Seasonal variation in climate and landcover niches of a migratory bird

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Abstract

Background: Resource utilization strategies of avian migrants are a major concern for conservation and management. Consequently, the ability to predict potential shifts in migratory species spatial use and migratory behaviour is a pressing challenge for predictive ecology under global changes. There are two main strategies of resource use adopted by migratory birds: niche tracking for similar environmental conditions and niche switching between different environmental conditions between seasons. Our objective was to examine whether the niche tracking/niche switching hypothesis would better explain seasonal variations in the ecological niche overlap of the American White Pelicans (AWPE, *Pelecanus erythrorhynchos*). We also tested whether recent changes in the non-breeding ground land-use have altered habitat selection and space use by AWPE.

Methods: We used Dirichlet-multinomial models to detect differences in habitat selection between regions and over times with the GPS locations of 36 tracked AWPEs. We estimated climatic and land-cover niche overlap between the breeding and non-breeding grounds to test for niche switches between seasons using ordination methods.

Results: Our habitat selection models did not detect shifts in habitat selection by AWPE after 2005. American white pelican strongly selected open water and wetland at the non-breeding and breeding grounds. American white pelicans showed little climatic niche overlap but substantial landscape niche overlap between breeding and non-breeding grounds.

Conclusions: Declines in aquacultural acreage did not change AWPE habitat selection in the Northern Gulf of Mexico. Our results did not support the hypothesis that AWPE would be a climatic niche tracker. However, AWPE tracked its foraging habitats, exhibiting strong selection for open water and wetland at both the breeding and non-breeding grounds. Climatic niche switching suggests that AWPE may adapt to future climate changes.

Background

Understanding habitat and resource selections by animals represents a key topic in ecology (Boyce and McDonald 1999, Manly et al. 2002, McLoughlin et al. 2010, Bell 2012). If resources are used by an organism more frequently than expected from availability, they are considered selected for by the organism (Aebischer et al. 1993). Organisms often exhibit seasonal and long-term shifts in habitat and resource selection in adaptation to fluctuating living environments, particularly under global changes and land-use changes (Martin 2001, Araujo et al. 2004, Tingley et al. 2009, Hoffmann and Sgro 2011, Gomez et al. 2016). In niche theory, the total environmental conditions in which populations of organisms survive and grow define the fundamental ecological niche (Hutchinson 1957). The occupied or selected portion of the fundamental niche is the realized niche (Hutchinson 1957). Furthermore, ecological niche has multi-dimensions, with a subset or axis (e.g., climatic conditions, food, and shelters) of the total environmental (abiotic and biotic) conditions defining a dimension of ecological niche (e.g., climatic

niche and land-cover niche; Hutchinson 1957, Sexton et al. 2009). Empirical studies of variations in the seasonal overlap of climatic and land-cover niches may provide insight into ecological mechanisms, which enable migratory species to shift their geographic ranges under anthropogenic disturbances (Tingley et al. 2009, Gomez et al. 2016).

The long-distance latitudinal migration between the breeding and non-breeding grounds represents a model system to study seasonal variations in the ecological niche of migratory species (Cox 1985, Newton 2008). Migration not only enables migrants to take advantage of resources (e.g., food and breeding habitat) available in different seasons, but also imposes physiological challenges (e.g., inclement climate and energetic costs of migration) to migrants (Marini et al. 2013, Gomez et al. 2016, Winger et al. 2019). Therefore, seasonal variation in climate and food availability between the breeding and non-breeding grounds may be two selective forces of the evolution of migration and annual resource utilization strategies (Newton 2008). The strategies that migratory birds use to cope with physiological challenges may vary between basic extremes: niche tracking and niche switching. Migrants either track a set of conditions year-round ("niche tracker") or adapt to the new environment when moving from one ecological regime to another ("niche switcher") (Nakazawa et al. 2004, Laube et al. 2015). However, few studies have determined the tracking or switching strategies for both climatic and land-cover niches of migratory birds (Engler et al. 2017).

The American white pelican (*Pelecanus erythrorhynchos*, hereafter AWPE) is a short-distance migrant and among the largest flying bird of North America (King et al. 2017). American white pelicans have been of conservation and restoration interests since the 1970s, and have become a substantial economic issue more recently due to their impacts on channel catfish (*Ictalurus punctatus*) aquaculture (King 2005). Before the 1980s, AWPE was of conservation concerns due to population declines caused by the DDT contamination (King and Michot 2002). Two-decades conservation and restoration efforts have successfully increased and restored AWPE populations at both the breeding and non-breeding grounds (King and Michot 2002). Consequently, since the 1990's, AWPEs have been known to use commercial aquaculture ponds consistently for feeding primarily on catfish in the Northern Gulf of Mexico (NGOM; King 2005). Because of the relatively shallow depth and high density of catfish, these commercial fish ponds have provided an ideal foraging environment for AWPE in Alabama, Arkansas, Louisiana, and Mississippi, USA (King and Werner 2001, King et al. 2010, King et al. 2016). Commercial aquaculture in the NGOM expanded with increased water acreage from 1980 to 2004 and has had a sharp decline due to rising feed prices and inexpensive foreign imported fish 2005. Furthermore, precipitation has steadily declined in the temperate regions (Walther et al. 2002, IPCC 2014). The decline may be exacerbated in the southern part of North America (Seager et al. 2007). The changes in precipitation regimes, in conjunction with the land-use changes (i.e., aquaculture rise and fall), are likely to affect the habitat selection and land-cover niche of waterbirds such as AWPE. For these reasons, we investigated the potential effects of reduced aquaculture activities in the non-breeding range on AWPE habitat selection patterns. We expected that AWPE may select alternative food and shelter resources due to the decline in aquaculture water acreage in the NGOM.

Our objective was to address the following predictions in this study: 1) that migratory behaviour of the AWPE populations would be better explained as niche trackers or niche switchers and 2) that there would be a greater land-cover niche overlap than climatic niche overlap between AWPE on the breeding and non-breeding grounds because of tracking similar foraging habitats in wetlands. We also tested for shift in habitat selection by AWPE before and after aquacultural decline.

Methods

Study areas and GPS tracking American white pelicans

American white pelicans are divided into eastern and western metapopulations by the Continental Divide (Anderson and King 2005). The AWPE eastern metapopulation migrates between the Northern Great Plains (the breeding grounds) and the NGOM (the non-breeding grounds) along the Mississippi and Ohio River Valleys (King et al. 2017, Shannon et al. 2002). We followed King et al. (2017) to delineate the boundaries of the breeding and non-breeding ranges (Fig. 1).

We used presence data from 36 AWPEs which had been tracked with the global positioning system (GPS) transmitters for one, two or a maximum of three years from 2002 to 2010 (King et al. 2016). Two different daily AWPE tracking schedules were used among the 36 AWPEs: 1) location recording from 0500 hr to 1900 hr and 2) for consecutive 24 hours. AWPE locations were recorded hourly during the daily GPS-on hours. American white pelicans were rarely active during the GPS-off hours of Schedule 1 (King and Werner 2001). We divided the recorded GPS locations into the AWPE breeding grounds (locations of migrants between the first arrival at and departure from the breeding grounds) and non-breeding grounds (including of migrants and year-round residents between the first arrival at and departure from the non-breeding grounds). A GPS-tracked individual was considered in spring migration (departure from the non-breeding range) when it crossed 35°N latitudinal line northward until it reached the breeding grounds (see King et al. 2017), and vice versa in autumn. For the purposes of this study, we assumed that migration ended when the given individual entered the breeding (spring) or non-breeding (autumn) region (King et al. 2017). We excluded AWPE GPS locations during seasonal migration from our analysis.

Processing and filtering of GPS data for the breeding and non-breeding grounds

We filtered and thinned the presence locations to control for spatial bias and unbalanced numbers of GPS locations among individual (Winton et al. 2018). First, we identified the GPS-tracked individual with the smallest number of GPS locations among the 36 AWPEs. We then reduced the number of GPS locations of the other individuals to the smallest number by randomly sampling from all available locations of an individual. Second, we resampled each of the 36 subsets of presence locations so that each location was separated from the nearest one by a minimum distance of 5 km for each animal. In a preliminary analysis, we found that average hourly movement distance of AWPE during the active hours (0900 – 1700 hr) on both the breeding and non-breeding grounds was about 5 km. Last, to ensure that we excluded those locations where AWPE were flying at higher altitude above ground, we also excluded from

analyses those locations in the upper decile of flying speed estimated by quantile regression from hourly location data (>4.45 m/s) (Illan et al. 2017).

To test for the effects of the aquaculture decline in AWPE habitat use and ecological niches, we divided our AWPE GPS location data into two subsets: before and after the 2005 peak of aquaculture activities on the non-breeding grounds. We used categorical variable for land-use change because of the lack of fine-scale data on aquacultural economy and fish-pond spatial distributions. All comparative analyses of habitat selection and ecological niche overlap were based on models developed with these two sets of data (hereafter, pre- and post-aquaculture). We expected that SDMs would show different land-cover niche breadth before and after the peak of aquaculture.

To assess the spatial dependence among the thinned GPS location data, we tested whether counts of AWPE occurrences (i.e., the numbers of times AWPE occurred at each unique AWPE GPS location) were correlated among the neighbouring locations using Moran's I index (Bivand et al. 2008). Moran's I index ranged from -1 (complete negative correlation) to +1 (complete positive correlation). If the value of Moran's I is zero or close to zero, spatial autocorrelation is weak. We used the "spdep" R package for the Moran's I test (Bivand 2006).

To further assess the spatial dependence of AWPE occurrences among the GPS locations of all 36 tracked AWPEs, we used Gaussian Markov random field (GMRF) to estimate the spatial range parameter (ρ) of Matern spatial covariance function (Lindgren et al. 2011). The range is the distance at which spatial autocorrelation is about 0.1. The GMRF model is a spatial statistical model for geospatial point data that are continuously registered over a geographic area. Spatially autocorrelated error is assumed to be generated by a continuous Gaussian random field (GF) on a 2-dimension plane (Lindgren et al. 2011). Stochastic partial differential equation (SPDE) is used to approximate the continuous GF with the GMRF, which is indexed discretely by the vertices of a mesh built with the Voronoi triangulation (Fig. 2) (Lindgren and Rue 2015). Therefore, the solution to the SPDE can be assumed to be a stationary GF with the Matern spatial covariance function (Lindgren et al. 2011). In SPDE, the continuous GF is approximated by the finite element method with linear piecewise functions, producing a sparse covariance matrix (Lindgren et al. 2011). The sparseness of GMRF covariance matrices allows the SPDE model to approximate continuous spatial stochastic process reliably with a fast runtime (Lindgren and Rue 2015; Rue et al. 2017). We implemented the GMRF models in R Template Model Builder (TMB), a C++ template-based statistical software (Kristensen et al. 2016), by modifying the codes publicly available from https://kaskr.github.io/adcomp/spde_8cpp-example.html. We first determined AWPE occurrence count y (i.e., the number of times AWPE occurred) at each unique AWPE GPS location using all GPS locations of 36 AWPEs. We assumed that AWPE occurrence counts (y) followed Poisson distributions with a spatial use intensity λ , that is, the Poisson parameter. The spatial use intensity of AWPE was represented as:

$$y_i \sim \text{Poisson}(\lambda_i),$$

$$\log(\lambda_i) = \beta_0 + \beta_{\text{change}} + u_i(1),$$

where λ_i is mean AWPE occurrence count at a geographic location i ; β_0 intercept; $\beta_{luchange}$ the coefficient of the main effect of land-use change; and u_i the GMRF variate evaluated at location i for spatial autocorrelation.

Environmental variables

We used two types of environmental predictors in raster format: (i) climate (14 variables) and (ii) land cover (six variables).

Climate: Climatic variables were obtained from the WorldClim (version 2) database (Hijmans et al. 2005; <http://www.worldclim.org>), which provides a variety of monthly climatic data averaged over the years 1970–2000. Three main reasons persuaded us to develop our models using the WorldClim data. First, the WorldClim data include part of the AWPE non-breeding range in the Southern GOM outside the USA, which is not encompassed by an alternative raster climatic data PRISM from Oregon State University (PRISM Climate Group 2012). Second, wind direction and wind speed are two main drivers of AWPE movements and behaviour (Illan et al. 2017). However, none of the alternative climate data sources included data on wind currents at the desired spatiotemporal scale. Last, we regressed data obtained from two alternative climate sources, Climate Research Unit (CRU) of University of East Anglia (Harris et al. 2014) and PRISM against the same variables from the WorldClim data. Linear regression demonstrated that pairs of same climate variables between the two climate data sets were highly significantly related ($R^2 > 0.8$; $p < 0.001$).

We selected July for the warmest month on the breeding grounds and January for the coldest month on the non-breeding grounds of AWPE (King et al. 2017). The arrival and departure dates of AWPE seasonal migration vary substantially from year to year. The two months correspond to the time of year when AWPEs are present on the breeding and non-breeding ranges (King et al. 2017). Initially selected climatic variables included minimum, maximum and average temperature, total precipitation, solar radiation, water vapour pressure and wind speed.

Land cover: We used *North American Land Change Monitoring System* (NALCMS, 2005; Homer et al., 2015) (<https://landcover.usgs.gov>) based on MODIS satellite imagery to obtain land cover data. The classification of land cover types was designed with three hierarchical levels using the Food and Agriculture Organization (FAO) Land Classification System (Homer et al, 2015). We reclassified original LULC classes needleleaf forest, broadleaf forest, temperate deciduous forest, mixed forest, and shrubland as woody cover and classes barren land and developed as developed cover. The reclassification resulted in six LULC classes cropland, grassland, developed, grassland, wetland, and woody. We aggregated 250-m LULC rasters by a factor 4 and calculated proportion of each LULC classes over 16 250-m grid cells to produce a 1-km resolution raster layer for each of six LULC classes. For each individual AWPE and for each GPS location, we extracted the selected land cover variables using ArcMap spatial analyst (ESRI, 2014).

To eliminate multicollinearity, we used a backwards stepwise process to calculate the variance inflation factor (VIF) starting from the initial pool of 20 predictor variables. We only selected predictors with $VIF < 4$ (Graham 2003, O'Brien 2007, Kock and Lynn 2012). With the resulting set of variables, we calculated a matrix of pairwise Pearson's correlation r and discarded any remaining predictors of $r > 0.7$. All raster files had 1-km spatial resolution. The 1-km resolution was chosen for a balance between the computational burdens and the accuracy of habitat selection models and ecological niche analysis. Our selected spatial resolution is less than the average hourly movement distance (5 km) of AWPE, sufficient for AWPE species distribution modelling, and is consistent with the spatial resolution of the climatic raster files (Table 1).

Ecological niche analysis

We used Dirichlet-multinomial distribution models (hereafter, D-M models) to habitat selection by the pelican following de Valpine and Harmon-Threatt (2013) and Wang et al. (2019). The spatially thinned data on pelican GPS locations were analysed by region (i.e., non-breeding or breeding ground) and period (i.e., before or after aquacultural decline). The distribution of GPS location counts over six different LULC classes was assumed to follow the multinomial distribution. The probability of selecting a LULC class was assumed to have a Dirichlet distribution (de Valpine and Harmon-Threatt 2013). The D-M models used in this study assumes that habitat selection is proportional to resource availability times a type-specific linear preference coefficient or index h ($h > 0$ and $\sum h = 1$). Resource availability was measured by the proportion of LULC classes within a non-convex polygon which encompassed all GPS locations at the non-breeding or breeding grounds (Fig. 2). The greater the coefficient h for an LULC class, the stronger the selection for the LULC class. Unknown parameter h for each LULC class was estimated in the Bayesian framework using software Rstan (Carpenter et al. 2017). Region- and period-specific h 's were estimated with a hyperprior Gamma (1, 0.01) for the Dirichlet parameters τ shared among the regions and periods, allowing for borrow strength among the four sets of data. The 95% credible intervals (CIs) of selection index h were generated over three Markov Chain Monte Carlo (MCMC) chains. Each MCMC chain had a total 2,000 iterations with the first 1,000 being discarded as a burn-in or tuning period. The convergence of MCMC chains were assessed with the Gelmen-Rubin split index R -hat and Rstan's `check_hmc_diagnostics()` function (Carpenter et al. 2017).

We also estimated the niche overlap between seasons using an ordination method based on principal component analysis (PCA, Broennimann et al. 2011). The ordination approach compares seasonal niches in the environmental space represented by the first two axes of PCA. Species occurrences are first mapped to a 100x100 grid on the environmental space; then, occurrence density is estimated by kernel smoothing methods for each cell and is rescaled to the range from 0 to 1 (Broennimann et al. 2011). Climatic condition or resource availability is smoothed and rescaled to the 0–1 range for each grid cell as well (Broennimann et al. 2011). Therefore, the ordination approach allows for direct niche comparisons between the regions and between seasons taking into account differences in resource availability, climatic condition, and geographic extent. The ordination method can also visualize ecological niche overlap between the breeding and non-breeding seasons in the first two PCA axes of the environmental

space. We used the “ecospat” R package to conduct the ordination analysis of AWPE seasonal niches (Di Cola et al. 2017). The niche space of a season or population is represented by a polygon in the environmental space with its limits of the two PCA scores being chosen to match with the geographic backgrounds for the two populations. As a result, the polygon may be truncated by the chosen limits of the two PCA axes (Bronnemann, personal communication). We used the I statistic and Schoener’s D to measure niche overlap (Schoener 1968, Warren et al. 2008). Both metrics were commonly used in ecological niche analysis and are available in the “ecospat” R package used in this study (Di Cola et al. 2017). Indices I and D range from 0 to 1, with 0 indicating no niche similarity between seasonal niches and 1 indicating complete similarity.

Results

The number of birds that fulfilled the filtering and inclusion criteria for analyses were 19 migrants on the breeding ground (eight individuals with 1,154 GPS locations before aquacultural decline; 11 individuals with 2,123 GPS locations after aquacultural decline) and 30 individuals on the non-breeding grounds (15 individuals with 1,584 GPS locations before aquacultural decline; 15 individuals with 1,494 GPS locations after aquacultural decline). Moran’s I value of both raw count and the residual of a Poisson regression with intercept only was 0.004 ($p = 0.01$) at the non-breeding ground. Likewise, Moran’s I of both raw count and the residual of a Poisson regression with intercept only was 0.02 ($p = 0.01$) at the breeding ground. Despite the p value of 0.01, Moran’s I was very close to zero, indicating a negligible, weak positive spatial autocorrelation among the thinned GPS locations. The range parameter, at which spatial correlation declines to 0.1, was 7.50 km (standard deviation [SD] = 1.10 km) and 5.74 km (SD = 1.32 km) for the non-breeding and breeding grounds, respectively, providing a further justification for our 5-km data thinning criterion. After the multicollinearity removal, the resulting final set of non-correlated environmental predictors included four climatic and four land cover variables (Table 1).

Proportions of six LULC classes did not change substantially at either the non-breeding and breeding grounds before and after aquacultural decline (Fig. 3a, b). The D-M model indicated that AWPE selected open water and wetland more than other LULC classes at both the breeding and non-breeding ground (Fig. 3c, d). American white pelicans exhibited the lowest selection for woody covers (Fig. 3c, d). The 95% CI of selection indices before and after aquacultural decline overlapped at the non-breeding ground, indicating no major shifts in habitat selection (Fig. 3c). The similar pattern was observed at the breeding ground, except that AWPEs selected more cropland after than before 2005 (Fig. 3d).

Ordination-based estimates of ecological niche overlap between the breeding and non-breeding grounds indicated that overlap of climate niche (Schoener’s D = 0.09; Fig. 4a, d) was much lower than that of land cover niche (Schoener’s D : Maxent-based = 0.88) between the breeding and non-breeding grounds (Fig. 4b, d). Schoener’s D for climate-landscape combined niche overlap was 0.35 (Fig. 4c, d). Mean I statistic was 0.24 for climatic niche overlap versus 0.73 for land-cover niche overlap. Our results suggest that migrating AWPE were likely to switch climatic niche and track land-cover niche.

Discussion

Ecological niche needs to be considered as a dynamic concept and have a time dimension in its quantification to better understand the responses of avian migrants to global change and anthropogenic disturbances (Martinez-Meyer et al. 2004, Tingley et al. et al. 2009, Eyres et al. 2017). Our results indicated that AWPEs were a climatic niche switcher, but tended to track similar land covers more than climatic conditions between the breeding and non-breeding grounds. American white pelicans may be forced to adapt to substantially different climatic conditions between the breeding and non-breeding grounds. The results of the D-M models did not support the prediction that AWPE would shift habitat selection after the aquacultural decline. AWPE appeared to select and track open water and wetland at the breeding and non-breeding grounds. Therefore, migratory species breeding in the northern temperate regions may need plastic climatic niches to adapt to dramatic differences in ecological conditions during the annual migration cycle.

Previous studies have found evidence of climatic niche trackers following the same climatic conditions year-round (e.g. Joseph and Stockwell 2000, Nakazawa et al. 2004, Gomez et al. 2016) as well as niche switchers switching climatic niches between seasons (Marini et al. 2013, Laube et al. 2015). This study rejects the hypothesis that AWPE would track climatic conditions between the breeding and non-breeding grounds (Shaw and Couzin 2012). On the contrary, the seasonal difference in the climatic niche of AWPE supported the hypothesis that the harshness of autumn temperatures on the northern temperate breeding grounds would force AWPE to migrate southward to the Gulf of Mexico sub-tropical climate to enhance winter survival (Bell 2000, Salewski and Bruderer 2007, Winger et al. 2014). Migrants adapt to more various climate conditions on the breeding grounds with greater climatic niche breadth than on the non-breeding grounds with less climatic variability (Marini et al. 2013, Laube et al. 2015, Pérez-Moreno et al. 2016).

Habitat provide birds with food, shelter or space, and nest sites for reproduction (Fuller 2012). Given little overlap of seasonal climatic niches as shown in this study, it is unlikely that AWPE tracked similar land covers for similar thermal conditions between the breeding and non-breeding grounds. Furthermore, there is no evidence that year-round AWPE residents breed in Alabama, Arkansas, Louisiana, and Mississippi. American white pelicans feed on fishes, salamanders, and crawfish living in the freshwater wetlands (King and Michot 2002). Therefore, selection of similar foraging habitat (e.g., open water and wetland) in both the breeding and non-breeding grounds may result in appreciable seasonal overlap of land-cover niches.

American white pelican is a soaring-flying bird and may fly a few hundred meters or higher above the ground (Shannon et al. 2002). We selected AWPE GPS locations of lower flying speed, suggesting relatively lower flying altitudes. However, without data on flying altitudes, we are not certain if AWPE takes advantage of thermal uplift for flying or foraging at a specific location. Scacco et al. (2019) used statistic topography and land cover as proxies to predict the uplift suitability of the white stork (*Ciconia ciconia*) across landscapes. American white pelicans exhibited some levels of selection for developed area

including barren lands. The use of developed area may be because of suitable thermal uplifts (Illan et al. 2017) or simply flying over. Future studies of AWPE need to consider landscape-atmospheric interactions with fine-scale data on soaring birds.

Conclusions

Our study addressed seasonal variations in habitat selection and ecological niche of a migratory foraging- and habitat-specialist bird between the breeding and non-breeding grounds. Instead of tracking climatic niche, AWPE tracked its foraging habitats in open water and wetland, exhibiting strong selection at both the breeding and non-breeding grounds. Future studies need to use fine-scale, real-time climatic data to determine whether APWE avoid or select certain climatic conditions during movement or habitat selection.

Declarations

Ethics approval and consent to participate

This research was conducted in accordance with the USDA guidelines of animal care and use. All experimental protocols of animal capture and handling were approved by the United States Department of Agriculture (USDA), National Wildlife Research Center, Institutional Animal Care and Use Committee (IACUC Protocol QA-1018). **Consent for publication**

Not applicable.

Availability of data and materials

All the datasets used during this study are fully available without restriction from the corresponding author upon request. AWPE gps-tracked locations, climate data and MaxEnt input files will be publicly and permanently accessible through Dryad repository (<https://datadryad.org>).

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

All authors conceived the ideas and designed methodology. DTK and FC collected the data. JGI and GW analysed the data. JGI led the writing of the manuscript. All authors contributed critically to the drafts and

gave final approval for publication.

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Abbreviations

AIC: Akaike Information Criterion; AWPE: American White Pelican; CRU: Climate research unit; FAO: Food and Agriculture Organization; GMRF: Gaussian Markov Random Field; LULC: Land Use and Land Cover; MCMC: Markov Chain Monte Carlo; NALCMS: North American Land Change Monitoring System; NGOM: Northern Gulf of Mexico; SPDE: stochastic partial differential equation; TMB: Template Model Builder; VIF: Variance inflation factor

References

- Aebischer NJ, Robertson PA, Kenward RE. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*. 1993;74(5):1313-25.
- Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*. 2004;10(9):1618-26.
- Bell CP. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology*. 2000;31(2):258-65.
- Bell WJ. *Searching behaviour: the behavioural ecology of finding resources*. Springer Science & Business Media; 2012 Dec 6.
- Bivand R. Implementing spatial data analysis software tools in R. *Geographical Analysis*. 2006; 38:23-40
- Bivand RS, Pebesma EJ, Gómez-Rubio V, Pebesma EJ. *Applied spatial data analysis with R*. Springer; 2008.
- Boyce MS, McDonald LL. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*. 1999 Jul 1;14(7):268-72.
- Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH. Measuring ecological niche overlap from occurrence and spatial

environmental data. *Global ecology and biogeography*. 2012 Apr;21(4):481-97.

Carpenter B et al. Stan: A probabilistic programming language *Journal of Statistical Software*. 2017; 76:1-32

Cox GW. The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist*. 1985 Oct 1;126(4):451-74.

de Valpine P, Harmon-Threatt AN. General models for resource use or other compositional count data using the Dirichlet-Multinomial distribution *Ecology*. 2013; 94:2678-2687

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., D'amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A. and Pellissier, L. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 2017; 40: 774-787.

E.S.R.I., ArcGIS, 2014. 10.2. 1 for Desktop. Redlands, CA: Environmental System Research Institute

Engler, JO, Stiels, D, Schidelko, K, Strubbe, D, Quillfeldt, P, and Brambilla, M. Avian SDMs: current state, challenges, and opportunities. *Journal of Avian Biology*. 2017; 48(12): 1483-1504.

Eyres, A, Böhning-Gaese, K, and Fritz, SA. Quantification of climatic niches in birds: adding the temporal dimension. *Journal of Avian Biology*. 2017; 48(12), 1517-1531.

Fuller, RJ. *Birds and habitat: relationships in changing landscapes*. Cambridge University Press, Cambridge, UK; 2012.

Gómez C, Tenorio EA, Montoya P, Cadena CD. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*. 2016 Feb 10;283(1824):20152458.

Graham MH. Confronting multicollinearity in ecological multiple regression. *Ecology*. 2003 Nov;84(11):2809-15.

Harris IP, Jones PD, Osborn TJ, Lister DH. Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 Dataset. *International journal of climatology*. 2014 Mar 15;34(3):623-42.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*. 2005 Dec;25(15):1965-78.

Homer C, Dewitz J, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold N, Wickham J, Megown K. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*. 2015 May 1;81(5):345-54.

Hoffmann AA, Sgro CM. Climate change and evolutionary adaptation. *Nature*. 2011 Feb;470(7335):479.

Hutchinson GE. Cold spring harbor symposium on quantitative biology. Concluding remarks. 1957; 22:415-27.

Illan JG, Wang G, Cunningham FL, King DT. Seasonal effects of wind conditions on migration patterns of soaring American white pelican *PloS One*. 2017 Oct 24; 12:e0186948

IPCC Synthesis Report 2014. Intergovernmental Panel on Climate Change (IPCC).

Joseph L, Stockwell D. Temperature-based models of the migration of Swainson's flycatcher *Myiarchus swainsoni* across South America: a new use for museum specimens of migratory birds. *Proceedings-Academy of Natural Sciences of Philadelphia*. 2000 Apr 14;150:293-300.

King DT. Interactions between the American white pelican and aquaculture in the southeastern United States: an overview. *Waterbirds*. 2005 Dec;28(sp1):83-7.

King DT, Michot TC Distribution, abundance and habitat use of American White Pelicans in the Delta Region of Mississippi and along the Western Gulf of Mexico Coast. *Waterbirds* 2002; 25:410-416

King DT, Werner SJ. Daily activity budgets and population size of American white pelicans wintering in south Louisiana and the delta region of Mississippi. *Waterbirds*. 2001 Aug 1:250-4.

King DT, Belant J, Harrel B, Glahn J. Superabundant food at catfish aquaculture facilities improves body condition in American White Pelicans. *Waterbirds*. 2010 Jun;33(2):221-8.

King DT, Wang G, Yang Z, Fischer JW. Advances and environmental conditions of spring migration phenology of American White Pelicans. *Scientific reports*. 2017 Jan 16;7:40339.

King DT, Fischer J, Strickland B, Walter WD, Cunningham FL, Wang G. Winter and summer home ranges of American white pelicans (*Pelecanus erythrorhynchos*) captured at loafing sites in the southeastern United States. *Waterbirds*. 2016 Sep;39(3):287-95.

Kock N, Lynn G. Lateral collinearity and misleading results in variance-based SEM: An illustration and recommendations. *Journal of the Association for Information Systems*. 2012 Sep 26;13(7).

Kristensen K, Nielsen A, Berg CW, Skaug HJ, Bell B. TMB: Automatic differentiation and laplace approximation *Journal of Statistical Software*. 2016; 70:1-21

Laube I, Graham CH, Böhning-Gaese K. Niche availability in space and time: migration in *Sylvia* warblers. *Journal of Biogeography*. 2015 Oct;42(10):1896-906.

Lindgren F, Rue H. Bayesian spatial modelling with R-INLA *Journal of Statistical Software*. 2015;63:19

- Lindgren F, Rue H, Lindström J. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*. 2011; 73:423-498
- Manly BF, McDonald L, Thomas DL, McDonald TL, Erickson WP. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media; 2002 May 8.
- Marini MÂ, Barbet-Massin M, Lopes LE, Jiguet F. Geographic and seasonal distribution of the Cock-tailed Tyrant (*Alectrurus tricolor*) inferred from niche modeling. *Journal of ornithology*. 2013 Apr 1;154(2):393-402.
- Martin TE. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts?. *Ecology*. 2001 Jan;82(1):175-88.
- Martínez–Meyer E, Townsend Peterson A, Navarro–Sigüenza AG. Evolution of seasonal ecological niches in the *Passerina buntings* (Aves: Cardinalidae). *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 2004 Jun 7;271(1544):1151-7.
- McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL. Considering ecological dynamics in resource selection functions. *Journal of animal ecology*. 2010 Jan;79(1):4-12.
- Nakazawa Y, Peterson AT, Martínez-Meyer E, Navarro-Sigüenza AG. Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. *The Auk*. 2004 Apr 1;121(2):610-618.
- Newton I. The migration ecology of birds. Academic Press, London, U; 2008.
- North American Land Change Monitoring System (NALCMS) at 250 m spatial resolution. 2005. Produced by Natural Resources Canada/Canadian Center for Remote Sensing (NRCan/CCRS), United States
- O'Brien RM. A caution regarding rules of thumb for variance inflation factors. *Quality & quantity*. 2007 Oct 1;41(5):673-90.
- Pérez-Moreno H, Martínez-Meyer E, Soberón Mainero J, Rojas-Soto O. Climatic patterns in the establishment of wintering areas by North American migratory birds. *Ecology and evolution*. 2016 Apr;6(7):2022-33.
- PRISM Climate Group 2012 Four-km monthly products. Oregon State University, Corvallis, OR, USA. <http://www.prism.oregonstate.edu/>. Accessed 04/25/2019.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Rue H, Riebler A, Sørbye SH, Illian JB, Simpson DP, Lindgren FK. Bayesian computing with INLA: a review Annual Review of Statistics and Its Application. 2017; 4:395-421
- Salewski V, Bruderer B. The evolution of bird migration—a synthesis. Naturwissenschaften. 2007 Apr 1;94(4):268-79.
- Scacco M, Flack A, Duriez O, Wikelski M, Safi K. Static landscape features predict uplift locations for soaring birds across Europe. Royal Society Open Science 2019; 6:181440
- Schoener TW. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology. 1968 Jul;49(4):704-26.
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang HP, Harnik N, Leetmaa A, Lau NC, Li C. Model projections of an imminent transition to a more arid climate in southwestern North America. Science. 2007 May 25;316(5828):1181-4.
- Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA. Evolution of ecological niche breadth. Annual Review of Ecology, Evolution, and Systematics 2017 48:1, 183-206
- Shannon HD, Young GS, Yates MA, Fuller MR, Seegar WS. American white pelican soaring flight times and altitudes relative to changes in thermal depth and intensity The Condor. 2002; 104:679-683
- Shannon HD, Young GS, Yates MA, Fuller MR, Seegar WS. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. Boundary-Layer Meteorology. 2002 Aug 1;104(2):167-99.
- Shaw AK, Couzin ID. Migration or residency? The evolution of movement behavior and information usage in seasonal environments. The American Naturalist. 2012 Nov 27;181(1):114-24.
- Tingley, MW, Monahan, WB, Beissinger SR, and Moritz, C. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences. 2009; 106 (Supplement 2): 19637-19643
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. Nature. 2002 Mar;416(6879):389.
- Wang G, McClintic LF, Taylor JD. Habitat selection by American beaver at multiple spatial scales Animal Biotelemetry. 2019; 7:10
- Winger BM, Barker FK, Ree RH. Temperate origins of long-distance seasonal migration in New World songbirds. Proceedings of the National Academy of Sciences. 2014 Aug 19;111(33):12115-20.
- Winger BM, Auteri GG, Pegan TM, Weeks BC. A long winter for the Red Queen: rethinking the evolution of seasonal migration. Biological Reviews. 2019 Jun;94(3):737-52.

Table

Table 1. List of the environmental variables included in the species distribution modelling of American white pelicans.

Environmental variable	Code	Mean (min-max)	Original resolution	Source	Units / classes
a) Climatic					
Minimum Temperature (July)	tmin07	11.3 (-21.7 - 40.8)	30 arc-sec	Worldclim	°C
Total Precipitation (July)	ppt07	71.2 (0 - 967)	30 arc-sec	Worldclim	mm
Total radiation (July)	rad07	20305 (123 - 28340)	30 arc-sec	Worldclim	kJ/m ² day
Wind speed (January)	wind01	3.5 (0.5 - 19.1)	30 arc-sec	Worldclim	m/s
b) Land cover					
		Data type			
Cropland	crop	proportion	250 m	MODIS	NA
Grassland	grass	proportion	250 m	MODIS	NA
Developed	developed	proportion	250 m		NA
Water	water	proportion	250 m	MODIS	NA
Wetland	wetland	proportion	250 m	MODIS	NA

Figures

Figure 1

Land cover and land use map of the study areas and the global positioning system (GPS) tracking locations of migrants (black dots) in the breeding range and migrants (white dots) and residents (blue dots) in the wintering range of American white pelicans (AWPE).

Figure 2

The meshes created by the Voronoi triangulation for the stochastic partial differentiation equation (SPDE) model for the GPS location density at the non-breeding (left panel) and breeding (right panel) grounds of American white pelicans. The mesh for the SPDE consisted of triangles and two outer polygons. The inner non-convex polygon encompassed all GPS locations at the non-breeding or breeding grounds defining the domain of the spatial effects. The area between the inner and outer polygons was used to account for the edge effect. The meshes were created for demonstrative purpose with the maximum edge length of 100 km and 200 km. The SPDE analysis used the maximum edge length of 40 km and 60 km.

Figure 3

Proportions of six land-use and land cover classes at the non-breeding (a) and breeding grounds and habitat selection index (h) of six different land-use and land cover classes at the non-breeding (c) and breeding (d) grounds of American white pelicans in the United States before (open circle) and after (open triangle) aquacultural decline in 2005. Vertical lines are 95% credible intervals.

Figure 4

Seasonal niche analysis of American white pelicans with the ordination method. Polygons represent ecological niche in the climate or landscape space depicted by the two principal components (PCs). Polygon overlap area (in blue) measures climatic (a), landscape (b) and climate-landscape combined (c) niche overlap between the breeding (green polygon) and non-breeding season (red polygon). The continuous and dashed contour lines represent 100% and 50% (most common conditions) of the

available environmental background, respectively. Schoener's D and I indices of seasonal niche overlap (d) were calculated for climate, landscape, and combined niche.