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 distribution 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 tracker” or “niche switcher” hypothesis would better explain seasonal variations in the ecological niche breadth and overlap of the American White Pelicans (AWPE, *Pelecanus erythrorhynchos*). We also tested whether recent changes in the non-breeding ground land-use have altered the land-cover niche breadth of AWPE.

Methods: We built Maximum Entropy Models (MAXENT) to predict the AWPE breeding and non-breeding ranges using GPS locations, climate variables, and land-cover variables. We then compared the estimated climatic and land-cover niche breadth and the overlap between the breeding and non-breeding grounds.

Results: Our climate, land-cover, and combined species distribution models had a good to excellent predictive performance. Our findings supported the hypothesis that AWPE would be climatic niche switchers. American white pelicans showed little climatic niche overlap between nesting and wintering seasons. Migrants on the breeding grounds showed broader climatic niche than both residents and migrants on the non-breeding grounds. Finally, declines in availability of food resources provided by commercial aquaculture on the non-breeding grounds appeared to increase land-cover niche breadth.

Conclusions: Climatic niche switching suggests that AWPE may adapt to future climate changes with unexpected spatial distributions under global change. Future declines in wetlands and food resources may restrict AWPE spatial distributions. Future studies need to investigate AWPE demographic consequences of climate and land-use 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 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 living 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 and land covers) of the total living environmental 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 breadth and 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). Niche switchers, therefore, may have a broad ecological niche with minimal overlap between the breeding and non-breeding grounds (Wiens et al. 2010). Niche trackers have more constant, narrow niches throughout the year (hence, greater niche overlap between seasons) than niche switchers. 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- to middle-distant migrant and 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). 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 questions in this study: (i) Is the migratory behaviour of the AWPE populations better explained as niche trackers or niche switchers? (ii) Do AWPE migratory populations on the breeding grounds show wider climate niche but narrower land-cover niche (temporally more stationary) compared to AWPE on the non-breeding grounds? (iii) Is there 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? and (iv) Has the land-cover niche of AWPE on the non-breeding grounds expanded after the decline of aquaculture activities?

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). Our study areas included the entire geographic distribution range of the eastern metapopulation of AWPE in North America (Fig. 1). We followed King et al. (2017) to delineate the boundaries of the breeding and non-breeding ranges.

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). We divided the recorded GPS locations into the AWPE breeding grounds (only migrants) and non-breeding grounds (including migrants and year-round residents). 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.

The potential usefulness of satellite tracked data in avian Species Distribution Models (SDMs) has been increasingly addressed in the ecological literature (Engler et al. 2017). Several studies have demonstrated that even a limited number of tracked individuals (six or seven birds) can produce accurate and reliable predictive models (Jiguet et al. 2011, Gschweng et al. 2012, Williams et al. 2017). Aebischer et al. (1993) suggested six radio-tracked individuals as the minimum number sampled for habitat selection with telemetry relocation data. In our study, the number of tracked individuals and the number of presence locations were above the minimum suggested or used for avian SDMs and habitat selection in the literature (Aebischer et al. 1993, Proosdij et al. 2016, Williams et al. 2017).

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 (Phillips et al. 2006, Williams et al. 2017). 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. 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 (> 4.45 m/s) (Illan et al. 2017).

In a preliminary analysis, we built SDMs using data on the GPS locations from migrants and year-round residents on the non-breeding grounds during winter. The results of SDM fitting and niche analyses did not differ in either direction or significance between the migrants and residents. Thus, in further analyses, we combined the winter GPS locations of the migrants and the residents at the non-breeding grounds.

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. All comparative analyses were based on SDMs 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.

Environmental variables

We used two types of environmental predictors in raster format: (i) climate (14 variables) and (ii) land cover (five 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 strength 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. Correlations were highly significant ($R^2 > 0.8$; $p < 0.001$) in all climatic variables considered.

The choice of climate predictors reflected energy and water constraints on the spatial distribution of birds. 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. We chose NALCMS also because the US Land Cover Data Base does not include the AWPE geographic range outside the USA. 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). Given the importance of the presence of water for AWPE foraging habitat, we used a layer called “wetlands” (which discriminates between different types of wetlands) from the Global Lakes and Wetlands Level 3 Database (GLWD-3) (Lehner and Döll, 2004). We also calculated the variable “distance to water” as the Euclidean distance from every tracked location to the nearest permanent water body. 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 19 predictor variables. We only selected predictors of $VIF < 4$ (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 land cover raster files were resampled to the same spatial resolution of climatic layers at the 30 arc-second grid cell size (equivalent to 1 km resolution). The 1-km resolution was chosen for a balance between the computational burdens and the accuracy of SDMs, given the spatial extent of North America in this study. 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).

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	tmin07	11.3 (-21.7–40.8)	30 arc-sec	Worldclim	°C
Minimum Temperature (July)	ppt07	71.2 (0–967)	30 arc-sec	Worldclim	mm
Total Precipitation (July)	rad07	20305 (123–28340)	30 arc-sec	Worldclim	kJ/m ² day
Total radiation (July)	wind01	3.5 (0.5–19.1)	30 arc-sec	Worldclim	m/s
Wind speed (January)					
b) Land cover	hidro	17.3 (0–174.5)	250 m	USGS	km
Distance to water	lc2005	categorical	250 m	MODIS	16
2005 land cover	lchange	categorical	250 m	MODIS	NA
Land cover change (2005–2010)					
Wetlands	wetland	categorical	30 arc-sec	GLWD	10

Species distribution modelling and ecological niche analysis

To estimate the potential spatial distribution, climatic niche, and land-cover niche of AWPE, we built SDMs using climate, land-cover and climate-land cover combined predictors, respectively. We used the Maximum Entropy Model (MAXENT) for AWPE SDMs (Phillips et al. 2006). MAXENT has become a benchmark SDM for presence-only data and has been shown to outperform other algorithms (Elith et al. 2006). Additionally, MAXENT software was designed to integrate with GIS software thus making data input and distribution map outputs easier to handle (Elith et al. 2010). MAXENT compares the environmental conditions measured by selected predictors at presence locations with those at randomly selected points (i.e., pseudo-absence), which quantify the available 'background' of environmental conditions. MAXENT estimates the spatial distribution (i.e., relative occurrence likelihood in each grid cell) by finding the largest spreading of occurrence conditions (i.e., maximum entropy), with the constraints of the observed mean and variance of environmental conditions at the presence locations (Warren et al. 2010). Maximum entropy is essentially the same as maximizing the log likelihood of the exponential family data associated with species presence (Renner and Warton 2013).

As proved by Renner and Warton (2013), MAXENT can be parameterized in a way equivalent to a Poisson Point Process Model (PPM) for spatial count data. Consequently, we changed the MAXENT default settings following recommendations from Renner et al. 2015 to develop our PPM to retain duplicate GPS records in the same grid cell. Then, the raw output can be interpreted as a relative habitat-use intensity for

each grid cell, proportional to a Poisson intensity (not the default logistic output), to create habitat suitability maps across the entire AWPE geographic range. All other MAXENT settings were left at their default values. We used 10,000 randomly selected background locations for MAXENT. Thirty percent of occurrence records were withheld from each model to be used as independent testing data in a cross validation. For our models, background points were selected within the boundaries of the breeding and wintering grounds of the AWPE eastern population, respectively, following King et al. (2016). Then we projected the models to Canada, the United States, and the Southern GOM to cover all areas potentially reachable by AWPE.

The overall performance of the models was evaluated via the True Skill Statistic metric (TSS) (Allouche et al. 2006). The TSS takes into account both omission and commission errors, and its value ranges from -1 to +1, where < 0 indicates indiscriminate; 0 no better than random models; 0–0.2 poor; 0.2–0.6 fair to moderate; > 0.6 good to excellent; and +1 perfect agreement (Jones et al. 2010). The TSS is not affected by either prevalence or the size of the validation set (Allouche et al. 2006). We calculated the TSS for each MAXENT using the R packages “rocr” (Sing et al. 2005) and “boot” (Canty and Ripley 2017) in the R environment (R Development Core Team 2017). We performed a 10-fold cross-validation procedure and calculated the average TSS values for each model.

We also used the Area Under the Receiver-Operating Characteristic (ROC) Curve (AUC) to assess and compare the performance of the three models. The AUC metric has been widely used to assess model performance in machine learning and species distribution modeling (e.g., Araujo and Guisan 2006, Marmion et al. 2009, Deblauwe et al. 2016), although potential limitations have also been identified (see Lobo et al. 2008). The AUC values range from 0.0 to 1.0, with 0.5 indicating fit no better than random; 0.6–0.9 good; >0.9 indicating excellent fitting to data; and 1.0 indicating perfect model performance (Pearce and Ferrier 2000).

We calculated niche overlap between the breeding and non-breeding AWPE populations using the I statistic and Schoener's D implemented in ENMTOOLS (Schoener 1968, Warren et al. 2008, 2010). Both metrics were calculated using habitat suitability scores in all grid cells after suitability index values were standardized. Indices I and D range from 0 to 1, with 0 indicating no niche similarity between seasonal niches and 1 indicating complete similarity (Broennimann et al. 2012, Warren et al. 2008). We calculated the niche breadth of the populations using the Levin's concentration metrics implemented in ENMTOOLS (Quintero and Wiens 2013). The Levin's concentration metric also ranges from 0 to 1, indicating minimum to maximum niche breadth, respectively. We developed 10 MAXENT models by bootstrapping 10 sets of training data for each of the breeding and non-breeding AWPE populations and then calculated the niche breadth and niche similarity (overlap), respectively (Warren et al. 2010).

Maxent models project living environmental conditions to suitable geographic areas using relationships between occurrence probability or intensity and observed living conditions of species (Elith et al. 2010, Boucher et al. 2014). Such geographic projection approaches may bias the estimation of ecological niches between different geographic regions (such as breeding and nonbreeding regions) and between

different periods (such as seasons). Estimation of niche breadth and overlap may be more problematic when comparing seasonal niches in migratory than non-migratory birds because of differences in geographic extent, sampling bias, and climatic regimes (Elith et al. 2010, Boucher et al. 2014, Gomez et al. 2016). To verify the estimation of niche overlaps with Maxent models, 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 100 × 100 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 R package *ecospat* to conduct the ordination analysis of pelican 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 (Bronnimann, personal communication). If estimates of ecological niche overlap with both Maxent-based and ordination-based methods supported our hypotheses concerning seasonal niche variation, we focused on interpreting the Maxent-based estimations because of the wide applications of Maxent-based models.

Results

The number of birds that satisfied the filtering and inclusion criteria for analyses were 19 migrants on the breeding ground (eight individuals with 1,154 GPS locations for the pre-aquaculture SDM; 11 individuals with 2,123 GPS locations for the post-aquaculture SDM) and 30 individuals on the non-breeding grounds (15 individuals with 1,584 GPS locations for the pre-aquaculture; 15 individuals with 1,494 GPS locations for the post-aquaculture). After the multicollinearity removal, the resulting final set of non-correlated environmental predictors included four climatic and four land cover variables (Table 1).

Model performance evaluation with the 10-fold cross-validation showed that the TSS values ranged from 0.64 to 0.90 for all different SDMs (Table 2), which were considered to be a good to excellent performance. The average AUC values of all different SDMs ranged from 0.85 to 0.95, which were also considered to be a very good to excellent performance. Climate and the combined models performed marginally better than the land-cover models (Table 2, Fig. 2).

Table 2
The performance evaluation of species distribution models for American white pelicans using the True Skill Statistic (TSS). Average values for the 10 replicates and the associated standard deviation are shown for each model.

Model	Pre-aquaculture	Post-aquaculture
a) Breeding	0.841 ± 0.012	0.872 ± 0.031
Climatic	0.806 ± 0.029	0.853 ± 0.024
Combined	0.654 ± 0.053	0.662 ± 0.037
Land cover		
b) Non-breeding	0.902 ± 0.022	0.901 ± 0.033
Climatic	0.898 ± 0.023	0.893 ± 0.026
Combined	0.637 ± 0.060	0.644 ± 0.048
Land cover		

Both Maxent- and ordination-based estimates of ecological niche overlap between the breeding and non-breeding grounds indicated that overlap of climate niche (Schoener' D: Maxent-based = 0.08; Ordination based = 0.06) was much lower than that of land cover niche (Schoener' D: Maxent-based = 0.47; Ordination based = 0.63) between the breeding and non-breeding grounds (Figs. 3a and 4). Subsequently, we present the niche analysis of the Maxent-based methods. Mean / statistic was 0.24 for climatic niche overlap versus 0.73 for land-cover niche overlap, suggesting that migrating AWPE were likely to switch climatic niche and track land-cover niche. Our results showed the lowest niche overlap for the combined models, which appeared to be more in agreement with the niche switcher hypothesis (Fig. 3a).

Niche breadth analyses demonstrated that the breeding population had a greater climatic niche breadth (pre-aquaculture: 0.070 ± 0.001 ; post-aquaculture: 0.055 ± 0.001) than the non-breeding population (pre-aquaculture: 0.025 ± 0.001 ; post-aquaculture: 0.022 ± 0.001) (paired *t*-test, $P < 0.01$, $n = 10$). However, the difference between the pre- and post-aquaculture peak was not significant. The breeding populations showed a significantly narrower land-cover niche (pre-aquaculture: 0.061 ± 0.005 ; post-aquaculture: 0.232 ± 0.007) than the non-breeding populations (pre-aquaculture: 0.113 ± 0.001 ; post-aquaculture: 0.251 ± 0.001) (paired *t*-test, $P < 0.01$, $n = 10$). Land-cover niche breadth significantly differed before and after the aquaculture peak, for both the breeding and non-breeding populations (paired *t*-test, $P < 0.01$, $n = 10$) (Fig. 3b). Finally, niche breadth for the combined models was significantly greater for the breeding than non-breeding populations (paired *t*-test, $P < 0.05$, $n = 10$), but there was no statistically significant difference between pre- and post- aquaculture peak.

Discussion

Ecological niche needs to be considered 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). Temporal variation in niche breadth and overlap may also shed light on the evolution of avian migration (Gomez et al. 2016). 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. Likewise, adaptation to more spatially heterogeneous climatic conditions may result in broader climatic niche in temperate breeding grounds than in sub-tropical non-breeding grounds. After the aquaculture decline, AWPEs might have diversified wetland habitat use to compensate for decreases in food availability, broadening land-cover niches. Therefore, middle- and long-distance 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 migratory behavior of AWPE would be motivated by tracking climatic conditions between the breeding and non-breeding grounds (Shaw and Couzin 2012). On the contrary, the climatic niche switching 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). Winter climate harshness is a driver of avian migration which shifts the wintering range to low latitudes (Bell 2000, Newton 2008).

Tracking food availability is an important driver of the evolution of avian migration (Newton 2008). 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 in both the breeding and non-breeding grounds may result in appreciable seasonal overlap of land-cover niches. It is plausible to hypothesize that the broader land-cover niches on the non-breeding grounds would be a product of ancestral exploratory movements when AWPE shifted their wintering range to the Gulf of Mexico. Additionally, nesting activities may also restrict habitat selection and movements on the breeding grounds. Therefore, AWPE migration may be an example of the northern home hypothesis that avian migration originated from the shift of wintering grounds from temperate to sub-tropical regions (Bell 2000).

Our findings support our expectation that the recent drastic decline in aquaculture activities starting around 2005 (King 2005) had broadened AWPE land-cover niche on both breeding and non-breeding grounds. We found that land-cover niche breadth had expanded considerably on the non-breeding grounds after 2005, suggesting that AWPE were forced to find additional sources of food and/or shelter due to the disappearance of the aquaculture ponds. However, we also found land-cover niche expansion on the breeding grounds. A plausible explanation is that migrants will broaden land-cover niche during their breeding season as a carryover from the non-breeding grounds. We believe this is one of the most important results of our study, and has considerable economic implications for fish farming in the South-eastern US. Aquaculture, apart from being an economic driver in the region, is possibly acting as a sustainable system to maintain viable long-term AWPE populations. Finding a balance between the economic viability of aquaculture and the maintenance of the near perfect foraging habitats for pelicans seems crucial for the sustainability of the ecosystem (Murphy 2005, King and Anderson 2005).

Conclusions

Our study addressed a major concern in the conservation and future management of avian migrants, including AWPE, regarding their ability to cope with ongoing climate change. Our results suggest that AWPE might respond to global change in unexpected ways as they might not track climatic niche (Barbet-Massin et al. 2009). American white pelicans may adapt to new climatic conditions, changing their migratory patterns and/or geographical distribution, like other taxa (Hickling et al. 2006, Marini et al. 2009). Furthermore, if global change and anthropogenic disturbances reduce wetlands and their food availability, AWPE would track land-cover niches altering their spatial distributions in North America. Further research should explore how global changes will potentially affect the migration, spatial distribution, and population dynamics of wetland-dwelling migratory birds.

Abbreviations

AWPE: American White Pelican; MAXENT: Maximum entropy; SDM: Species distribution model; VIF: Variance inflation factor; CRU: Climate research unit; NALCMS: North American Land Change Monitoring System; FAO: Food and Agriculture Organization; GLWD: Global Lakes and Wetlands; AIC: Akaike Information Criterion; PPM: Poisson point process model; TSS: True Skill Statistic metric; ROC: Receiver-Operating Characteristic; Area under the curve: AUC;

Declarations

Ethics approval and consent to participate

The authors declare that no animal was harmed or hurt during the development of the present study.

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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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 predictions of maximum entropy models for the breeding and non-breeding ranges of American white pelicans by (a, b) climate, land covers (c, d), and climate – land covers combined (e, f). The left column (panels a, c, e) is for the breeding range and the right column (b, d, f) for the non-breeding range. Maps show in warmer colours the higher habitat suitability for each model and each range.

Figure 3

Seasonal niche analyses of American white pelicans with Maxent models. The niche overlap between breeding and wintering populations (panel a) and niche breadth (panel b) were determined for each of the climatic, land-cover, and combined models before (gray) and after (black) the aquaculture peak in the wintering grounds. Niche overlap is measured via Schoener's D (D) and the I statistic (I). Niche breadth is measured via the Levin's concentration metrics in all cases. In panel b, letter 'b' denotes breeding and letter 'w' denotes wintering.

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. The solid red arrows represent the displacement of the centre of the niche between the seasons.