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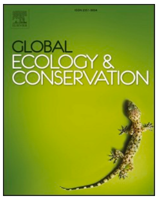

Seasonal variation and tracking of climate niche of a migratory bird

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ABSTRACT

Migratory birds inhabit different areas during breeding and non-breeding seasons. Depending on the time of the year, they may utilize different resources available in seasonal habitats, but also are subjected to changing climate regimes during their annual life cycle. Migratory birds may adopt ecological niche tracking to cope with different environmental conditions between breeding and non-breeding grounds. The American White Pelican (*Pelecanus erythrorhynchos*, hereafter 'AWPE') is a short-distance migrant between the Gulf of Mexico coastal regions (non-breeding grounds) and the Northern Great Plains (breeding grounds) of Canada and the US. The American White Pelican is a piscivore, feeding on fish, crayfish, and salamanders in inland freshwater wetlands. Cold, icy winter weather conditions substantially reduce and limit food resource availability at the breeding grounds during winters. Thus, we hypothesize that AWPEs would migrate between the breeding and non-breeding grounds to track climatic conditions that allow easier availability of resources. However, the niche tracking strategies have not been tested in AWPEs mainly due to the lack of reliable tracking data. Our objectives were to test whether the niche tracking or niche switching hypothesis would better explain seasonal variations in ecological niche overlap of AWPEs using the GPS locations of 19 tracked migrating birds, which had GPS locations at both breeding and non-breeding grounds. We estimated overlap of climate niche to test for seasonal niche tracking behaviors at both individual and population levels. Our results indicate that six out of 13 GPS-tracked AWPE individuals tracked climatic niche during the annual migration cycle. The analysis of the combined data of all 19 tracked AWPEs demonstrated that AWPEs tracked seasonal climate niche at the population level. Cold winter temperatures below zero (℃) may freeze the water surface of wetlands and shallow waterbodies, preventing AWPEs from acquiring sufficient food. The coupling of winter food resources with winter climatic conditions may result in climate niche tracking. Variation in climate niche tracking among individuals may offer ecological plasticity for AWPEs to cope with climatic changes.

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1. Introduction

Climate and environmental conditions vary from season to season, exerting profound effects on life history strategies, behaviors, and ecology of organisms, particularly in the northern temperate regions (Boyce, 1979; Roff, 2002; Stenseth et al., 2003). Organisms adapt to seasonal climatic variations physiologically, behaviorally, and ecologically (Roff, 2002; Thorup et al., 2017). Migratory birds make seasonal movements in distances spanning from hundreds to thousands of kilometers between their breeding and non-breeding grounds to exploit resources available in different seasons (Newton, 2008; Thorup et al., 2017). For instance, common cuckoos (*Cuculus canorus*), long-distant migrants, track vegetative greenness probably to maximize resource availability during their annual cycle (Thorup et al., 2017). These long-distance migratory movements are risky, making birds vulnerable to global changes (Dufour et al., 2020; Zurell et al., 2018b). Therefore, long-distance migrants must obtain important benefits for engaging in migration.

Studies of seasonal variation in ecology can help understand why birds migrate (Somveille et al., 2015; Winger et al., 2019) and assess the impacts of climate changes on migratory bird populations (Lamb et al., 2020; Ruegg et al., 2021; Zurell et al., 2018b). Although there are many studies of the ecology of migratory birds at both non-breeding (or wintering) and breeding grounds (Dufour et al., 2020; Fandos et al., 2020; Gómez et al., 2016; Joseph and Stockwell, 2000; Winger et al., 2019), previous studies tended to ignore non-breeding ranges due to lack of knowledge (Eyres et al., 2017). Studies of avian migration ecology at the breeding and non-breeding grounds often rely on IUCN range maps to define breeding and non-breeding areas, which do not reflect the dynamics of the ranges. The recovery and resighting of banding rings have been also used in studies of seasonal ecological niche overlap of migratory birds (Dunning et al., 2020; Fandos and Tellería, 2020). The aforementioned data are not suitable for studies of individual-level responses of migratory birds to climatic and environmental changes. Satellite or GPS tracking has revolutionized the acquisition of movement data of migratory birds, and has become a widely used method for studies of animal movement ecology (Cagnacci et al., 2010; Tucker et al., 2018). The GPS or satellite tracking of migratory birds can provide the locations data and ecological information of individuals or populations during the annual cycle, including the delineation of the breeding and non-breeding ranges.

Hutchinsonian niche theory defines the total environmental conditions, which enable populations of organisms to survive and

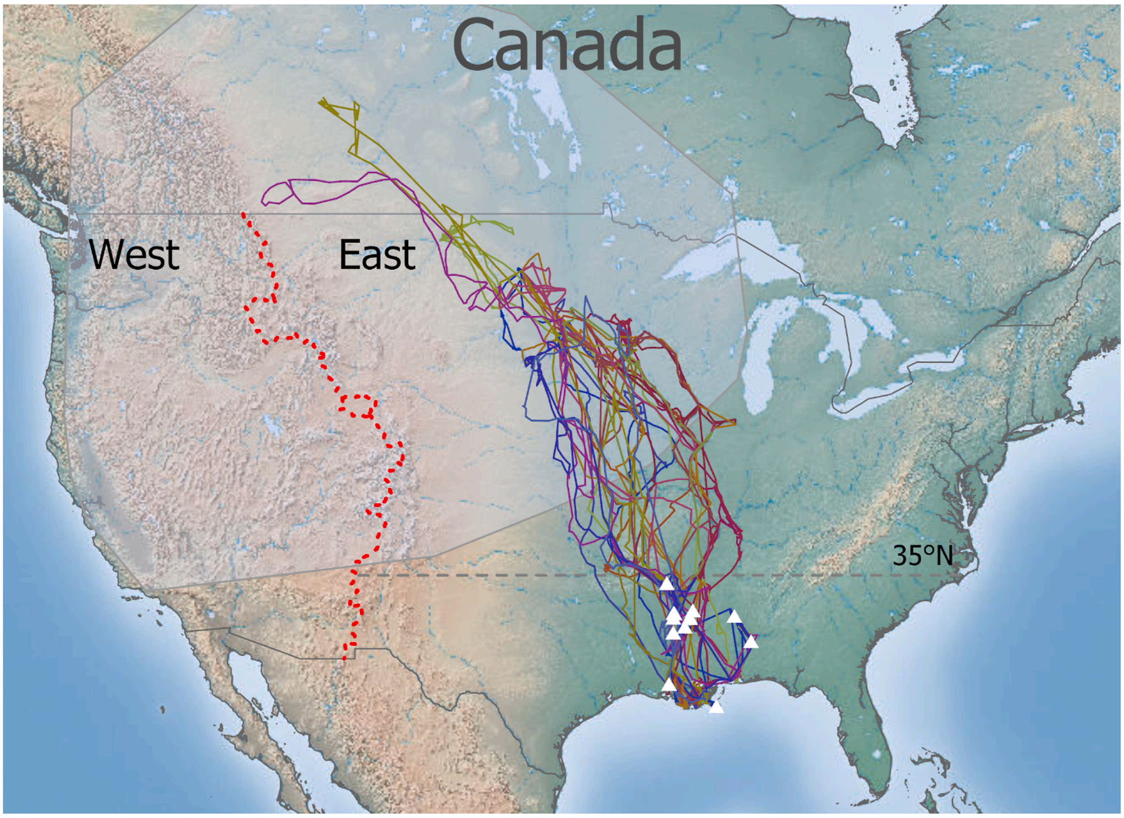

Fig. 1. The breeding range and the northern boundary (35° N latitudinal line) of the non-breeding grounds of American White Pelicans. The polygon of light-blue color delineates the area encompassing all known nesting grounds. The white triangles mark the capture locations of American White Pelicans in the non-breeding grounds from October to March from 2002 to 2009. The red dotted line is the Continental Divide which separates American White Pelicans into the eastern (East) and western (West) metapopulations. The solid lines that run between the breeding and non-breeding grounds are migration trajectories of 19 American White Pelicans. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

grow, as the fundamental ecological niche (Hutchinson, 1957). The Hutchinsonian niche is a multi-dimensional hypervolume of abiotic and biotic environments including different niche dimensions or axes (Sexton et al., 2017). Habitats and resources actually occupied by organisms represent parts of their realized ecological niche (Hutchinson, 1957). Temporal variation and flexibility (e.g., niche shift) of ecological niche may allow organisms to adapt to environmental changes (Tingley et al., 2009; Winger et al., 2019). Migration imposes physiological challenges to migrants with different climatic regimes along their migration routes, resulting in different seasonal ecological requirements during the annual cycle (Gómez et al., 2016; Marini et al., 2013; Winger et al., 2019). Studies of seasonal variation and overlap in climate niche can help us understand the impacts of ongoing climate changes on migratory birds (Gómez et al., 2016; Tingley et al., 2009).

Migratory birds may track seasonal ecological niche or resources to cope with physiological challenges and resource availability during the annual cycle. Migrants either track a set of environmental conditions (e.g., climate) year-round (niche tracker) or adapt to different environments when moving from one ecological regime to another (niche switcher) (Gómez et al., 2016; Laube et al., 2015). Earlier studies of seasonal climate niches primarily focused on population-level niche behaviors. For instance, Ponti et al. (2020) found that 80% of 355 migratory birds migrating through Eurasian–African flyways were climate niche switchers. However, Fandos and Tellería (2020) demonstrated that European Robins (*Erithacus rubecula*) and Eurasian Blackcaps (*Sylvia atricapilla*) tracked climate niche. The inconsistencies of the relationship between niche tracking or switching and migratory behaviors may be due to variations in life history traits among migratory birds (Eyres et al., 2020; Zurell et al., 2018a). Furthermore, migratory birds are likely to switch to different seasonal climate niche if they travel long distances between seasons (Dufour et al., 2020). Recent studies have demonstrated that ecological niche tracking of migratory birds may be scale-dependent (e.g., individuals and populations). Carlson et al. (2021) found that white storks (*Ciconia ciconia*) had individual environmental niche variation and specialization. Individual white storks track weather conditions, whereas climate niche tracking emerges at the population level (Fandos et al., 2020). Variation in individual niche tracking behaviors may ameliorate the detrimental impacts of global changes on migratory birds. However, little is known about the ability of individuals to adjust climate niche tracking (such as yearly variation) in response to global changes (Thorup et al., 2017).

The American White Pelican, *Pelecanus erythrorhynchos* (hereafter 'AWPE'), is a short-distance migrant (King et al., 2017). American White Pelicans wintering in the lower Mississippi River Valley migrate to the Northern Great Plains in spring (Fig. 1; King and Anderson, 2005; King et al., 2017; Strait and Sloan, 1975). Furthermore, AWPEs are habitat specialists primarily using inland freshwater wetlands. Although AWPEs are mainly piscivorous, they also feed on salamanders and crawfish (King et al., 2010; King and Michot, 2002; Sibley, 2001). Cold winter temperatures freeze the surface water of wetlands and shallow waterbodies in the AWPE breeding grounds in late autumn and winter, preventing AWPEs from accessing food. Zurell et al. (2018a) found that seasonal niche overlap of migratory birds is inversely related to migration distance and that large-sized birds are likely to track seasonal ecological niche. It is plausible to predict that AWPEs, a large-sized short-distance migrant, would track climate niche during their migration. However, no studies, to the best of our knowledge, have tested for ecological niche tracking or switching behaviors of AWPEs at the individual or population levels. Our objectives were to: (1) evaluate seasonal variation in climate niches of AWPEs between the breeding and non-breeding grounds at both individual and population levels; and (2) test the hypothesis that AWPEs would track climate niche between breeding and non-breeding grounds and that population-level climate niche tracking may be stronger than at individual levels (Fandos et al., 2020).

2. Methods

2.1. Study areas and GPS tracking of American White Pelicans

American White Pelicans are divided into eastern and western metapopulations by the Continental Divide (Fig. 1; King and Anderson, 2005). The AWPE eastern metapopulation migrates between the Northern Great Plains (the breeding grounds) and the Gulf of Mexico (the non-breeding grounds) along the Mississippi and Ohio River Valleys (King et al., 2017; Shannon et al., 2002). We defined the breeding grounds as the areas delineated by the boundaries of the breeding range to encompass the geographic locations of all known AWPE colonies from King and Anderson (2005) and the North America Breeding Bird Survey transects of non-zero AWPE relative abundance (Fig. 1; King et al., 2017). The breeding grounds delineated by the boundary of the breeding range are the known nesting grounds, in which climatic and habitat conditions are suitable for the breeding activities of AWPEs (King and Anderson, 2005). We followed King et al. (2017) in using the 35°N latitudinal line as the northern boundary of the AWPE non-breeding grounds (Fig. 1), which was determined by the spatial threshold method and the net squared displacement method (Soriano-Redondo et al., 2020). During winter, AWPEs spent extended periods in the area surrounding aquacultural facilities where they were initially captured in the Mississippi Alluvial Valley south of the 35°N latitudinal line (King et al., 2017). Furthermore, field observations and eBird data demonstrated that AWPEs have been observed in an extended area south of the 35°N latitudinal line between November and February (King et al., 2017).

American White Pelicans were captured at sites near aquaculture-intensive areas in Alabama, Arkansas, Louisiana, and Mississippi, USA using rocket nets and modified soft catch foot-hold traps during March and April from 2002 to 2009 (Fig. 1; King et al., 1998). Captured AWPEs were aged (>3 yr. old = adult; <3 yr. old = immature) by plumage and eye and skin color characteristics and were sexed by culmen length (Dorr et al., 2005). Captured AWPEs were fitted with 70-g solar-powered GPS transmitters (PTT-100, Microwave Telemetry, Columbia, Maryland, USA) using a backpack harness (Dunstan, 1972). 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).

We used the GPS locations of 19 GPS-tracked AWPEs in the population-level ecological niche analysis because each of the 19 birds had the GPS location data at both the breeding and non-breeding grounds. For individual-level ecological niche analysis, we used 13 birds that had at least 100 GPS locations at both the breeding and non-breeding grounds. Two different daily AWPE tracking schedules were used among the 19 AWPEs: (1) location recording from 05:00 h. to 22:00 h. ($n = 19$) and (2) for consecutive 24 h ($n = 3$, Table S1). The GPS tracking was programmed to record the AWPE locations hourly during the daily GPS-on hours (i.e., maximum 18 or 24 locations a day). American White Pelicans were rarely active during the GPS-off hours of Schedule 1 (King and Werner, 2001). The recorded GPS locations were divided into the AWPE breeding grounds and non-breeding grounds. For the purpose of this study a GPS-tracked individual was considered in spring migration when it crossed 35^{o}N latitudinal line northward until the bird entered the breeding range (King et al., 2017). A bird was in autumn migration from when it departed from the breeding range until the bird crossed the 35^{o}N latitudinal line southward. Thus, breeding-ground locations included those between the first arrival at the breeding range in spring and the departure from the breeding range in autumn, whereas non-breeding ground locations included those (south of the 35^{o} N latitudinal line) between the first arrival at the non-breeding ground in autumn and following spring departure. We excluded AWPE GPS locations during seasonal migration from our analysis, only including AWPE GPS locations at the breeding and non-breeding grounds in our analysis. It is possible that our method may result in the inclusion of some migratory movement locations in our datasets for the breeding and non-breeding grounds. However, as a short-distance migrant, seasonal migration trip lasts for 3–17 days on average, whereas AWPEs spend about four months at their breeding grounds and about seven months at the non-breeding grounds (King et al., 2017). Migratory movement locations included in the datasets may only constitute a small part of the entire dataset for either breeding or non-breeding grounds. Furthermore, the flyover area covered by those migratory movement locations are either the wintering (south of 35^{o}N latitudinal line) or the nesting habitats of AWPEs. Therefore, the inclusion of some numbers of migratory movement locations does not misrepresent climatic conditions of the breeding or non-breeding grounds for climate niche analysis.

2.2. *Climate variables at the GPS locations of American White Pelicans*

Climatic variables were obtained from Climatologies at high resolution for the earth's land surface areas (*Chelsa*) database version 2.1 (https://chelsa-climate.org/downloads/). The *Chelsa* climate database provides a high resolution (30″, about 1 km) of monthly minimum, mean, and maximum temperatures (°C) and total monthly total precipitation (mm) for the entire earth land surface from 1979 through 2013 (Karger et al., 2017). Water levels, soil moisture, and total acreage of wetlands are related to amounts of seasonal precipitation (Donnelly et al., 2020; Millett et al., 2009). Increased precipitation can influence the quantity and quality of wetlands, by improving streamflow and groundwater recharge (Haig et al., 2019; Millett et al., 2009). Freshwater species richness is positively related to precipitation (Dodds et al., 2019). Therefore, increases in precipitation can influence the number of wetlands and amount of food availability within wetlands. The GPS tracking of AWPEs spanned from 2002 to 2010 in this study; thus, we used the time series of the monthly values of the four climate variables in climate niche analysis. We extracted the values of the monthly climatic variables for each GPS location according to the month and year of the time stamp of each GPS location using the function *extract* of the package *raster* (Hijmans, 2016). We standardized the four climate variables so that they have the mean of zero and standard deviation of 1.

2.3. *Seasonal climate niche analysis*

We estimated the overlap of climate niche between seasons using an ordination method based on principal component analysis (PCA; Broennimann et al., 2012). The ordination approach compares seasonal niches in the environmental space represented by the first two principal components (PCs) of PCA. Each PC is a linear combination of the four climate variables with the loading factor being the coefficients. 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. Climatic condition is smoothed and rescaled to 0–1 range for each grid cell as well (Broennimann et al., 2012). The ordination approach allows for direct niche comparisons between regions and seasons correcting for differences in geographic extent, environmental or climatic conditions, with occurrence density being divided by the background density of available resources. We used the R package *ecospat* to conduct the ordination analysis of AWPE seasonal climate niche (Di Cola et al., 2017). We calculated Schoener's *D* to measure niche overlap using the R package *ecospat* (Schoener, 1968). Index *D* ranges from 0 to 1, with 0 indicating no niche overlap and 1 indicating complete overlap.

We used the niche similarity test to evaluate whether observed ecological niche overlap between the breeding and non-breeding grounds were greater than that between simulated ecological niches selected at random from observed AWPE occurrences in the breeding and non-breeding grounds, respectively (Broennimann et al., 2012). The niche similarity test simulates ecological niches by randomly shuffling the centers of the niche space in the available environmental space of the breeding and non-breeding grounds, respectively. The simulated niche space of the breeding ground is compared to the observed niche space of non-breeding grounds, and vice versa. The niche similarity test estimates Schoener's *D* between the observed niche of the breeding ground and the simulated niche of the non-breeding ground as well as between the observed niche of the non-breeding ground and the simulated niche of the breeding ground. This random permutation is repeated 1000 times for the breeding and non-breeding grounds, respectively. We estimated Schoener's *D* at both individual and population levels. For the individual niche analysis, we used migrating AWPEs in ecological niche analysis with each migrant having > 100 GPS locations at breeding and non-breeding grounds, respectively. To avoid the overfitting of each individual with more GPS locations (Carlson et al., 2021; Fandos et al., 2020), we took a random sample of 100 locations for the breeding and non-breeding grounds, respectively. One hundred presence locations are more than the minimum number of locations recommended for ecological niche analysis (Guisan et al., 2017; Zurell et al., 2018a). The *P* value of the niche similarity test was estimated with 1000 permutations (Fandos et al., 2020; Zurell et al., 2018a). We concluded that individual pelicans tracked ecological niche if the observed niche overlap was significantly greater than the randomly simulated niche overlap. We also pooled all GPS locations over the 19 GPS-tracked AWPEs at the breeding and non-breeding grounds, respectively, to estimate Schoener's *D* to determine population-level climate niche tracking using the same methods for individual-level niche analysis.

3. Results

We used a total of 36,088 GPS locations for the 19 GPS-tracked AWPEs for the population-level ecological niche analysis in this study, including 20,789 locations at the non-breeding grounds and 15,299 locations at the breeding grounds (Tables S1 & S2). Out of the 19 GPS-tracked AWPEs, 13 birds were used for individual-level ecological niche analysis because they had at least 100 GPS locations at both the breeding and non-breeding grounds. The ID number, sex, age, tracking schedules, and the number of GPS locations of the tracked birds were included in Table S1.

Thirteen AWPEs generated the data of 17 spring-autumn migration events for individual ecological niche analysis. Out of 13 birds, six AWPEs had observed climate niche overlap between the breeding and non-breeding grounds being significantly greater than that of randomly simulated climate niche, indicating climate niche tracking at the individual level (Fig. 2a). Some AWPE individuals exhibited variation in niche tracking between years. For instance, AWPE ID # 36045, 86864, and 86865 differed in climate niche tracking behaviors between two different years, changing from the tracking to the switch and vice versa. Average individual climate niche overlap D was 0.3 (standard deviation [SD] = 0.17, $n = 17$). AWPEs tracked climate niche at the population level with the data of 13 APWEs each having > 100 GPS location per season (D = 0.44, P = 0.01, Fig. 2b). The first PC explained 74% of total variability with the eigenvalue being 2.969, and the second PC explained 24% with the eigenvalue of 1. Principal component 1 represented temperature more than precipitation with the loading factors being −0.997, −0.984, −0.983, and 0.082 for average temperature, min temperature, max temperature, and precipitation, respectively. Principal component 2 primarily represented precipitation with the loading factors being 0.042, 0.112, −0.071, and 0.996 for average temperature, min temperature, max temperature, and precipitation, respectively. Ecological niche analysis with all GPS locations from 19 migrating AWPEs also demonstrated that AWPEs tracked climate niche (Schoener's $D = 0.40$, $P = 0.001$).

4. Discussion

Animals may exhibit seasonal variations in ecological niche with seasonal variations in climatic conditions and resource availability at both individual and population levels (Fandos et al., 2020; Gómez et al., 2016; Ruegg et al., 2021; Winger et al., 2019). Difficulties of collecting data on spatial use and movement during the annual migration cycle have hindered studies of seasonal ecological niches of migratory birds (Fandos et al., 2020; Laube et al., 2015). This study is among the few studies which used GPS

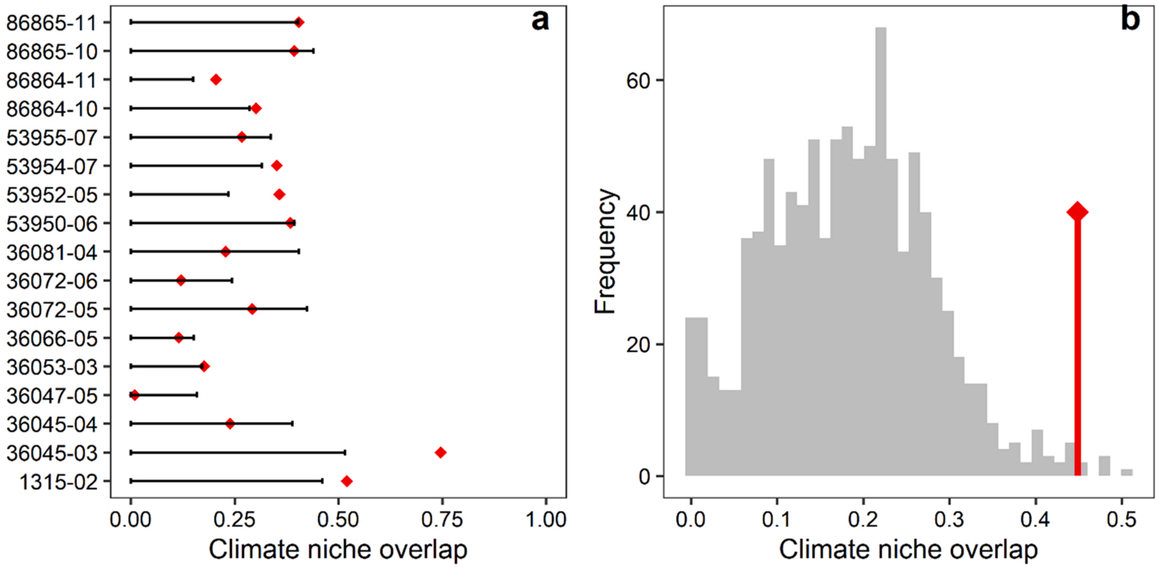

Fig. 2. Individual seasonal climate niche overlap of 13 American White Pelicans between the breeding and non-breeding grounds (a) and climatic niche overlap (Schoener's D) of American White Pelican populations (b). In panel (a), horizontal error range lines of panel (a) are 90% of empirical confidence intervals of Schoener' D (x axis) with the lower and upper limits being 5% and 95% percentiles, respectively; the red diamonds are observed Schoener's D of migration events. Tick labels of the y axis are animal ID and last two digits of year connected by hyphen "-". In panel (b), histogram is for randomly simulated climate niche overlap. The red diamond is observed Schoener's D. D ranges from 0 to 1, with 0 indicating no overlap and 1 complete overlap. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tracking or other presence data of the same individuals at both breeding and non-breeding grounds to estimate climate niche overlap at the individual and population levels (Carlson et al., 2021; Fandos et al., 2020; Torney et al., 2018). Our findings support the climate-niche tracking hypothesis that AWPEs track similar climatic conditions between the breeding and non-breeding grounds at individual and population levels. We also found evidence for the prediction that the niche-tracking behavior of AWPEs was stronger at the population level than at the individual levels. Migratory birds may have different requirements each season or need plastic climate niches to adapt to space-time differences in ecological conditions during the annual migration cycle (Gómez et al., 2016; Ruegg et al., 2021; Thorup et al., 2017).

Studies of niche tracking or switching behaviors need to have data on climate, movement, and resource use of the same migratory individuals living in their spatially disjunct seasonal habitats hundreds or thousands of kilometers apart. Like Carlson et al. (2021) and Fandos et al. (2020), our study has used> 15,000 AWPE locations from the breeding and non-breeding grounds, respectively, to assess seasonal climate niche of AWPEs. However, the possible detrimental effects of transmitter attachment on the behavior, movement, and physiology of tracked birds always concern avian ecologists (García et al., 2021). Although the PTT transmitters weighed 70 g (< 1% of average body mass of AWPEs), the potential effects of GPS transmitter deployment on the movement and space use of AWPEs have not been assessed in this study. Nevertheless, Lamb et al. (2017) found that transmitter attachment did not affect the behavior and demography of Brown pelicans (*Pelecanus occidentalis*). Furthermore, our study used the spatial threshold methods to divide the GPS locations into segments for the breeding season, non-breeding season, spring migration, and autumn migration partially because of our sparse GPS location data during the migration seasons, which does not account for the modes (e.g., migratory flight, nesting, and foraging) of movements. Future studies need to use unsupervised or supervised classification to segment the seasonal locations for individual niche analysis (Carlson et al., 2021; Wang, 2019).

Previous studies have found evidence for climate niche trackers following the similar climatic conditions year-round (Fandos and Tellería, 2020; Gómez et al., 2016; Joseph and Stockwell, 2000; Nakazawa et al., 2004) and climate niche switchers living in different climatic conditions between the seasons (Laube et al., 2015; Marini et al., 2013). This study supports the hypothesis that AWPE would track climatic conditions between the breeding and non-breeding grounds at both individual and population levels. Our PCA analysis demonstrated that temperature was a primary factor representing the climatic conditions under which AWPEs live, with the temperature-dominant PC explaining the variability of the climatic conditions about twice more than the precipitation-dominant PC. Harshness of autumn temperatures at the northern temperate breeding grounds may drive avian migrants to migrate southward to subtropical or tropical regions to enhance winter survival (Gómez et al., 2016; Somveille et al., 2015). American White Pelicans forage in shallow water lakes and wetlands. Cold winter temperatures may freeze surface water at the nesting grounds during winter, preventing AWPEs from acquiring sufficient food and forcing AWPEs to migrate southward in late autumn. Cold temperatures and frozen wetlands also reduce food availability of other waterbirds in North America, which subsequently determines the departure timing of autumn migration and spatial distribution of wintering waterbird populations (Schummer et al., 2010). Warming up to 2 ℃ increases in air temperatures and frequent flooding events have been projected for North America through the 21st century (IPCC, 2021). Future studies need to monitor and determine whether AWPEs respond to warming with an extended breeding season in the Northern Great Plains.

Our findings demonstrated that 35% of annual migration events made by six of the 13 birds examined tracked climate niches. Fandos et al. (2020) found that 10–25% of white stork individuals tracked climate niche. Such individual-level variation in ecological niche tracking behaviors may be due to individual niche specialization and interactions between environmental conditions and life-history traits (Carlson et al., 2021). Individual variation in environmental niche may result from individual variation in habitat selection (Carlson et al., 2021). Johnson et al. (2013) show that the strength and even direction (i.e., positive or negative) of resource selection for sea surface temperature by northern fur seals (*Callorhinus ursinus*) differed among individuals. Wild turkeys (*Meleagris gallopavo*) also exhibit substantial differences in the strength and direction of their selection of land cover types among individual birds (Almond, 2019). Population-level responses of habitat or resource selection by animals to resource availability may differ from individual-level responses (Newediuk et al., 2022), similar to the observation that climate niche tracking of white storks emerged at the population levels (Fandos et al., 2020; Zurell et al., 2018a). Individual variation in ecological niche and behavior may enable species or populations to adapt to environmental changes (Bolnick et al., 2003; Carlson et al., 2021; Van Valen, 1965).

Migratory birds may shift their habitats or use different core habitats at the breeding or non-breeding grounds between years. For instance, whinchats (*Saxicola rubetra*) use multiple sites at the wintering grounds (Blackburn and Cresswell, 2016). It is plausible that individual niche tracking may vary due to the use of different sites between years. We also found that individual niche tracking of AWPEs varied between years. American white pelicans wintering in the Mississippi Alluvial Valley exhibit population-level wintering site fidelity (Fig. 1 of King et al., 2017). However, AWPE individuals may use different numbers and sizes of core habitat areas at the breeding and non-breeding grounds between years. Yearly variation in the number and size of the core habitats of migratory individuals may result in temporal variation in individual niche tracking, providing a means to cope with climatic changes. There were more immatures than adults in our tracked AWPEs. Young migrants may make exploratory movements after their first migration trip to the non-breeding grounds and return to wintering locations which promote survival in future years (Cresswell, 2014). Migrating Marsh Harrier (*Circus aeruginosus*) make substantial post-migration movements (up to 632 km) after arriving at wintering grounds (Strandberg et al., 2008). Immature AWPEs have larger winter home ranges than mature birds probably due to the exploratory sampling of their winter habitats (King et al., 2016). Immature AWPEs may have more flexibility in movement and resource use than mature AWPEs, which may result in bias (e.g., underestimate) in our inference of climate niche tracking of AWPEs.

5. Conclusions

Our findings provide a case study of niche tracking strategy in the migration of large-sized birds of passive flight (Zurell et al., 2018a). Seasonality and harshness of winter climate in the temperate breeding grounds may force AWPE to migrate southward to non-breeding grounds in subtropic or tropic regions for overwintering. American White Pelicans tracked climate niche between the breeding and non-breeding grounds with substantial variation among individuals. Long-term population trends of migratory birds are influenced by climate changes at the breeding grounds (Howard et al., 2020). Future studies need to assess whether individual variation in climate niche tracking behaviors can improve the adaptation of AWPEs to global change, ameliorating the impacts of global changes.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

Data used in this study will be archive in a public data-sharing repository after the manuscript is accepted for publication.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02155.

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