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Large- and Small-Scale Climate Influences Spring Migration Departure Probability of American White Pelicans

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Abstract: Endogenous (e.g., age and sex) and exogenous (e.g., climate and resource availability) factors influence avian migration phenology. However, little is known regarding the migration ecology of birds at the non-breeding grounds, including the American white pelican (*Pelecanus erythrorhynchos*). We used Global Positioning System transmitters to track the movements and migration of 51 pelicans from 2002 to 2012. We used the Kaplan–Meier model to estimate pelican spring migration probabilities to quantify partial migration with 94 spring migration events and used the Cox proportional hazards model to evaluate the effects of the North Atlantic Oscillation index (NAOI), Southern Oscillation Index (SOI), and spring daily precipitation on the propensity of pelican spring migration departures. Increases in the NAOI and SOI enhanced the propensity of pelican spring departure. The propensity of spring departure was also positively related to daily precipitation. Male pelicans have greater spring migration probabilities than female pelicans. Spring migration departure probabilities of adult pelicans are greater than those of immature pelicans. Therefore, both large-scale and local climatic conditions affect pelican spring departure probabilities. Advanced migratory phenology of pelicans caused by climate changes with warming temperature and increased precipitation may result in the mismatch of pelican spring arrival with food resource availability of breeding grounds and subsequent pelican population declines.

Keywords: global positioning system transmitter; north Atlantic oscillation; southern oscillation; spring migration

1. Introduction

Migratory birds move seasonally between the breeding and non-breeding grounds to utilize resources available during different seasons and escape inclement winter climatic conditions in the temperate region [1]. Multiple intrinsic (e.g., age, sex, body condition, and genetics) and extrinsic factors (e.g., climate, predation risk, and resource availability) influence avian migration phenology [1–3]. Climatic conditions such as temperature and precipitation may cue birds to initiate spring migration [4–6]. Spring temperature is believed to be the most influential exogenous factor of spring migration timing [6]. Springtime warming at the non-breeding grounds may enhance the migratory propensity of migratory birds [7]. Haest, Hüppop, and Bairlein [6] found that spring precipitation at the wintering grounds was needed to better explain the observed trends of spring migration phenology of nine species of migratory birds, which migrate between western Europe and coastal northwest Africa. However, multiple climate variables may be integrated and act in concert to influence avian migration timing.

Indices of large-scale atmospheric circulation, such as Southern Oscillation (SO) and North Atlantic Oscillation (NAO), are proxies for climate conditions—representing a package of weather for global climate changes [8]. The NAO is associated with changes in the

surface westerlies between the sub-polar and sub-tropic regions across the North Atlantic onto Europe [9]. The SO is the atmospheric circulation of the air mass in the Pacific between the eastern and western hemispheres, centering in the tropical and subtropical latitudes. Migratory birds move a long distance during a relatively short period. The NAO index (NAOI) and SO index (SOI) may be appropriate climate proxies for studies of avian migration phenology because the NAO and SO influence climatic variability at the global scale, resulting in teleconnection in climate phenomena over a long distance between breeding and non-breeding grounds [10,11].

The influences of the NAO and SO on local climate may differ in different parts of the Earth [10,12]. Positive NAOI values are related to strong westerly winds moving northward, corresponding to warmer wintertime temperatures and increased precipitation in the southeastern United States (US), whereas negative NAOI values are related to weakened winds with cooler wintertime temperatures and precipitation in the southeastern US [8,9]. Stronger northward-moving winds and warmer temperatures associated with higher NAOI would increase spring departure probability. Although high NAOI values are related to early departure and arrival of long- and short-distance migratory birds in Europe [11,13], relationships between spring migration phenology and NAOI were inconsistent among North American migratory birds [14–16].

The SO is associated with two well-known climate anomalies—the El Nino (extremely negative SOI < −8) and the La Nina (extremely positive SOI) [8,10]. Gilford et al. [17] found that the El Nino winter daily temperature (16.1 °C) was likely to be twice more than that (8.3 °C) of the La Nina winter in the southeastern US including Alabama, Florida, and Georgia. The more positive SOI values are correlated with less precipitation and higher temperature in winter, while more negative SOI values correspond to more precipitation and lower temperature in the southern US in winter [8,10]. Despite some spatial variation, it has been validated that winter mean SOI was positively related to winter mean precipitation in the southeastern US, including Alabama, Florida, Georgia, and Mississippi [18]. It is plausible to hypothesize that warmer, drier spring climates of more positive SOI would generate more thermals (rising warm air mass) to facilitate the spring migration of soaring birds. Previous studies primarily used winter or monthly mean NAOI and SOI values to predict mean departure and arrival dates at population levels. However, it is uncertain which temporal scales or time windows of climatic conditions influence spring migration decisions of migrants.

The American white pelican *Pelecanus erythrorhynchos* (hereafter, pelican) is among the largest native flying birds of North America [19]. Pelicans wintering in the lower Mississippi River Valley and along the Northern and Southern Gulf of Mexico (GOM) are short-distance partial migrants, migrating to the Northern Great Plains with soaring flying in spring [20–22]. King, Wang, Yang, and Fischer [21] investigated the migration phenology of pelicans wintering in the Northern Gulf of Mexico using global positioning system (GPS) transmitters. Illan et al. [23] found that pelican hourly flying speed was positively related to tailwind speed in both spring and autumn migration, but was positively related to thermal updrafts only during spring migration. However, no studies, to the best of our knowledge, have estimated the effects of climate on the spring daily migration probability of pelicans at the non-breeding grounds. In this study, we tested the three predictions that pelican migration probability in the GOM: (1) would increase with increasing NAOI which is related to strong northward-moving winds and warm climate; (2) would be positively related to the SOI; and (3) would be positively related to interaction of temperature and precipitation. Global positioning system (GPS) tracking enabled us to assess the effects of the NAO and SO on pelican spring departure probabilities and evaluate the relative importance of large- and small-scale climates in pelican migration phenology.

2. Materials and Methods

2.1. Global Positioning System Tracking for Determining Spring Departure Timing

We used GPS relocation data to determine the timing of pelican spring migration at the wintering grounds. Thirty-two 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 [21,24]. Nineteen pelicans were captured near Chase Lake, North Dakota, USA. Captured pelicans were aged ($\geq$3 y old = adult; <3 y old = immature) and sexed [25]. Captured birds were fitted with 70 g solar-powered GPS satellite transmitters (PTT-100, Microwave Telemetry, Columbia, MD, USA; <3% of body mass) using a backpack harness [26].

We used two different daily pelican tracking schedules: (1) GPS-on from 0500 h to 1900 h (30 birds) and (2) for consecutive 24 h (21 birds). One GPS location per hour was recorded during the daily GPS-on hours. American white pelicans were rarely active during the GPS-off hours of Schedule 1 [27]. The N 35° latitude line was determined as the northern boundary of the pelican non-breeding range with the methods later called spatial threshold method and net squared displacement method by Soriano-Redondo et al. [28]. Spring departure date of pelicans was defined as the first date when pelicans cross the N 35° latitude line northward and continue to move northward during spring [21].

2.2. Daily North Atlantic Oscillation Index and Daily Southern Oscillation Index

The NAOI is a standardized index. The NAO can be measured by the difference between winter sea level barometric pressure in Gibraltar and the winter sea level barometric pressure over Iceland. The daily NAOI was calculated by the interpolation using the least squares regression method. Daily NAOI time series was downloaded from the NOAA National Weather Service Climate Prediction Center (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html, accessed on 30 June 2021). Daily NAOI values vary between −3.254 and 2.751.

The SOI is a standardized index measuring the difference of the barometric pressures between Darwin, Australia, and Tahiti [29]. Daily SOI data were downloaded from the Open Data Portal of Queensland Government, Australia (https://www.data.qld.gov.au/dataset/the-southern-oscillation-index-soi-daily, accessed on 30 June 2021). We used the daily SOI time series since 1999 calculated using the 1933–1992 base period. Daily SOI ranges from −76.05 to 224.84. We standardized NAOI and SOI to make them have a mean of 0 and standard deviation of 1.

2.3. Daily Ambient Temperature and Precipitation of the Non-Breeding Grounds in the Southeastern US

We acquired data on daily temperatures (°C) and precipitation (cm) recorded at 40 weather stations located within the winter range boundaries from the National Oceanic and Atmospheric Administration National Center for Environmental Information (http://www.ncdc.noaa.gov/cdo-web/, accessed on 1 January 2018). The wintering range boundary was defined with the GPS locations of pelicans which skipped spring migration remaining in the Northern GOM year-round [21]. We then calculated averages of daily mean temperatures and daily precipitation over all the weather stations for each day from 1 January 2001 to 31 December 2012. Daily temperatures and daily precipitation were centered by long-term daily means to remove seasonal trends using the formula $\Delta w_t = w_{t,j} - \overline{w}_j$, where Δw_t is the deviate of a weather variable w_t in day t (t = 1, 2, . . . , 4389) from long-term daily mean $\overline{w}_j$ (i.e., the mean of a weather variable of the Julian day j of a year over 12 years from 2001 to 2012, j = 1, 2, . . . , 365).

2.4. The Cox Proportional Hazards Regression for the Propensity of Spring Departures

We first used the Kaplan–Meier (K-M) estimator, a time-to-event model, to estimate the daily probability of pelicans remaining sedentary at the non-breeding grounds until spring departures [30]. The K-M model had spring departure as the event and estimated

the probability of remaining from spring departure. Thus, the K-M model estimated the complement of migration probability (i.e., 1-migration probability). We estimated the region-specific probability of remaining sedentary for the Northern and Southern GOMs, respectively.

We then used the Cox proportional hazards (PH) regression to evaluate the relationships: (1) between spring departure propensity and the average of daily SOI, daily NAOI, daily temperature, and daily precipitation of previous *n* days (i.e., a time window between the starting day *t-n m* and ending day *t-m*), where m is the number of days between departure day t and the end day of the time window [31,32]. Pelican spring departure days varied from 16 February to 23 June from 2002 to 2012 (King et al. 2017 [21]). To avoid using climate data after spring departures to predict spring migration propensity of some individuals, we used the R package *climwin* to determine the soft time window length *n* and the value of *m* (see the description below) [33].

Each observation in the K m and Cox PH models consisted of an event (e.g., spring departure in this study), the starting day of annual monitoring or tracking, and the ending day when an event (i.e., spring departure) takes place in a year. An observation was right censored if the event of interest (i.e., spring departure) did not take place when observations ended (e.g., when annual migration season was over), or tracking individuals dropped off studies (e.g., due to the failure of transmitters) before observations ended. The starting day was the first tracking day (after the initial capture) in the first tracking year or the first tracking day of the subsequent calendar year if a bird was tracked more than one year. A bird which did not depart in spring was right censored on day 174 or the last tracking day of a year before day 174 (i.e., a drop-off). The latest spring departure day observed was Julian day 173 from 2002 to 2010 [21].

We used the instantaneous rate of event occurrence *h(t)* of the Cox PH model to measure pelican spring departure propensity [30]. The Cox PH model represents propensity as a time-varying baseline propensity $h_0(t)$ adjusted by the effects of time-varying covariates in the following form:

$$h(t) = h_0(t) \exp\left(\sum_{i=1}^{p} \beta_i z_i(t)\right) \tag{1}$$

where exp () is the exponential function, $z_i(t)$ is the ith covariate of which values are constant or vary over time, and β_i is the regression coefficient of the ith covariate. The Cox PH models of time-varying covariates have been used to model the phenology of avian reproduction and migration [34,35]. Quantity *h(t)* approximates departure probability in a tiny time interval Δt. The greater the hazard *h(t)*, the greater the departure propensity. We used animal identification (ID) numbers as random effects in Cox mixed models to account for repeated appearances of the same birds over years [32].

We selected the best approximating models using Akaike information criterion (AIC) [36]. The best model has the lowest AIC value. Competing models have ΔAIC values < 2.0 [36]. We used a 2-step procedure to select large-scale and local climate variables. We included both NAOI and SOI to select local climate variables daily temperature, daily precipitation, and their interaction by examining the AIC values of eight models of all possible combinations of three climate variables. Similarly, we included all local climate variables including daily temperature, daily precipitation, and temperature–precipitation interaction to select large-scale climate variables NAOI and SOI by examining the AIC values of three models of three possible combinations of NAOI and SOI. In the second step, we select the best model and competing models using the AIC values of the models of all possible combinations of large-scale and local climate variables selected in the first step. The K m and Cox PH mixed models were built using R package *survival* [30] and the function *coxme* of R package *coxme* [32]. We used variance inflation factor (VIF) to detect multicollinearity among the covariates of Cox mixed models. We removed any covariates of which the VIF was greater than 5 [37]. We calculated the VIF using the R package rms [38].

The size (*n*), beginning (*t-n-m*), and end (*t-m*) of time window for climatic conditions were determined by the AIC values with a Cox PH model without climate variables as

the baseline model varying the window size from 1 day to 150 days before each spring departure day. We included age, sex, and wintering ground (southern or northern GOM) in the Cox PH baseline models to determine the window size using the *slidingwin* () function of the R package *climwin* [33]. The function *slidingwin* () uses nested for-loops to vary the beginning and end of time window from 1 to 150 days before each spring departure day to produce a series of climate variables of different time windows. The *climwin* package automatically fits a Cox PH model to each time window and uses AIC to determine the beginning *t-n* and end *t* m of the time window, which leads to the lowest AIC [33].

3. Results

A total of 94 annual observations from 51 GPS-tracked pelicans (5 female immatures, 8 female adults, 22 male immatures, and 16 male adults) were used in this study. Male pelicans started migration earlier than female pelicans in the Northern GOM (Figure 1a). Although the sedentary probability of males declined more rapidly than females (Figure 1b), pelicans wintering in the southern GOM did not pass the N35° line earlier than those wintering in the northern GOM (Figure 1a,b).
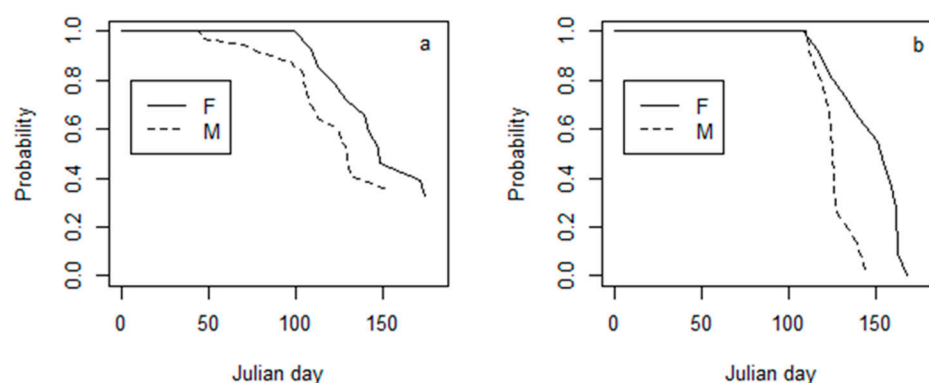
Figure 1. Kaplan–Meier estimates of the daily probability for remaining sedentary at the non-breeding grounds of American white pelicans (*Pelecanus erythrorhynchos*) in (**a**) the Northern and (**b**) Southern Gulf of Mexico, USA, during spring from 2002 to 2011.

Among 11,476 automatically fitted models of different time windows for SOI, the time window was 1 day long (11 days before spring departure days) in the best model, which had the lowest AICc (ΔAICc = −13.92) compared to the baseline model without climatic variables (AICc = 477.92). The best model (ΔAICc = −10.92) among 11,476 models for the NAOI indicated that time window was 46 days long from 0 to 46 days before spring departure day. The time window of daily temperature was 46 days long (1 day before spring departure day. Daily precipitation had a time window of 29 days from day 85 to day 114 before spring departure days.

Variance inflation factor ranged from 1.07 to 2.0 among age, sex, ground, NAOI, SOI, daily temperature, daily precipitation, and temperature–precipitation interaction. Therefore, there was no multicollinearity in our Cox regression models. With both NAOI and SOI being included, daily precipitation was the only local climate variable selected with the lowest AIC values among seven different models (Table A1). Large-scale climate variables NAOI and SOI were included in the best model with all three local climate terms daily temperature, daily precipitation, and temperature–precipitation interaction being included (Table A2).

The best model included NAOI, SOI, and daily precipitation (Table 1). The pseudo R^2 of the best model was 65%. Spring migration departure propensity was influenced by large-scale climatic variables NAOI and SOI. Spring departure propensity increased with increasing NAOI and SOI. Additionally, spring migration propensity increased with increasing daily precipitation, that is, local climate variable (Table 1). The migration propen-

sity of immature birds was lower than that of adult pelicans. The migration propensity of male pelicans was higher than that of female pelicans (Table 1).

Table 1. The Cox proportional hazards regression for the propensity of spring departures of American white pelicans (*Pelecanus erythrorhynchos*) from the non-breeding grounds in the Gulf of Mexico from 2002 to 2011.

Model	NAO	SOI	PREC	Sex (M)	Age (im)	Ground (South)	AIC
m1	1.94	0.04	0.59	0.73	−2.74	−0.62	421.38
m2	1.18	0.05		1.18	2.29	−0.63	440.71
m3		0.05	0.53	0.92	−2.58	−0.66	424.73
m4	1.52		0.51	0.38	−2.24	−0.30	446.96
m5		0.05		1.32	−2.28		436.49
m6	1.29			0.92	−2.13	−0.48	458.66
m7			0.51	0.73	−2.31	−0.49	448.68

Symbol PREC stands for the daily precipitation (mm). Words Sex, Age, and Grounds are the covariates of sex, age, and wintering sites of tracked birds. Symbol "im" stands for immature age and "south" for the southern Gulf of Mexico. Initial AIC represents Akaike information criterion.

4. Discussion

Large- and small-scale climatic variability influences avian migration phenology [6,11,13]. Our study is among the few studies which assessed the relative importance of large- and small-scale climatic forces in determining avian spring migration phenology. Our results supported the three predictions that pelicans would be more likely to depart from the non-breeding grounds for spring migration with increasing NAO, SOI, and daily precipitation. To the best of our knowledge, our study was the first study which used the probability of remaining sedentary at the non-breeding ground to quantify the partial migration of avian migrants. We found evidence that adult pelicans would be more likely to depart from the non-breeding grounds than immature pelicans during spring. We also found that male pelicans would be more likely to depart from the non-breeding grounds than female pelicans. Pelicans are a partial migrant with more than 30% probability of skipping spring migration in the Northern GOM at the end of spring [2]. Both endogenous (e.g., age and sex) and exogenous (e.g., climate) factors may determine the propensity of spring migration in American white pelicans.

Local climatic variable spring temperature at the non-breeding grounds has been proposed to be the main factor influencing the spring migration timing of birds [39]. Nevertheless, several studies have found that spring temperature alone was insufficient to explain the observed variability in spring migration phenology [6,40]. The findings of our study did not support the suggestion that daily temperatures affect spring migration probabilities of pelicans. Pelicans primarily feed on fish, crayfish, and salamander in wetlands. Increased precipitation improves the hydrology, number, and quality of wetlands [41]. Furthermore, freshwater fish species richness and abundance are positively related to precipitation at the continental scale [42]. A wet winter climate may improve the habitat conditions and food availability of pelicans. Consequently, increased daily precipitation may improve the survival and body conditions of pelicans, increasing their spring migration propensity. The positive relationship between spring migration propensity and precipitation is consistent with that between NAOI and spring departure propensity, both suggesting that wetter weather may increase the departure probability.

Large-scale climatic indices have been used to investigate the effects of global changes on avian spring migration phenology for at least two decades [12]. Our findings suggested that SOI explained more variability in spring departure probabilities than the NAOI. Inclusion of SOI explained 15% of the total variability, whereas NAOI explained 9% of the total variability. Teleconnections among NAO, SOI, and local climate have been confirmed in the southeastern USA [9,17,18]. Increases in the SOI predict warmer and drier weather, which is in favor of the formation of thermals and uplift intensity for pelican soaring flying.

On the other hand, a more positive NAOI indicates warmer, wetter, and windier weather. Our study demonstrated that windier, warmer, and wetter local climate enhanced spring departure probability. Illan, Wang, Cunningham, and King [23] found that pelican flying speed was positively related to tailwind speed. The NAOI and SOI may be integral climatic proxies representing the "package of weather" to predict the effects of future global changes on pelican spring migration in the GOM [10].

Cotton [43] investigated the effects of NAOI, SOI, and local temperature on the spring migration phenology of 20 trans-Saharan migratory birds and found those birds were unlikely to use large-scale sub-Saharan climate indexed by the NAOI and SOI to cue spring departure timing. Spring migration advancement of Afro-Palearctic migratory birds is not only related to spring temperature increases, but also increase in wind speed [44]. Precipitation amount in the southeastern USA is closely related to ocean moisture blown by southerly winds and is more influenced by large-scale atmospheric circulation [18]. It is possible that soaring pelicans use large-scale climate to predict temperature and wind speeds to adjust spring departure phenology. Close teleconnection among large-scale atmospheric circulation, local precipitation, and wind in the southeastern USA may cause the consistent responses of pelicans to large- and small-scale climatic variabilities, contrary to those of Afro-Palearctic avian migrants in the Sahara.

Pelicans migrate northward from the Gulf of Mexico to the breeding grounds in the Northern Great Plains in spring [21]. Elevation of the breeding habitat within pelican summer home ranges was 252–735 m (above sea level) higher than that of their wintering grounds [23]. Although elevation increased gradually along the spring migration route, climbing up against rising elevation during the spring migration may impose physiological or energetic challenges to inexperienced large-sized soaring birds such as immature pelicans. This may explain why immature pelicans had substantially lower propensity of spring migration departure than adult pelicans. On the other hand, young-of-the-year pelicans may be able to utilize potential energy caused by the higher elevation at northern latitudes for soaring down southward during the autumn migration [23]. Javier et al. (2017) also found that wind directions affected movement speed during autumn migration [23]. Once arriving at the non-breeding grounds, immature pelicans may skip spring migration for 1–2 years until they become physically strong and experienced in soaring flying. Immature pelicans do not breed until they are 3 or more years old [19]. Remaining at the non-breeding grounds allows immature birds to avoid migration-related mortalities without losing the reproductive component of fitness. Non-migratory immature pelicans may make exploratory movements with multiple core areas of annual home ranges covering a large area at the non-breeding grounds [45]. By the end of spring, pelicans had a probability of 0.4 to skip spring migration remaining at the non-breeding grounds. Future studies of soaring flying strategies for varying winds, thermal conditions, and associated energetic costs are needed for better understanding the partial migration of American white pelicans at the non-breeding grounds.

Appendix A

Table A1. Model selection for local climate variables using Akaike information criterion (AIC) with both large-scale climate variables NAOI and SOI being included.

Model	Model Terms	AIC
ms1	age + sex + g + soi + nao + temp + prec + t × p	426.09
ms2	age + sex + g + soi + nao + temp + t × p	447.26
ms3	age + sex + g + soi + nao + prec + t × p	425.75
ms4	age + sex + g + soi + nao + temp + prec	424.52
ms5	age + sex + g + soi + nao + temp	446.77
ms6	age + sex + g + soi + nao + prec	421.38
ms7	age + sex + g + soi + nao + t × p	444.31

Symbol g stands for ground, soi Southern Oscillation Index, nao Northern Oscillation Index, temp daily temperature, prec daily precipitation, and t × p temperature–precipitation interaction. Word age stands for age group of pelicans (i.e., immature and mature) and sex for the sex of pelicans.

Table A2. Model selection for large-scale climate variables using Akaike information criterion (AIC) with all three local climate variables being included.

Model	Model Terms	AIC
ms8	age + sex + g + soi + nao + temp + prec + t × p	426.09
ms9	age + sex + g + soi + temp + prec + t × p	426.58
ms10	age + sex + g + nao + temp + prec + t × p	435.10
ms11	age + sex + g + temp + prec + t × p	438.62

Symbol g stands for ground, soi Southern Oscillation Index, nao Northern Oscillation Index, temp daily temperature, prec daily precipitation, and t × p temperature–precipitation interaction. Word age stands for age group of pelicans (i.e., immature and mature) and sex for the sex of pelicans.

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