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ABSTRACT

Natural history museum collections (NHCs) represent a rich and largely untapped source of data on demography and population movements. NHC specimen records can be corrected to a crude measure of collecting effort and reflect relative population densities with a method known as abundance indices. We plot abundance index values from georeferenced NHC data in a 12-month series for the new world migratory passerine *Passerina ciris* across its molting and wintering range in Mexico and central America. We illustrate a statistically significant change in abundance index values across regions and months that suggests a quasi-circular movement around its non-breeding range, and use enhanced vegetation index (EVI) analysis of remote sensing plots to demonstrate non-random association of specimen record density with areas of high primary productivity. We demonstrate how abundance indices from NHC specimen records can be applied to infer previously unknown migratory behavior, and be integrated with remote sensing data to provide a deeper understanding of demography and behavioral ecology across time and space.

INTRODUCTION

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Natural history museum collections (NHCs) represent a rich and largely untapped source of data on demography, behavioral ecology, and population movements. (Lister and Group 2011, Suarez and Tsutsui 2004). Housed in museums and herbaria worldwide, NHCs are unique among extant biological datasets in their breadth, depth, and, for the most part, in lacking biases intrinsic to data collected for a specific research goal. NHCs are particularly valuable in that the oldest specimens in collections predate even the longest running ecological surveys (Magurran et al. 2010), and that the majority of specimens are associated with detailed provenance data (Lister and Group 2011). The combination of these records into sortable databases spanning multiple institutions provides an invaluable resource in approaching a wide range of biological questions through careful scrutiny and meta-analysis.

NHCs have traditionally been used to assess biogeographic range changes (Boakes et al. 2010), phenological shifts (Robbirt et al. 2011), hybridization (Rohwer and Wood 1998) and evolutionary change in morphology. Applications of molecular techniques to NHCs have extracted DNA from historic specimens to use in phylogenetic analyses (Paabo et al. 2004), performed stable isotope analyses to track diet and migration in birds (Inger and Bearshop 2008), and examined environmental contamination through trace element analysis (Berg et al. 1966, Hickey and Anderson 1968). While specimen collections have obvious utility in addressing questions of population biology, particularly in gaining access into otherwise-unknown historical population dynamics, a major shortcoming of these data is the absence of information on collecting effort associated with any individual specimen.

One method of overcoming this shortcoming is the application of indices that are corrected to a crude measure of effort (Miki et al. 2000, Barry et al. 2009). These abundance indices are calculated by use of electronic natural history museum catalogs (such as VertNet.org) to aggregate records of specimens from a particular region and time period that are expected to have been collected in a similar manner to the focal species of a study. Abundance indices have been successfully applied to show molt migration (Barry et al. 2009), population dynamics in medicinal plants (Miki et al. 2000), and in assessing migratory double-breeding (Rohwer et al. 2012) and changes in community composition from massive environmental pertubations (Rohwer et al. 2015). A logical extension of these analyses is to examine spatial and temporal changes in abundance index values to infer month-to-month population-level movements, where

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technology, cost and unpredictable behavior often prohibit geotagging individuals. However, such use of aggregated collection records remains untested.

Here, we demonstrate how abundance indices can be applied to infer population-level movements from month to month across a migratory species' non-breeding range. We plot abundance index values from georeferenced NHC data in a 12-month series for the new world migratory passerine *Passerina ciris* across its molting and wintering range in Mexico and central America. We illustrate a statistically significant change in abundance index values across regions and months that suggests a quasi-circular movement around its non-breeding range, and use enhanced vegetation index (EVI) analysis of remote sensing plots to demonstrate non-random association of specimen record density with areas of high primary productivity.

METHODS

Study species. The Painted Bunting (*Passerina ciris*) is a migratory New World passerine in the family Cardinalidae. Current taxonomy recognizes two subspecies of Painted Bunting but the boundary between these races does not coincide with a nearly 500km gap separating the east coast and the Midwestern breeding populations of Painted Buntings (Thompson 1991). Further, these isolated breeding populations differ dramatically in their molt scheduling, with the eastern population molting on its breeding range prior to migration and the Midwestern population moving to the monsoon region of the southwestern United States and northwestern Mexico where it pauses to molt before proceeding to its wintering range in southern Mexico and Central America (Thompson 1991, Rohwer et al. 2005, V.G. Rohwer et al. 2009).

Across their range, Painted Buntings favor ecotones, brushy, weedy habitats in second growth, and dense forest understory. Relatively little is known in detail about the species' movements following molt stopover, but progressive southward movements of populations along the west coast of Mexico have been observed in the autumn (Rohwer 2014, pers. comm.; Contina et al. 2013).

Calculating Abundance Indices. To track spatial and temporal changes in Painted Bunting population densities during the wintering season, we employed a method of inferring relative population densities from specimen collections data known as Abundance Indices. The method, proposed in Rohwer et al. 2011 and developed independently by Miki et al. (2000), adjusts for a major shortcoming of specimen collections data -- the absence of associated information on collecting effort -- by producing an index that is corrected to a crude measure of effort. This index is calculated by using electronic natural history museum catalogs (such as VertNet.org) to aggregate records of specimens from a particular region and time period that are expected to have been collected in a manner similar to the methods used to collect the focal species of a study.

We used the formula for abundance index calculation proposed in Rohwer et al. (2015):

$$AI_{kr} = 100 \frac{x_{kr}}{\sum_{j=1}^{n} x_{jr}}$$

where x_{kr} is number of specimens of the k^{th} species collected in r, the region and time period of interest, and n is the number of specimens of all species that would be "expected" to be collected using the same methods in that region and time period of interest.

Reference data. In order to calculate abundance indices for Painted Buntings, we accessed two databases of specimen collection records: the Mexican Bird Atlas, and VertNet. The Mexican Bird Atlas began compilation by A. Navarro and T. Peterson in the 1990s, and now represents the most complete reference of study skins of Mexican birds residing in natural history museums worldwide (Navarro et al 2003). The Atlas now contains records of more than 370,000 specimens from 71 museums, and is completely georeferenced. We used records for the Mexican Bird atlas for all indices calculated within the political boundaries of Mexico. The VertNet data portal (vertnet.org) is an NSF-funded collaborative project to make biodiversity information, including specimen collections records, freely and easily accessible to the public. We also used records from VertNet to examine raw bunting counts by month for the Central American countries of Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Subsetting and data cleaning. We produced abundance indices for Painted Buntings for each month of the year. These indices were produced on a relatively fine spatial scale for Mexico (see section *GIS* below), but were only produced on a country-wide level for Central America, due to limitations in properly georeferenced in the VertNet data. To calculate abundance indices, we referenced Painted Bunting collections against the combined records of species collected using similar methods, as in Rohwer et al. 2012: Passerines (order Passeriformes), Cuckoos (order Cuculiformes), and Woodpeckers (order Piciformes; family Picidae).

While the majority of specimen collections records accessed from the Mexican Bird Atlas were both dated and georeferenced, a subset (<10% in both Painted Bunting and reference specimen data) had either missing or obviously erroneous values for date or latitude and longitude coordinates. These were excluded from all subsequent analyses.

Analyzing migration patterns. We used a Geographic Information Systems (GIS) approach to plot all specimen collections records from the Mexican Bird Atlas, for both Painted Buntings and reference specimens. A 5’ raster grid was initially overlayed on plotted reference specimens, which were then transformed into a scaled density map of all collected specimens in a particular region and month. In any grid square where Painted Bunting specimens were collected, an abundance index was calculated and plotted as a circle, its diameter proportional to the value of the index. While abundance indices were produced for Central America, we did not incorporate these into our geospatial analysis due to exceedingly few Painted Bunting specimens and corresponding low AI values.

To determine the statistical significance of any observed patterns of spatial and temporal change, we divided Mexico into three regions corresponding with contiguous bands of Painted Bunting habitat, (NW, NE, and S, defined by the 20th parallel north and the 103rd meridian West, respectively; **Figure 1**). Among these regions, we performed four Pearson’s chi-square tests for changes in abundance indices in Painted Buntings and reference specimens during three time periods: the molt-stopover period (July-October), winter (November-April), and spring migration (May and June). Specifically, we asked 1) whether Painted Bunting records were significantly more numerous than expected by chance (relative to reference specimens) in NW Mexico during the molting season; 2) whether Painted Bunting records were significantly more numerous than expected by chance in Southern Mexico during the winter; and 3) whether Painted Bunting records were significantly more numerous than expected by chance along the Gulf of Mexico during spring migration. While lacking resolution, this aggregated measure of abundance change allowed us to more rigorously test our interpretation of the direction of migration (**Figure 1**). Additionally, we performed a chi-square test to determine whether Painted Bunting records were significantly more numerous below 500m in elevation.

Finally, to provide additional ecological context to our findings, and offer evidence of a possible explanatory factor for population movement, we investigated the correlation between bunting abundance and primary productivity. We downloaded monthly means for the Enhanced Vegetation Index (EVI) compiled from 2000 to 2010 from the North American Vegetation Index and Phenology Lab website (http://vip.arizona.edu). We used EVI, as opposed to the more widely used Normalized Difference Vegetation Index (NDVI), as an index of primary productivity because of EVI's enhanced sensitivity in high biomass regions (such as the Painted Buntings' wintering sites) and its robustness against atmospheric influences (Liu and Huete, 1995; Matsushita et al., 2007). The downloaded data for each monthly mean consisted of a georeferenced HDF raster file at a 0.05° resolution. We extracted the EVI data layer and clipped it to the area of interest (Latitude: 10 to 40°, Longitude: -125 to -70°).

For each month, we extracted EVI values for pixels within a 10 km radius of each collection site. We included data from each specimen such that locations from which multiple specimens were collected were represented multiple times in the data set. We assume that collection sites that yielded multiple birds are indicative of the most suitable or desirable habitat for Painted Buntings, and that they should be overrepresented among all the collection sites when evaluating the correspondence between EVI and Painted Bunting distributions. The data extraction yielded an average of 10.3 pixels per collecting location (range = 3 to 14). Locations near coastlines often had fewer pixels than inland site as the EVI data did not extend into water bodies.

To test the simple null hypothesis that specimen locations for Painted Buntings were random with respect to EVI, we generated 500 uniformly random locations within the borders of Mexico and repeated the extraction process described above with each monthly EVI map and the 500 random points. Extractions from random locations yielded an average of 11.1 EVI pixels (range: 2 to 15).

We averaged the pixels from each location and then compared the set of EVI values for each month from the specimen locations to the corresponding EVI values associated with the random locations. We performed a t-test for each monthly data set and calculated 95% confidence intervals for each overall mean. Initial manipulation of EVI data was performed using the gdal translator library (http://www.gdal.org). All subsequent analysis were performed in R version 3.1.0 (R Core Team, 2014) with extensive use of the following packages: raster (Bivand

and Rundel, 2015), maptools (Bivand and Lewin-Koh, 2015), plyr (Wickham, 2011), rgeos (Bivand and Rundel, 2015), and ggplot2 (Wickham, 2009).

RESULTS

Migration analysis. Our plotted monthly abundance indices for *P. ciris* confirm a pattern of population-level movement across Mexico throughout the year (Figure 2). AI values plotted for July illustrate an east-west split during mid-summer, with high AI values forming two clusters in Northern Mexico: an eastern cluster in Nuevo Leon and Tamalpais, and a western cluster in Sinaloa and Durango. In August and September, these associations persist, with the western cluster increasing both by number of raster grid squares reporting an abundance index, and by value of plotted abundance indices. October, November, and December show the southward movement and diffusion of plotted AI values on both coasts of Mexico. Abundance indices again hug the states of both coasts, forming a loose western cluster in Guerrero, Michoacán, Oaxaca, Jalisco, and Colima, and a loose eastern cluster in the Veracruz, Tabasco, Campeche, and Yucatån. There is then no observable pattern in plotted AI values from January to April within or among these clusters, followed by a strong association of AI values in northeast Mexico (Coahuila, Nuevo Leon, Tamalpais) and an absence of values elsewhere in the month of May. South of Mexico, specimen records indicate the presence of Painted Buntings at extremely low densities, mostly restricted to the winter months of November to March. Pooled raw counts of buntings for all records in this region (including Belize, El Salvador, Honduras, Guatemala, Nicaragua, Costa Rica, and Panama) confirm the near absence ($n<10$ per month) of bunting specimens collected during the July-October stopover period (**Figure 3**).

Statistical tests. Our chi-sq tests confirm significantly higher Painted Bunting record density than expected for all four analyses. Painted Buntings were significantly more numerous in NW Mexico during the molt-stopover period than expected, compared to reference specimens (question 1; X-squared = 108.8395, df = 1, p-value < 2.2e-16), were significantly more numerous in southern than NW Mexico in the winter than reference specimens (question 2; X-squared = 122.772, df = 1, p-value < 2.2e-16), were significantly more numerous along the Gulf of Mexico than along the west coast of Mexico, compared to reference specimens during spring migration (question 3; X-squared = 63.6554, df = 1, p-value = 1.482e-15), and were significantly more numerous below 500m elevation (question 4; X-squared = 122.772, df = 1, p-value < 2.2e-16).

Remote sensing. For almost every month of the year, Painted Bunting collection sites in Mexico had higher EVI scores (i.e. higher primary productivity) than randomly generated locations within Mexico (**Figure 4**, $p < 0.01$). The only exceptions were May and June, when Painted Buntings are on their breeding grounds and are relatively scarce in Mexico. The highest monthly EVI average associated with the specimen data was from the month of October, which corresponds with high Painted Bunting densities in the states of Sinaloa and Sonora, where many if not most Painted Buntings undergo feather molt. It is also in the month of October that we observed the greatest difference between the mean EVI value for collection sites and for random sites.

DISCUSSION

The spatial and temporal changes in plotted abundance indices presented in **Figure 2** illustrate that an abundance index approach can be applied to NHC datasets to infer population-level movements across a species' range from month to month. The advantages of this approach in determining general trends within or among taxa are numerous. Analyzing spatial and temporal changes in abundance indices allows for the repurposing of a comprehensive and pre-existing source of species occurrence data into a tool for investigating questions about behavior and population movement. In doing so, the approach also circumvents the need for costly and potentially error-prone geologger tagging studies (Contina et al. 2013). Perhaps most importantly, the use of NHC datasets allows for the potential of describing *historical* population-level movements, phenomena that might otherwise go undescribed due to an absence of contemporary observers, and the disturbance of decades of anthropogenic pressure on populations and land-use change that may have changed historic movement patterns.

Our results also shed light on previously unconfirmed migratory behavior in *P. ciris.* The initial clustering of high AI values in July-September in northwestern Sinaloa (**Figure 2**) correlate to evidence of molt-migration stopover in agricultural habitats in NW Sinaloa for subspecies *P. c. pallidor* (Contina et al. 2013, Rohwer 2013, Rohwer et al. 2009, Rohwer et al 2005). We believe subsequent southward progression and diffusion visible in abundance index values across the southern half of Mexico from October to April is consistent with anecdotal observations by Rohwer (2015, pers comm) describing a complete absence of wintering Painted Buntings in regions where they had been previously been abundant during the molting period, as well as geologger tag and isotope evidence from Contina et al. (2013) of similar movement. The limited number of specimen records elsewhere in Central America provides additional support for this movement, as the timing of Painted Bunting presence in countries south of Mexico is consistent with a post molt-migration stopover arrival to the southern extent of the species' range (**Figure 3**). A reduction in individual grid-square AI values and increase in overall number of grid squares filled also correlates with expected migratory behavior: in the absence of sedentary behavior associated with molt stopover sites during molt-migration, and associated high population densities during this time period, individuals should move independently and avoid competition for limited resources. Finally, plotted AI values in May and June illustrate the high population densities in NE Mexico in the Gulf Coast migration corridor to be expected during spring migration through this region to breeding grounds in the United States.

Taken in sum, monthly plotted abundance indices (**Figure 2**) indicate a quasi-circular movement of *P. ciris* populations around coastal and Southern Mexico. We believe these patterns can be partially explained by the EVI analysis of remote sensing data presented in Figure 3. A period of peak live green vegetation in Mexico in the months of July - September correlates with the cluster of abundance indices representing the molt-migration stopover site in Sinaloa for *P. c. pallidor* identified for the same period in Figure 1. After a period of reduction in green vegetation from October - March, a second peak in live green vegetation in Mexico correlates with the location of *P. ciris* abundance indices in NE Mexico representing an increase in population densities in a migration corridor immediate prior to spring arrival on their principle midwestern breeding grounds in the United States.

EVI plots indicating peaks in live green vegetation can be thought of as a rough indicator of primary productivity and corresponding resource availability. *P. ciris* population densities therefore appear to shift in tangent with precipitation and plant growth, a logical correlation given *P. ciris* feeds primarily on grass seeds during the winter, and supported by our comparison with randomly generated localities. The comparison of EVI data associated with collection sites and randomly generated sites (**Figure 4**) confirms that the dynamic distribution of Painted Buntings as evinced by museum collection data corresponds in a non-random manner with increased primary productivity across the landscape. Numerous studies have documented similar associations including studies of Painted Buntings (Bridge et al, in press) and various tests of the green-wave hypothesis (Drent et al., 1978; Owen, 1980, Shariatinajafabadi et al., 2014, Si et al., 2015). Therefore, we present this finding as validation that our specimen based distribution mapping yields rather than a novel correlative observation. Likely also due to resource limitation, our finding that Painted Bunting specimen records were significantly more numerous below 500m supports claims that *P. ciris* primarily winters in the lowlands (Rohwer 2015, pers. comm.; Howell and Webb 2007).

While we demonstrate the utility of NHC abundance indices in inferring population level movements, we reiterate that the technique in no way reflects the movements of individual birds. AI values represent stationary population densities at a particular time and place, and as such, caution must be taken not to over interpret findings, while keeping an open mind to alternate hypotheses. These include the existence of sedentary populations with geographically distinct distributions, and the potential of results being an historical artifact of a particular collecting expedition in regions with limited collecting effort. However, assuming thorough background collecting, the absence of target species at a particular time and place almost certainly represents the mass movement of individuals (rather than huge die-offs). In light of this, we believe the method can be applied to significantly more complex cases than the one described above. We are particularly interested to see studies with well-sampled species in regions where anthropogenic disturbance has substantially altered migratory corridors in recent years. We hope in the future AI values will shed light on avian demographics, behavior, and distribution, and continue to illustrate the immense value of NHCs worldwide.

CONCLUSIONS

Our study illustrates the utility of NHC specimen collection records in inferring population-level movement through abundance index analysis. We find evidence of quasi-circular movement from month to month in *Passerina ciris* populations across its non-breeding range, with abundance index values non-randomly distributed in regions with high EVI values (indicating high primary productivity).

ACKNOWLEDGEMENTS

Thanks to John Klicka, Cooper French, Dave Slager, C.J. Battey, and Kevin Epperly for reading and providing helpful feedback on the manuscript. Thanks to Alejandro Gordillo for coordinating geolocation of specimen records.Additionally, thanks is due to the following collections for specimen records in the portion of the Mexican Bird Atlas used for this study: American Museum of Natural History; Academy of Natural Sciences of Philadelphia; Bell Museum of Natural History, University of Minnesota; Natural History Museum (Tring, UK); Zoologische Forschungsinstitut und Museum Alexander Koenig; Übersee-Museum Bremen; Carnegie Museum of Natural History; California Academy of Sciences; Canadian Museum of Nature; Coleccion Ornitologica Centro de Investigaciones Biológicas UAEM; Cornell University Museum of Vertebrates; Denver Museum of Natural History; Delaware Museum of Natural History; Fort Hays State College; Field Museum of Natural History, Senckenberg Museum Frankfurt, Colección Nacional de Aves Instituto de Biología UNAM; Instituto de Historia Natural y Ecología; University of Kansas Natural History Museum; Los Angeles County Museum of Natural History; Natuurhistorische Musem Leiden; Louisiana State University Museum of Zoology; Museo de las Aves de México; Museum of Comparative Zoology; Moore Laboratory of Zoology; Museum Nationale D'histoire Naturelle Paris; Zoological Museum Moscow State University; Museum Mensch und Natur Munich; Museum of Vertebrate Zoology; Museo de Zoología Facultad de Ciencias UNAM; Royal Ontario Museum; San Diego Natural History Museum; Staatliche Museen fur Naturkunde, Stuttgar;, Southwestern College, Kansas; Universidad Autónoma de Baja California; University of Arizona; University of British Columbia Museum of Zoology; University of California Los Angeles; Florida Museum of Natural History; University of Michigan Museum of Zoology; United States National Museum of Natural History; University of Washington Burke Museum; Western Foundation of Vertebrate Zoology; and, Yale University Peabody Museum.

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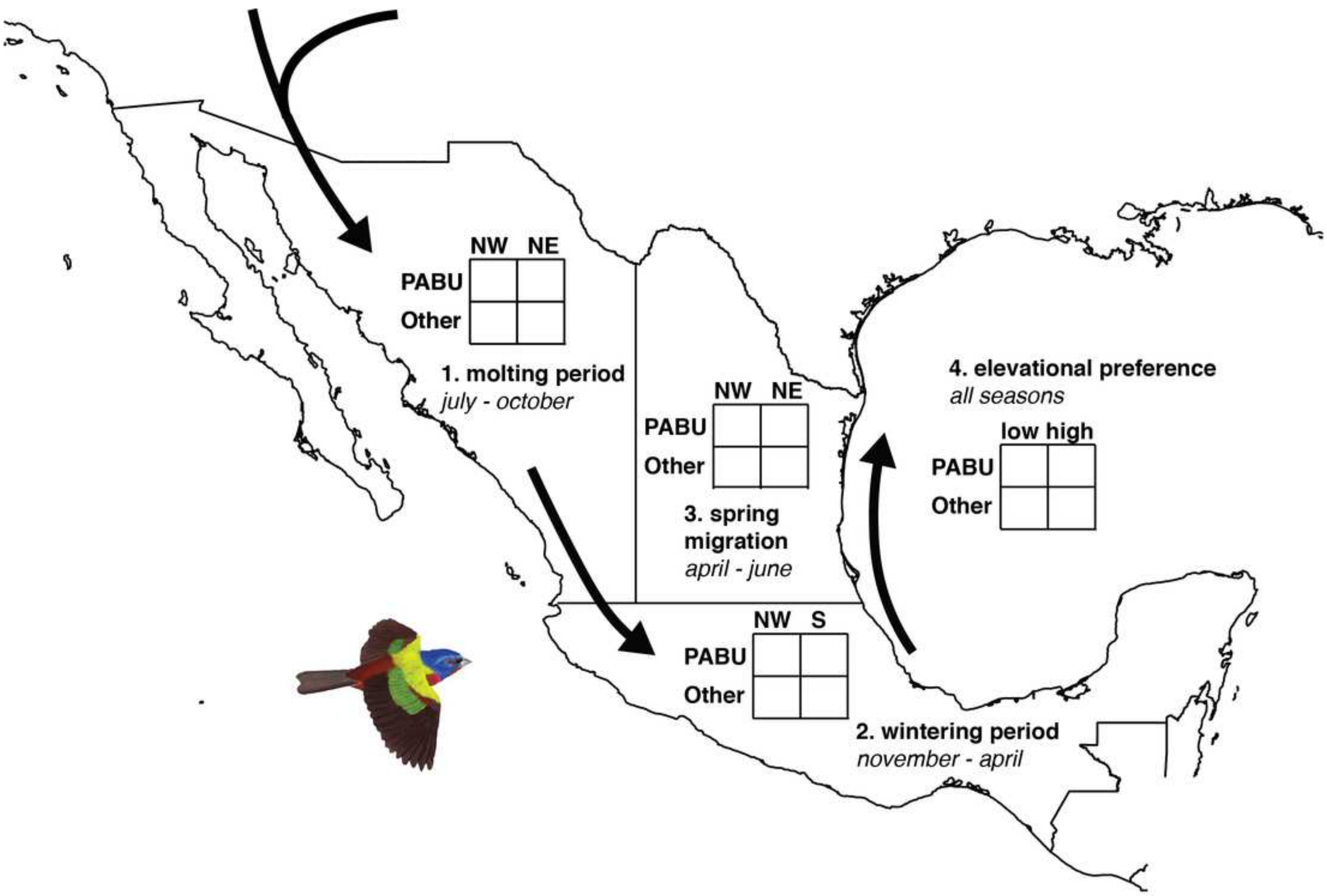
1

Diagram of Chi-square tests of seasonal changes in *Passerina ciris* specimen record densities

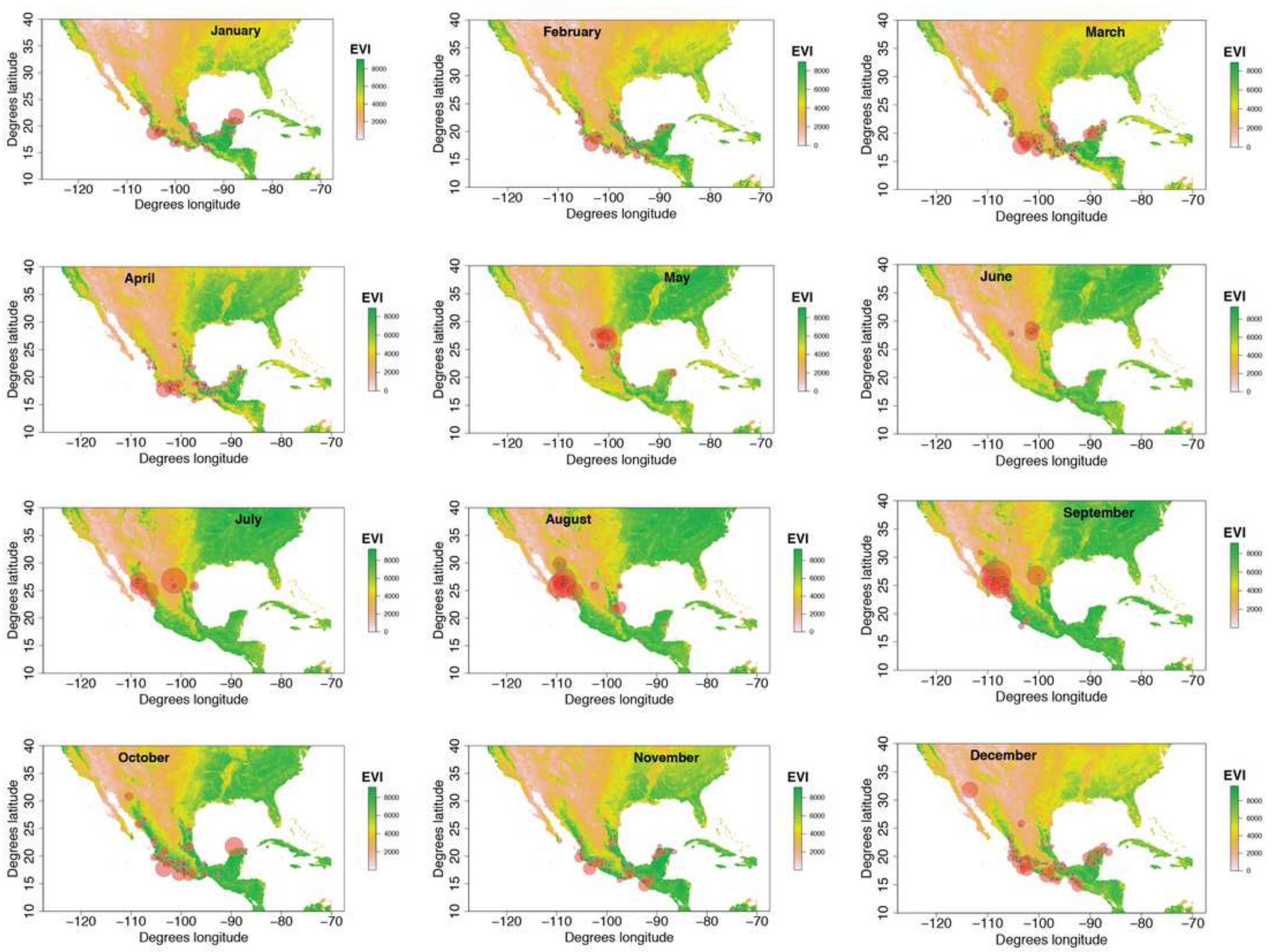
Figure 1. Chi-square analysis of *Passerina ciris* population movements around Mexico. 2x2 grids illustrate Pearson's chi-square tests asking whether Painted Bunting ("PABU") populations were significantly greater in a particular region (NW, NE, and S, divided by 20 degrees N and 103 degrees west and marked on the plot) and a particular time (molting period, wintering period, and spring migration) than expected with respect to reference specimen populations ("Other").



2

Monthly changes in *Passerina ciris* abundance index values with EVI analysis of remote sensing data

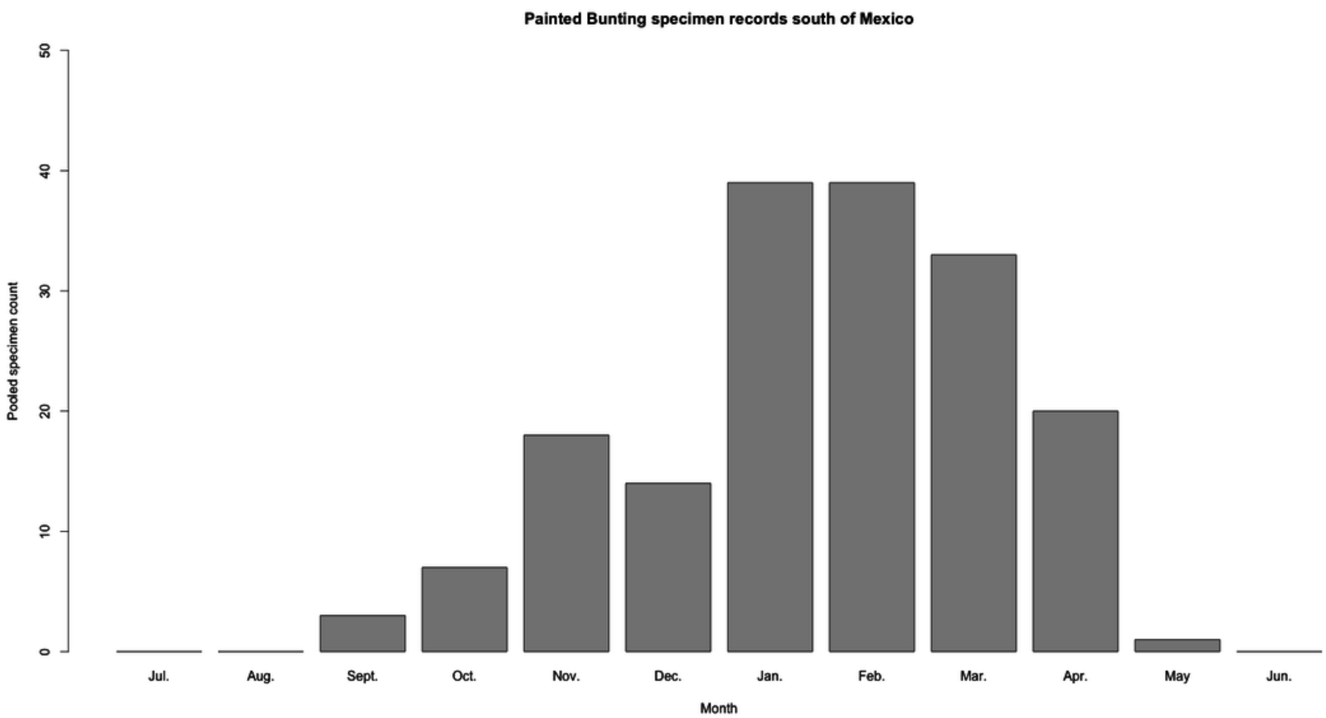
Figure 2 (also provided as .gif animation in supplemental files). Abundance index (AI) values for *Passerina ciris* specimens in Mexico by month, plotted against EVI analysis of remote sensing data. Red circles indicate the occurrence of *P. ciris* specimens, with the diameter of the circle proportional to value of Abundance Index. Green areas indicate high EVI values, correlated with regions with a high density of live green plants (photosynthetically active vegetation).



3

Histogram of raw *Passerina ciris* specimen counts in Central America

Figure 3. Raw Painted Bunting specimen records pooled from Belize, Guatemala, El Salvador, Honduras, Nicaragua, Panama, and Costa Rica, and totaled by month of collection.



4

Mean EVI values of specimen data compared to mean EVI values of randomly distributed points, by month

Figure 4. Mean EVI values of specimen records compared to mean EVI values of 500 randomly distributed points within Mexico.