versa) cannot be rejected.

season (summer) and in the winter season as has already been suggested for other species (Hedenström 2008). For example, during winter, some populations are found at higher altitude areas (such as in the Mexican Volcanic Belt). In contrast, others are distributed in lowlands (such as on the eastern coasts of Mexico and the United States). Similar behaviors have been observed concerning other migratory species of hummingbirds, such as *S. rufus*, *S. sasin*, and *Stellula calliope* (Phillips 1975; Calder 1993; Calder and Calder 1994). The similarities with these species could even have a phylogenetic component (Licona-Vera and Ornelas 2014 2017).

For *S. platycercus*, based on the niche similarity test, we can conclude that there is no significant climatic niche similarity (Di Cola et al. 2017) between summer and winter niches, given the environments of the areas and the seasons that were compared. That is, it is possible a selection of different environmental conditions between seasons during their migratory cycle. This selection could confer certain evolutionary advantages to populations (Lincoln et al. 1998). A particular case of these advantages has been demonstrated in several species of hummingbirds. It has been suggested that migration has caused an increase in the size of the niche (Battey 2015). Or, as indicated by Williamson and Witt (2021), the various forms of migration evolved to take advantage of the seasonal pulses of resources. Although no genetic differences were found within this lineage, Malpica and Ornelas (2014) described that migratory hummingbirds were larger than sedentary hummingbirds, probably favored by climatic conditions that have been recognized as a factor that differentiates geographic groups in other hummingbirds (*e.g.*, Licona-Vera and Ornelas 2014 2017; Licona-Vera et al. 2018; Godwin et al. 2020; Myers et al. 2021; Rodríguez-Gómez et al. 2021), showing an acceptable predictive value. However, long-distance migratory populations do not follow the same conditions between the reproductive and winter seasons could suggest a greater complexity about the origin of migratory populations. The idea that most of the migratory populations recently originated from sedentary populations in Central Mexico due to climatic events during the last interglacial period (Malpica and Ornelas 2014), could be complemented with another set of evidence that explains the divergence of niches between the reproductive and winter seasons (*e.g.*, Zink and Gardner 2017). In this sense, the fact that the Trans-Mexican Volcanic Axis is a site with long-distance populations that visit during the winter, residents and probably summer breeding populations that migrate during the winter stands out. These characteristics make the area potentially important and highlight the need to continue studying seasonal movements on a finer scale, which would help clarify local seasonal presence patterns and the origin and evolution of migration in *S. platycercus*.

Our analysis assumed that the sample we used (n = 1176 occurrence records) was representative of the accurate spatial distribution patterns of broad-tailed hummingbirds during migration. Still, the lack of metadata on the annual occurrence of this hummingbird species through its distribution makes it impossible to infer the results to all populations of the species. Our scope of inference is thus limited to the hummingbird records used in this study. Several biases are likely to present. First, our data were analyzed, excluding the populations from the subspecies *S. p. guatemalae*. Thus, our data may misrepresent the accurate distributions of all *S. platycercus* populations during migration. Second, this spatial misrepresentation problem is exacerbated because we have no data supporting the described behaviors related to the reported migration patterns, only occurrence data from public databases. Thus, our results could be entirely driven by the frequency of records in some regions of its distribution and confounded by records in the eastern United States potentially related to recent expansion and misidentifications by data collectors. Although these limitations are important, they do not necessarily preclude studying the relative differences among populations during migration. For the last few years, citizen science observations have made around 50% of the biodiversity knowledge on the GBIF network (Troudet et al. 2017). For example, the eBird dataset is by far the most significant contributor. However, despite these efforts, it is a fact that knowledge about the migratory patterns of hummingbirds is still scarce in the literature, which renders our analysis a reasonable first attempt at estimating these parameters.

Even though no major threats are known to the Broad-tailed Hummingbird, global change impacts are particularly pressing in the case of migratory species, which are forced to shift their migratory behaviors in response to changes in the suitability of their breeding and wintering habitats (Wilcove and Wikelski 2008). For example, in the U.S., McKinney et al. (2012) showed that climate change affects the phenology of hummingbird nectar resources. These authors characterized west-central Colorado as near the northern limit of the breeding range and suggested that continued climate change could make the area unsuitable for broad-tailed hummingbird breeding. They indicated that this climate-change-driven phenological alteration, combined with increased warming at lower latitudes, could result in an overall shrinkage of the species' breeding range through a contraction at the northern end of the range. These behavioral changes can affect these species' interactive networks throughout their migratory routes (Bauer and Hoye 2014). In the case of hummingbirds, it has been shown that migrant species are vital players that increase plant-hummingbird network cohesiveness by interacting with a diverse set of plant species (Martín-González et al. 2018; Magrach et al. 2020). Thus, obtaining information on climate preferences of the niche that shape the migratory movements of hummingbirds through their distribution is of great importance due to possible impacts on many other species, including plants and other pollinators, given the interdependencies of species within natural communities.

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Availability of data and materials: The original datasets analyzed for this study can be found in the platform GBIF: https://doi.org/10.15468/dl.g3naz6.

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REFERENCES

Anderson RP, Lew D, Peterson AT. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol Modell **162:**211–232. doi:10.1016/S0304-3800(02)00349-6.

Arizmendi MC. 2001. Multiple ecological interactions:nectar robbers and hummingbirds in a highland forest in Mexico. Can J Zool **79:**997–1006. doi:10.1139/z01-066.

Arizmendi MC, Berlanga H. 2014. Colibríes de México y Norteamérica. CONABIO. México, 160 pp.

Battey CJ. 2015. Migration Increases Niche Breadth in North American Hummingbirds. Electron J Appl Multivar Stats **8:**1–10.

Bauer S, Hoye BJ. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science **344:**1242552. doi:10.1126/science.1242552.

Bell CP. 1996. The relationship between geographic variation in clutch size and migration pattern in the yellow wagtail. Bird Study **43:**333–341. doi:10.1080/00063659609461026.

Bröennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Graham CH. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr **21:**481–497. doi:10.1111/j.1466-8238.2011.00698.x.

Calder WA. 1987. Southbound through Colorado: migration of rufous hummingbirds. Natl Geogr Res **3:**40–51.

Calder WA. 1993. Rufous hummingbird (*Selasphorus rufus*). *In*: Poole A, Gill F (Eds.), The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Calder WA. 2004. Rufous and broad-tailed hummingbirds Pollination, migration, and population biology. Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, Arizona, USA.

Calder WA, Calder LL. 1994. Calliope hummingbird (*Stellula calliope*). *In*: Poole A, Gill F (Eds.), The Birds of North America, No. 135, Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.

Camfield AF, Calder WA, Calder LL. 2013. Broad-tailed Hummingbird (*Selasphorus platycercus*). *In*: Poole AF (Ed.), The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Chesser RT, Levey DJ. 1998. Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. Am Nat **152:**311–319. doi:10.1086/286171.

Cobos ME, Peterson AT, Barve N, Osorio-Olvera L. 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ **7:**e6281. doi:10.7717/peerj.6281.

Di Cola V, Bröennimann O, Petipierre B, Breiner FT, D'Amen CR, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A. 2017. Ecospat: and R package to support spatial analyses and modeling of species niches and distributions. Ecography **40:**774–787. doi:10.1111/ecog.02671.

Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. Methods Ecol Evol **1:**330–342. doi:10.1111/j.2041-210X.2010.00036.x.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol **37:**4302–4315. doi:10.1002/joc.5086.

Global Biodiversity Information Facility (GBIF). 2021. Available at: http://data.gbif.org/species. *Selasphorus platycercus*. Accessed 3 Feb. 2021.

Godwin BL, LaCava ME, Mendelsohn B, Gagne RB, Gustafson KD, Stowell SML, Engilis A Jr, Tell LLA, Ernest HB. 2020. Novel hybrid finds a peri-urban niche: Allen's Hummingbirds in southern California. Conserv Genet **21:**989–998. doi:10.5061/dryad.zgmsbcc84.

Gómez C, Tenorio EA, Montoya P, Cadena CD. 2016. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). Proc Royal Soc B **283:**20152458. doi:10.1098/rspb.2015.2458.

González-García JM, Lara C, Quesada J, Chávez-Zichinelli CA, Serrano-Meneses MA. 2018. Superciliums in white-eared hummingbirds as badges of status signaling dominance. Sci Nat **105:**31. doi:10.1007/s00114-018-1553-1.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. Ecol Lett **8:**993–1009. doi:10.1111/j.1461-0248.2005.00792.x.

Hagan JM III, Johnston DW. 1995. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C. USA.

Hedenström A. 2008. Adaptations to migration in birds: behavioral strategies, morphology, and scaling effects. Philos Trans R Soc Lond, B Biol Sci **363:**287–299. doi:10.1098/rstb.2007.2140.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high-resolution interpolated climate surfaces for global land areas. Int J Climatol **25:**1965–1978. doi:10.1002/joc.1276.

Jahn AE, Cueto VR, Fontana CS, Guaraldo AC, Levey DJ, Marra P, Ryder TB. 2020. Bird migration within the Neotropics. The Auk **137:**1–23. doi:10.1093/auk/ukaa033.

Kaufman K. 2005. Kaufman field guide to birds of North America. Houghton Mifflin Harcourt, USA.

Lara C. 2006. Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. Ecoscience **13:**23–29. doi:10.2980/1195-6860(2006)13[23:TDOFUB]2.0.CO;2.

Laube I, Graham CH, Böhning-Gaese K. 2015. Niche availability in space and time: migration in *Sylvia* warblers. J Biogeogr **42:**1896–1906. doi:10.1111/jbi.12565.

Licona-Vera Y, Ornelas JF. 2014. Genetic, ecological, and morphological divergence between populations of the endangered Mexican Sheartail Hummingbird (*Doricha eliza*). PLoS ONE **9(7):**e101870. doi:10.1371/journal.pone.0101870.

Licona-Vera Y, Ornelas JF. 2017. The conquering of North America: dated phylogenetic and biogeographic inference of migratory behavior in bee hummingbirds. BMC Evol Biol **17:**1–17. doi:10.1186/s12862-017-0980-5.

Licona-Vera Y, Ornelas JF, Wethington S, Bryan KB. 2018. Pleistocene range expansions promote divergence with gene flow between migratory and sedentary populations of *Calothorax* hummingbirds. Biol J Linn Soc **124:**645–667. doi:10.1093/biolinnean/bly084.

Lincoln C, Fredrick C, Peterson SR, Zimmerman JL. 1998. Migration of birds. Washington, DC: United States Fish and Wildlife Society.

Magrach A, Lara C, Luna, UM, Díaz-Infante S, Parker I. 2020. Community-level reorganizations following migratory pollinator dynamics along a latitudinal gradient. Proc Royal Soc B **287:**20200649. doi:10.1098/rspb.2020.0649.

Malpica A, Ornelas JF. 2014. Postglacial northward expansion and genetic differentiation between migratory and sedentary populations of the broad-tailed hummingbird (*Selasphorus platycercus*). Mol Ecol **23:**435–452. doi:10.1111/mec.12614.

Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005. The influence of climate on the timing and rate of spring bird migration. Oecologia **142:**307–315. doi:10.1007/s00442-004-1725-x.

Martín-González AM, Ornelas JF, Dalsgaard B, Márquez-Luna U, Lara C. 2018. Meta-networks for the study of biogeographical traits in ecological networks: the Mexican hummingbird-plant assemblage. Sci Nat **105:**1–11. doi:10.1007/s00114-018-1578-5.

McKinney AM, CaraDonna PJ, Inouye DW, Barr B, Bertelsen CC, Waser NM. 2012. Asynchronous changes in phenology of migratory broad-tailed hummingbirds and their early-season nectar resources. Ecology **93:**1987–1993. doi:10.1890/12-0255.1.

Mérő TO, Žuljević A, Lengyel S. 2015. Latitudinal, longitudinal, and weather-related variation in breeding parameters of Great Reed Warblers in Europe: a meta-analysis. Bird Study **62:**411–416. doi:10.1080/00063657.2015.1042357.

Myers BM, Burns KJ, Clark CJ, Brelsford A. 2021. The population genetics of nonmigratory Allen's Hummingbird (*Selasphorus sasin sedentarius*) following a recent mainland colonization. Ecol Evol **11:**1850–1865. doi:10.1002/ece3.7174.

Nakazawa Y, Peterson, AT, Martínez-Meyer E, Navarro-Sigüenza AG. 2004. Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. The Auk **121:**610–618. doi:10.2307/4090425.

Németh Z, Moore FR. 2012. Differential timing of spring passage of Ruby-throated Hummingbirds along the northern coast of the Gulf of Mexico. J Field Ornithol **83(1):**26–31. doi:10.1111/j.1557-9263.2011.00352.x.

Newton I. 2008. The Migration Ecology of Birds. Elsevier, London, UK.

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Peterson AT. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Modell **263:**10–18. doi:10.1016/j.ecolmodel.2013.04.011.

Papes M, Peterson AT, Powell GV. 2012. Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling. J Biogeogr **39(4):**652–664. doi:10.1111/j.1365-2699.2011.02632.x.

Peña-Peniche A, Ruvalcaba-Ortega I, Rojas-Soto O. 2018. Climate complexity in the migratory cycle of *Ammodramus bairdii*. PLoS ONE **13(8):**e0202678. doi:10.1371/journal.pone.0202678.

Pérez-Moreno H, Martínez-Meyer E, Soberón J, Rojas-Soto O. 2016. Climatic patterns in the establishment of wintering areas by North American migratory birds. Ecol Evol **6:**2022–2033. doi:10.1002/ece3.1973.

Peterson AT. 2001. Predicting 'Species' Geographic Distributions Based on Ecological Niche Modeling. The Condor **103:**599–605. doi:10.1650/0010-5422(2001)103[0599:PSGDBO]2.0.CO;2.

Peterson AT, Ball LG, Cohoon KP. 2002. Predicting distributions of Mexican birds using ecological niche modelling methods. Ibis **144:**E27–E32. doi:10.1046/j.0019-1019.2001.00031.x.

Peterson AT, Papes M, Soberón J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecoll Modell **213:**63–72. doi:10.1016/j.ecolmodel.2007.11.008.

Peterson AT, Soberón J. 2012. Species distribution modeling and ecological niche modeling: getting the concepts right. Nat Conserv **10(2):**102–107. doi:10.4322/NATCON.2012.019.

Peterson AT, Soberón J, Pearson R, Martinez-Meyer E, Nakamura M, Araujo M. 2011. Ecological niches and geographical distributions. Princeton University Press. USA.

Phillips AR. 1975. The migrations of Allen's and other hummingbirds. The Condor **77:**196–205. doi:10.2307/1365790.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol Modell **190:**231–259. doi:10.1016/j.ecolmodel.2005.03.026.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Rappole JH. 1995. The ecology of migrant birds: A Neotropical perspective. Smithsonian Institution Press, Washington D.C., USA.

Rodríguez-Gómez F, Licona-Vera Y, Silva-Cárdenas L, Ornelas JF. 2021. Phylogeography, morphology and ecological niche modelling to explore the evolutionary history of Azure-crowned Hummingbird (*Amazilia cyanocephala*, Trochilidae) in Mesoamerica. J Ornithol **162:**529–547. doi:10.1007/s10336-020-01853-x.

Ruíz-Sánchez A, Renton K, Landgrave-Ramírez R, Mora-Aguilar EF, Rojas-Soto O. 2015. Ecological niche variation in the Wilson's warbler (*Cardellina pusilla*) complex. J Avian Biol **46:**516–527. doi:10.1111/jav.00531.

Saupe EE, Barve V, Myers CE, Soberón J, Barve N, Hensz CM, Lira-

Noriega A. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. Ecol Modell **237:**11–22. doi:10.1016/j.ecolmodel.2012.04.001.

Schoener TW. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology **51:**408–418. doi:10.2307/1935376.

Schondube JE, Martínez del Rio C. 2004. Sugar and protein digestion in flower-piercers and hummingbirds: a comparative test of adaptive convergence. J Comp Physiol B **174:**263–273. doi:10.1007/s00360-003-0411-3.

Schuchmann KL. 1999. Family Trochilidae (Hummingbirds). Handbook of the birds of the world **5:**468–680.

Soberón JM, Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform **2:**1–10. doi:10.17161/bi.v2i0.4.

Somveille M, Rodrigues AS, Manica A. 2015. Why do birds migrate? A macroecological perspective. Glob Ecol Biogeogr **24:**664–674. doi:10.1111/geb.12298.

Somveille M, Bay RA, Smith TB, Marra PP, Ruegg KC. 2021. A general theory of avian migratory connectivity. Ecol Lett **24:**1848–1858. doi:10.1111/ele.13817.

Terborgh J. 1989. Where have all the birds gone?: Essays on the Biology and Conservation of birds that migrate to the American tropics. Princeton University Press, New Jersey, USA.

Toews DPL. 2017. Habitat suitability and the constraints of migration in New World warblers. J Avian Biol **48:**1614–1623. doi:10.1111/jav.01157.

Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F. 2017. Taxonomic bias in biodiversity data and societal preferences. Sci Rep **7:**1–14. doi:10.1038/s41598-017-09084-6.

Vuilleumier F. 2011. Birds of North America. Eastern region. American Museum of Natural History. New York: DK Pub.

Warren D, Seifert S. 2011. Ecological niche modeling in MaxEnt: the importance of model complexity and the performance of model selection criteria. Ecological Applications **21:**335–342. doi:10.1890/10-1171.1.

Wilcove DS, Wikelski M. 2008. Going, going, gone: Is animal migration disappearing. PLoS Biology **6:**e188. doi:10.1371/journal.pbio.0060188.

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol Evol **17:**76–83. doi:10.1016/S0169-5347(01)02380-1.

Williams HM, Willemoes M, Thorup K. 2017. A temporally explicit species distribution model for a long-distance avian migrant, the common cuckoo. J Avian Biol **48:**1624–1636. doi:10.1111/jav.01476.

Williamson JL, Witt CC. 2021. Elevational niche-shift migration: Why the degree of elevational change matters for the ecology, evolution, and physiology of migratory birds. Ornithology **138:**1–26. doi:10.1093/ornithology/ukaa087.

Zenzal Jr TJ, Moore FR. 2016. Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration. The Auk **133(2):**237–250. doi:10.1642/AUK-15-160.1.

Zenzal Jr TJ, Moore FR, Diehl RH, Ward MP, Deppe JL. 2018. Migratory hummingbirds make their own rules: The decision to resume migration along a barrier. Animal Behav **137:**215–224. doi:10.1016/j.anbehav.2018.01.019.

Zink RM. 2002. Towards a framework for understanding the evolution of avian migration. J Avian Biol **33:**433–436. doi:10.1034/j.1600-048X.2002.03081.x.

Zink RM, Gardner AS. 2017. Glaciation as a migratory switch. Sci Adv **3(9):**e1603133. doi:10.1126/sciadv.1603133.

Supplementary Materials

Appendix 1. MESS (Multivariate Environmental Similarity Surface) analysis. (download)