

Differential migratory movements of geographically distinct wintering populations of a soaring bird

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Abstract

Background: Migratory soaring birds exhibit spatiotemporal variation in their circannual movements. We hypothesized that the circadian and seasonal movements of soaring migrants may depend primarily on exogenous factors such as thermals and wind conditions. Nevertheless, it remains uncertain how different winter environments affect the circannual movement patterns of migratory soaring birds. Here, we investigated annual movement strategies of American white pelicans *Pelecanus erythrorhynchos* (hereafter, AWPE) from two geographically distinct wintering grounds in the Southern and Northern Gulf of Mexico (GOM).

Methods: We calculated average and maximum hourly movement distances and seasonal home ranges of GPS-tracking AWPEs. We then evaluated the effects of circadian hours, seasons, two wintering regions in the Southern and Northern GOM, human footprint index, and relative AWPE abundance from Christmas Bird Count data on AWPE hourly movement distances and seasonal home ranges using linear mixed models and generalized linear mixed models.

Results: American white pelicans moved at the highest speed near 1200 hours at breeding grounds and during spring and autumn migrations. Both wintering populations in the Northern and Southern GOM exhibited similar hourly movement distances and seasonal home ranges at the shared breeding grounds and during spring and autumn migrations. However, AWPEs wintering in the Southern GOM showed shorter hourly movement distances and smaller seasonal home ranges than those in the Northern GOM. Hourly movement distances and home ranges of AWPEs increased with increasing human footprint index.

Conclusions: Winter hourly movements and home ranges of AWPEs differed between the Northern and Southern GOM; however, the difference in AWPE winter movements did not carry over to the shared breeding grounds during summers. Therefore, exogenous factors may be the primary drivers to shape the flying patterns of migratory soaring birds.

Background

Migration is the seasonal movement of animals between their breeding and non-breeding grounds, and allows animals to exploit resources available in different seasonal habitats during a year [1]. Seasonal migration of birds may span vast distances from hundreds to thousands of kilometers, a phenomenon studied for nearly two centuries [2]. Flying patterns of avian migrants (e.g., circadian variation in speed and flying modes) and movement strategies (e.g., spatiotemporal variation in the duration and frequency of flying, foraging, and stopover) are fundamental behavioral mechanisms underlying long-distance migration [3]. However, there is a paucity of studies of movement patterns and strategies used by migratory birds throughout the entire annual cycle [4, 5].

Birds may alter their flying patterns in response to circadian and seasonal variation in weather or climatic conditions [6–8]. Flight is the most physically challenging and energetically expensive avian activity (per

unit time), particularly for large-sized migrants over long distances [9]. Duration and timing of flight are critical factors influencing the energy budgets [10], but also the competitiveness of migrating individuals for breeding and foraging opportunities [11]. Optimality theory has been proposed to be a major conceptual framework of movement ecology [2] and migration strategies [12, 13]. Optimality predicts that avian migrants may adjust the speed, mode, duration, frequency, timing, and route (path) of flights to minimize energetic costs or total migration time, often with trade-offs, suggesting the fitness benefits of reproductive success and survival enhancement [8, 14]. Therefore, morphological and physiological traits of migrants and wind and climatic conditions may collectively shape the movement patterns and strategies of migratory birds, resulting in different movement patterns between geographically distinct populations [8, 15]. However, few empirical studies have assessed geographic variation in movement patterns and strategies of the same migratory species.

Plastic migratory movement strategies may optimize the fitness of wintering individuals [16–18]. Soaring birds take advantage of rising hot air masses (i.e., thermals) to gain altitude and glide distances, and then return to the ground [19]. Soaring and gliding are energetically cheaper than flapping and are the main flying mode of large-sized land migratory birds [20, 21]. For instance, the energy costs of soaring and gliding are estimated to be < 50% of flapping in Himalayan (*Gyps himalayensis*) and Eurasian (*G. fulvus*) griffons [22]. Large-sized, obligate soaring birds often soar with no or few wing strokes to save energy [23]. Compared to flapping flight, soaring flight may be influenced more by thermal and wind conditions, and topography along the flying path [6, 24]. It is plausible to hypothesize that sub-populations of soaring birds that winter at different non-breeding grounds may exhibit different movement patterns and migratory strategies. Nevertheless, it is uncertain if flying patterns of geographically separated wintering populations would converge at the shared breeding grounds under the same wind and thermal conditions.

Multiple factors other than winds and thermals may also affect soaring bird movements. Availability and spatial distributions of food resources may influence animal movements. Increases in ecosystem productivity would reduce bird movements and home ranges [25, 26]. Additionally, increases in animal population size may result in the “crowding” effects on animal individuals, reducing movement distance [27]. Anthropogenic disturbances also can affect bird and mammal movements [28, 29]. Human footprints index quantifies the degree of human disturbance to natural systems with the composite scores of man-made environments (e.g., urban development), human population density, electric infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways [30]. Human footprint index has been found to be inversely related to the movements of mammals [28] and affect the projected spatial distribution of birds [31]. However, few studies have related individual migratory bird movement to human footprint index.

American white pelicans (*Pelecanus erythrorhynchos*, hereafter AWPE) are among the largest flying birds of North America [32]. Average body mass of AWPEs ranges from 4.54 kg to 7.72 kg [32], and soaring is their primary flying mode due to large body size [33]. The allometric scaling exponent of required energy for flapping flight is approximately double that of available energy, limiting the flapping flight capacity of

large-sized birds [34]. Like other large-sized birds, AWPEs have relatively longer wingspan and smaller wing areas, making them suitable for soaring and gliding [19, 34]. King et al. (2017) investigated the migration phenology of AWPEs that wintered in the Northern Gulf of Mexico (GOM) [35], and Illan et al. (2017) studied the effects of winds and thermals on the spring and autumn migration speed of the same migratory population of AWPEs [36]. However, no studies have investigated the movement patterns and migration strategies of AWPEs during the entire annual cycle.

The majority of AWPEs that breed in the Northern Great Plains east of the Continental Divide, United States, winter in the Northern or Southern GOM [37]. The Northern and Southern GOMs differ in climate, ecosystem, landscape, and anthropogenic disturbance [38, 39]. However, it has been uncertain whether movement patterns vary between the Northern and Southern GOM wintering populations of AWPEs. Furthermore, an unexplored question was whether movement patterns of the Northern and Southern GOM wintering populations of soaring AWPEs would converge at the shared breeding grounds.

In this study, we aimed to test the predictions of hypotheses concerning spatiotemporal variation in the movement patterns of two geographically distinct wintering populations of AWPEs. We hypothesized that flying and movement of large-sized soaring birds would mainly be influenced by exogenous environmental and thermal conditions. Therefore, we predicted that two AWPE populations wintering in the Northern and Southern GOMs would exhibit similar flying patterns and spacing behaviors (e.g., hourly movement distances and seasonal home ranges) at the shared breeding grounds, but would differ in these two aspects between the Northern and Southern GOMs. Relative abundance of AWPEs in the Southern GOM increased rapidly during the years of our study and on average was double that in the Northern GOM (Fig. S1). Therefore, we predicted that AWPEs in the Southern GOM with higher ecosystem productivity, greater AWPE relative abundance, and lower human disturbance would have shorter hourly movement distances and smaller seasonal home ranges than birds using the Northern GOM during winters. Lastly, we hypothesized that migratory populations wintering farther from the breeding grounds would fly faster than those nearer breeding grounds during spring migration. In essence, hourly movement distances of AWPEs from the Southern GOM would exceed those of birds occupying Northern GOM during spring migration.

Methods

Description of study regions

American white pelicans of the Central and Mississippi Flyway winter either in the Southern or Northern GOM. The boundaries of the Northern and Southern GOMs were delineated based on the marine ecoregions in North America [38, 39]. The Northern GOM spans from Gullivan Bay on the west coast of Florida through Alabama, Mississippi, Louisiana, and Texas, US to Tamaulipas, Mexico. The Southern GOM extends from Veracruz through Tabasco and Campeche to Yucatan, Mexico [38, 39]. The Northern and Southern GOMs differ in sea surface temperatures in winter. Winter ambient air temperatures in the Northern GOM range from 14 to 24°C, while those in the Southern GOM from 24 to 25°C [39]. The

Northern GOM has tidal estuaries, fresh and salt marsh, and river inlets, which create wetland complexes that serve as important habitat and provide food resources for migratory waterbirds [39, 40]. The Southern GOM contains coastal lagoons and mangroves, river deltas, and emergent freshwater marshes, also comprising the habitat of wintering migratory birds [39, 40]. The Southern GOM ecosystems are more productive than the Northern GOM ecosystems owing to more precipitation, higher temperature, and mangrove ecosystems [41].

Capture Sites And Capture Methods

We captured AWPEs on both breeding and non-breeding grounds with rocket nets and modified foot-hold traps [42, 43]. On the breeding grounds in 2005 and 2006, we captured birds at three major colonies, Bitter Lake, South Dakota (45°14'N, 97°20'W), Chase Lake, North Dakota (47°01'N, 99°27'W), and Medicine Lake, Montana (48°30'N, 104°30'W) (see Sovada et al. 2008 for capture site details and information on sampled AWPEs). On the non-breeding grounds of Alabama, Arkansas, Louisiana, and Mississippi from 2002 to 2010 we also captured AWPEs near aquaculture facilities [43]. We used culmen length to sex captured AWPEs [45] and placed birds as immature (≤ 3 years old) or mature based on plumage and eye and skin color characteristics (D. T. King, unpublished data). We attached 70-g backpack solar-powered Global Positioning System (GPS) transmitters (PTT-100, Microwave Telemetry, Inc., Columbia, MD, USA) to captured AWPEs [46]. GPS transmitters were programmed to record one location per hour for a 24-hour duty cycle or from 0600 hour to 1900 hour.

We classified all captured AWPEs into two wintering populations, those wintering in either the Northern or Southern GOM. We used the marine ecoregions in North America to delineate the boundaries of the Northern and Southern GOMs [38, 39].

GPS location, Christmas Bird Count, and Human footprint data acquisition and processing

We did not have data on the reproductive condition or breeding status of tracked AWPEs. Therefore, instead of using the terms “breeding” and “non-breeding seasons,” we divided all GPS locations of AWPEs into four different biological seasons of a year: on the breeding grounds (hereafter, summer), autumn migration, on the non-breeding grounds (hereafter, winter), and spring migration in this study. The terms “summer” and “winters” referred to AWPE annual biological seasons in this study. We used net squared displacement to determine the start and end dates of each season for each tracked AWPE using the “as.ltraj” function in R package “adehabitatLT” [47, 48]. Net squared displacement is a squared geographic distance between the first location and each subsequent location of a tracked animal [47]. Net squared displacement remains relatively constant on the breeding grounds during summer and on the non-breeding grounds during winter, but varies during spring and autumn migrations [35]. For sedentary AWPEs that remained at the non-breeding grounds year-round, we set their wintering seasons from median autumn arrival date at those non-breeding grounds to median spring departure date of AWPE migrants. We also examined whether the departure and arrival dates of spring migration would differ between the two wintering populations of AWPEs in the Northern and Southern GOMs using a t-test.

To examine the effects of AWPE relative abundance on their spacing behaviors and movements, we obtained Audubon Christmas Bird Count data from National Audubon Society to calculate AWPE relative abundance within AWPE wintering grounds around GOM [49]. We used count per party hour as a relative abundance index of AWPEs. The Christmas Bird Count is a volunteer-based survey, during which volunteers count birds across North America from December to January each year [49]. We used Christmas Bird Count data only from survey sites on the wintering grounds in the Northern and Southern GOMs from 2002 to 2012. To account for variation in survey effort among sites and years, we built generalized additive mixed models with Poisson distributions and log link functions to predict AWPE counts at each survey location using “`gamma4`” function in R package “`gamma4`” [50]. To account for survey efforts and spatial autocorrelations between survey sites, we included log-transformed survey effort hours as an offset and a smoothing term of survey year and x- and y-coordinates of survey locations [51]. We then used the predicted annual relative abundance index of AWPEs within AWPE wintering grounds around GOM in the analysis of hourly movement distances and seasonal home ranges.

To quantify anthropogenic disturbances in the two wintering regions, we obtained the human footprint index raster file from Socioeconomic Data and Applications Center [30]. Human footprint index uses built environments, human population density, electric infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways to score the human pressure levels in the 1-km spatial resolution [30]. We used human footprint index calculated in 2009 for our birds tracked from 2002 to 2012 [52].

We calculated hourly movement distances (km/h) during each season (i.e., winter, spring migration, summer, and autumn migration) and seasonal home ranges (km²) for each tracked AWPE each year. We calculated hourly movement distances between successive hourly locations of individual AWPEs and then calculated mean hourly movement distance for each hour of a day by season for each tracked AWPE. To estimate unbiased geographic distances, we calculated the great circle distances using “`distVincentyEllipsoid`” function in R package “`geosphere`” [53]. We determined maximum hourly movement distances for each hour of a day by season for each tracked AWPE. Therefore, our statistical sample unit of hourly mean and maximum distances was individual bird in a season.

We estimated the 95% seasonal home ranges of AWPEs for summer, winter, spring migration, and autumn migration seasons, respectively, using dynamic Brownian bridge movement models (DBBMM) with the “`Brownian.bridge.dyn`” function in R package “`move`” [54]. The DBBMMs estimate animal home ranges accounting for heterogeneous changes in animal behavior [55]. The DBBMM is appropriate for estimating AWPE home ranges mainly because AWPEs are highly mobile and their movement lacks central tendency during migration. To parameterize the DBBMM, we set location error, window size, margin, and time step of the DBBMM to 30 m, 23 hours (approximately one day), 11 hours (approximately half time of window size), and 15 steps per hour, respectively. We then extracted and averaged human footprint indices within the boundary of each seasonal home ranges to examine the effects of anthropogenic disturbance on the hourly movement distances and seasonal home ranges of each AWPE in each season.

Statistical Analyses

(i) Daily maximum and average hourly movement distance or speed

We used generalized linear mixed models (GLMMs) to assess the effects of season, wintering population (i.e., the Northern or Southern GOM), population relative abundance, year, and human disturbance on the hourly movement distances of AWPEs. We built GLMMs with the Gamma distribution and log link function for movement distances [56]. We included season, wintering population, winter relative abundance index, year, and human footprint index as fixed effects and animal identity as a random effect. Year and relative abundance index were correlated with each other (Pearson's correlation $r = 0.88$; Fig. S2); therefore, we built two sets of models to include only one of the two covariates in each set of models, respectively (Figs. S3 and S4, and Tables S1, S2, and S3). To account for circadian variations in hourly movement distances of AWPEs, we incorporated Fourier transformations of time (i.e., hours) using the sine and cosine functions of time in the frequencies of 1/24 and 1/12 cycles per hour into our models. The two frequencies corresponded to the daily (i.e., a 24-hr cycle) and daytime (a 12-hr cycle) rhythms, respectively. To investigate region-specific seasonal variations in the hourly movement distances of AWPEs between the Northern and Southern GOMs, we included interactions among circadian hour, wintering population, and season in GLMMs.

We used Akaike information criterion (AIC) for model selection with the most parsimonious model having the lowest AIC among a set of candidate models [57]. We conducted model selection in a backward manner, starting with a full model including all fixed effects and their interactions. We considered models with ΔAIC of < 2.0 as competing models [57].

If there was an interaction between wintering population and season in the selected models, we estimated the marginal means of movement metrics and their 95% confidence intervals (CIs) for each wintering population. If the 95% CIs of two marginal means did not overlap, we concluded the two means differed. If the 95% CI of a regression coefficient did not include zero, we concluded that the coefficient was non-zero.

(ii) Seasonal home ranges

We built linear mixed models (LMMs) to evaluate the effects of season, wintering population, relative population abundance index, year, and human footprint index on seasonal home ranges with bird identity as a random effect. We log-transformed the home ranges for the normality assumption. We also included interactions between annual population abundance index, wintering ground, and season as well as between season and human footprint index. We used the same model approaches to the model selection and pairwise comparisons of LMMs as those to the aforementioned GLMMs.

We used the R package glmmTMB in the R 3.6.2 environment for LMMs and GLMMs and R package MuMIn to calculate ΔAIC [58, 59]. The marginal means and their 95% CIs were calculated using the R package emmeans [60].

Results

We analyzed hourly location data of 72 GPS-tracked AWPEs from 2002 to 2012. Twenty-four birds were captured on the breeding grounds at Chase Lake, Medicine Lake, and Bitter Lake, while the remaining 48 birds were captured on the non-breeding grounds. Effects of years on hourly movement distances and seasonal home ranges of AWPEs were similar to those of AWPE relative abundance (Supplemental Information, Fig. S2, Tables S1 and S2). Subsequently, we only reported the effects of AWPE relative abundance on movement distances and home ranges. Neither departure nor arrival dates of spring migration differed between the wintering Northern and Southern GOM populations (departure: $t = 0.92$, $df = 46.02$, $p = 0.36$; arrival: $t = 0.90$, $df = 45.97$, $p = 0.38$).

Seasonal Hourly Movement Distance

The best GLMM of average hourly movement distance included human footprint indices (hfp) and interactions between circadian hours, seasons, and wintering populations plus interactions among seasons, wintering populations, and AWPE relative abundance indices. The second-best model included a season-hfp interaction and had ΔAIC of 1.08 (Table 1). We chose the simpler (i.e., the best model) between the two competing models as the final model to represent average hourly movement distance.

Table 1

Generalized linear mixed models of average hourly movement distances of American white pelicans. Symbol ΔAIC is difference in Akaike information criterion between a model and the most parsimonious model.

Model	df	ΔAIC
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc} + \text{hfp}$	51	0.00
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc} + \text{ssn} * \text{hfp}$	54	1.08
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc}$	50	13.57
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * \text{cbc} + \text{hfp}$	47	13.72
$(\sin + \cos) * \text{ssn} * g + (g + \text{ssn}) * \text{cbc} + \text{hfp}$	48	15.36
$(\sin + \cos) * \text{ssn} * g + \text{cbc} + \text{hfp}$	44	32.61
$(\sin + \cos) * \text{ssn} * g + g * \text{cbc} + \text{hfp}$	45	34.64
$(\sin + \cos) * \text{ssn} * g + \text{hfp}$	43	38.15
$(\sin + \cos) * (g + \text{ssn}) + \text{ssn} * g * \text{cbc} + \text{hfp}$	39	53.04
$(\sin + \cos) * \text{ssn} + \text{ssn} * g * \text{cbc} + \text{hfp}$	35	69.68
$(\sin + \cos) * g + \text{ssn} * g * \text{cbc} + \text{hfp}$	27	794.13
$(\sin + \cos) + \text{ssn} * g * \text{cbc} + \text{hfp}$	23	801.75
Note: $(\sin + \cos)$: Circadian hours with Fourier transformation of sine and cosine function		
ssn: Season (i.e., summer and winter seasons and spring and autumn migration)		
g: Wintering population group (the Northern or Southern Gulf of Mexico)		
cbc: Population relative abundance index estimated by Christmas Bird Count		
hfp: Human footprint index within seasonal home ranges of pelicans		
All models with interactions include main effects.		

American white pelicans exhibited a 12-hour cycle of movement rhythm with a peak speed around 1200 hours at the breeding grounds and during spring and autumn migrations (Fig. 1). Marginal means of winter average hourly movement distance were greater in the Northern than in the Southern GOM (Northern GOM: distance = 1.62 [km], 95% CI [1.43–1.84]; Southern GOM: distance = 0.81 [km], 95% CI [0.63–1.05]). However, marginal mean hourly movement distance did not differ between Northern and Southern GOMs during summer, spring migration, and autumn migration (Fig. 2). Marginal mean hourly movement distances were greater during spring and autumn migration than during summer and winter; however, marginal mean hourly movement distances did not differ between spring and autumn migration (Fig. 2).

Average hourly movement distances of AWPEs were positively related to human footprint indices ($\beta = 0.06$, 95% CI [0.03– 0.09]). Average hourly movement distances of the Northern GOM wintering population were inversely related to winter AWPE relative abundance indices during summer and autumn migration (summer season: $\beta = -0.05$, 95% CI [-0.07– -0.03]; autumn migration: $\beta = -0.04$, 95% CI [-0.06– -0.01]; Fig. 2a and d), but were not inversely related to winter AWPE relative abundance either in the winter or during spring migration (winter season: $\beta = -0.001$, 95% CI [-0.02– 0.02]; spring migration: $\beta = -0.001$, 95% CI [-0.02– 0.02]; Fig. 2b and c). Average hourly movement distances of the Southern GOM wintering population were inversely related to AWPE relative abundance in winter (winter season: $\beta = -0.11$, 95% CI [-0.17– -0.05]; Fig. 2b), but were not inversely related to winter AWPE relative abundance either in summer or during spring and autumn migration (summer season: $\beta = -0.03$, 95% CI [-0.07– 0.01]; spring migration: $\beta = -0.01$, 95% CI [-0.07– 0.09]; autumn migration: $\beta = 0.03$, 95% CI [-0.02– 0.07]; Fig. 2a, c, and d).

Seasonal Maximum Hourly Movement Distance

Among the top three models ranked by AIC, we chose the second-best model ($\Delta AIC = 0.11$), the simplest model, to represent maximum hourly movement distance (Table 2). Maximum hourly movement distances also had a 12-hour cycle of rhythm with a peak speed around 1300 hours at the breeding grounds and during spring and autumn migrations (Fig. 3). The 95% CIs of maximum hourly movement distance overlapped during the summers, winters, and spring and autumn migration (Fig. 3). Maximum hourly movement distances of the Northern GOM wintering population were inversely related to winter AWPE relative abundance indices during summer ($\beta = -0.06$, 95% CI [-0.08– -0.04]), winter ($\beta = -0.03$, 95% CI [-0.05– -0.01]), and spring ($\beta = -0.04$, 95% CI [-0.07– -0.02]) and autumn migration ($\beta = -0.03$, 95% CI [-0.06– -0.01]) (Fig. 4). Likewise, maximum hourly movement distances of the Southern GOM wintering populations were inversely related to winter AWPE relative abundance during summer ($\beta = -0.05$, 95% CI [-0.08– -0.01]), winter ($\beta = -0.14$, 95% CI [-0.20– -0.09]), autumn migration ($\beta = -0.07$, 95% CI [-0.10– -0.03]), but not during spring migration ($\beta = -0.06$, 95% CI [-0.14– 0.02]) (Fig. 4).

Table 2

Generalized linear mixed models of maximum hourly movement distances of American white pelicans. Symbol ΔAIC is the difference in Akaike information criterion between a model and the most parsimonious model.

Model	df	ΔAIC
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc} + \text{ssn} * \text{hfp}$	54	0.00
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc}$	50	0.11
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * g * \text{cbc} + \text{hfp}$	51	0.66
$(\sin + \cos) * \text{ssn} * g + \text{cbc}$	43	7.71
$(\sin + \cos) * \text{ssn} * g + g * \text{cbc}$	44	8.16
$(\sin + \cos) * \text{ssn} * g + \text{ssn} * \text{cbc}$	46	11.89
$(\sin + \cos) * \text{ssn} * g + (g + \text{ssn}) * \text{cbc}$	47	12.45
$(\sin + \cos) * (g + \text{ssn}) + \text{ssn} * g * \text{cbc}$	38	19.46
$(\sin + \cos) * \text{ssn} + \text{ssn} * g * \text{cbc}$	34	34.22
$(\sin + \cos) * \text{ssn} * g$	42	45.19
$(\sin + \cos) * g + \text{ssn} * g * \text{cbc}$	26	322.99
$(\sin + \cos) + \text{ssn} * g * \text{cbc}$	22	330.48
Note: $(\sin + \cos)$: Circadian hours with Fourier transformation of sine and cosine function		
ssn: Season (i.e., summer and winter seasons and spring and autumn migration)		
g: Wintering population group (the Northern or Southern Gulf of Mexico)		
cbc: Population relative abundance index estimated by Christmas Bird Count		
hfp: Human footprint index within seasonal home ranges of pelicans		
All models with interactions include main effects.		

Seasonal Home Range

American white pelicans wintering in both the Northern and Southern GOMs shared the breeding grounds in the Northern Great Plains (Fig. 5a). American white pelicans wintering in the Southern GOM had a single relatively linear flying corridor from south Texas to the breeding grounds during spring migration (Fig. 5c). The spring migration routes of the Northern GOM wintering population forked between the Mississippi River and Arkansas River, covering larger areas than those of the Southern GOM population (Fig. 5c).

The best LMM of seasonal home ranges included human footprint index, interaction between AWPE relative abundance and wintering grounds, and interaction between seasons and wintering grounds (Table 3). The second-best model was a competing model ($\Delta\text{AIC} = 1.11$), including AWPE relative abundance, human footprint index, and interaction between seasons and wintering grounds (Table 3). We chose the simpler second-best model to represent seasonal home range. Seasonal home ranges of AWPEs were positively related to human footprint indices ($\beta = 0.50$, 95% CI [0.32– 0.68]), but were inversely related to AWPE relative abundance ($\beta = -0.33$, 95% CI [-0.56 – -0.09]). The marginal mean of winter home ranges was larger in the Northern GOM (log-home-range [km^2] = 8.72, 95% CI [8.35– 9.10]) than in the Southern GOM (log-home-range [km^2] = 6.39, 95% CI [5.68– 7.11]) during winter seasons (Fig. 5b).

Table 3

Linear mixed models of seasonal home ranges of American white pelicans. Symbol ΔAIC is difference in Akaike information criterion between a model and the most parsimonious model.

Model	df	ΔAIC
ssn * g + g * cbc + hfp	13	0.00
ssn * g + cbc + hfp	12	1.17
ssn * g + g * cbc + ssn * cbc + hfp	16	3.78
ssn * g + ssn * cbc + hfp	15	5.56
ssn * g + hfp	11	5.73
ssn * g * cbc + hfp	19	9.40
ssn * g * cbc + ssn * hfp	22	10.78
ssn * g	10	29.51
ssn * g * cbc	18	38.49
ssn + g * cbc + hfp	10	45.58
g * cbc + ssn * cbc + hfp	13	47.41
ssn + g	7	70.94
Note: ssn: Season (i.e., summer and winter seasons and spring and autumn migration)		
g: Wintering population group (the Northern or Southern Gulf of Mexico)		
cbc: Population relative abundance index estimated by Christmas Bird Count		
hfp: Human footprint index within seasonal home ranges of pelicans		
All models with interactions include main effects.		

Discussion

Avian migrants often exhibit spatiotemporal variation in the mode, speed, and duration of flights in response to changes in climate, wind, and food availability [15, 61–63]. Migratory birds may fly faster in spring migration than in autumn migration for timely arrival at the breeding ground [64]. Long-distance avian migrants may change stopover duration to minimize overall migration time [63]. Wing-flap flight may allow migratory birds to minimize spring migration time at the cost of increased energy expenditure with winter fat storage and stopover refueling [20]. Alternatively, large-sized soaring birds may primarily use external sources of energy for migration flights [65]. Our results supported the hypothesis that hourly flying speed of soaring AWPEs would be primarily affected by exogenous factors; however, our findings did not support the hypothesis that AWPEs departing from the Southern GOM would fly faster than those departing from the Northern GOM despite comparable departure and arrival dates of spring migration between the two populations. Furthermore, we also found evidence that AWPE reduced hourly average and maximum flying speed with increasing AWPE relative abundance when we accounted for wintering region (for possible different ecosystem productivity and human disturbances). Individual AWPEs may gather in resource rich areas that required less movement to meet daily energy needs through more efficient foraging [25, 66]. Increased anthropogenic disturbances also increased hourly mean flying speed and seasonal home ranges of AWPEs.

Temperatures, winds, thermals, and individual differences affect bird flying performances [7, 21, 36, 67]. Illan et al. (2017) found that tailwind speed and uplift intensity affected flying speed of AWPEs during spring and autumn migrations [36]. In our study, AWPEs in the Northern GOM had greater hourly flying speeds and larger home ranges than in the Southern GOM, after accounting for circadian rhythm, anthropogenic disturbances, AWPE relative abundance, and individual random effects. As most tracked AWPEs used in this study had at least one migration trip with observations at both breeding and non-breeding grounds, the difference in hourly flying speed between the two wintering populations may be attributable to unmeasured differences in climatic conditions and food availability between the two regions. Furthermore, AWPEs that were subject to similar climate and wind conditions on the shared breeding grounds and migration corridors did not differ in flying speed. Therefore, exogenous environmental factors such as food availability, thermals, air uplift intensity, and wind conditions (e.g., speed and direction) may dictate the flying speed of AWPEs [68].

Avian migrants may have greater total flying speed during spring migration than during autumn migration for timely arrival at the breeding grounds [63]. We found that AWPEs flew faster during spring and autumn migration than during winter and summer. However, hourly flying speed did not differ between spring and autumn migration. The similar hourly flying speed may be because AWPEs mainly use soaring flight to complete spring and autumn migration without much flapping flight [33]. High reliance of soaring flight on thermals and wind conditions may result in comparable flying speed of AWPEs between spring and autumn migration. Although AWPEs wintering in the Southern GOM did not

fly faster than those in the Northern GOM, the birds of different wintering populations may differ in the number of stopover sites and stopover duration, which can be used to adjust total flying duration [63], given the similar spring departure and arrival timing between the two AWPE populations. Our GPS data had gaps along migratory tracks, preventing us from measuring stopover duration during spring migration. Future studies are needed to use fine-resolution GPS location data to better understand AWPE migration strategies.

Hourly flying distance and home ranges of AWPE increased with increasing human footprint index. Anthropogenic disturbances may affect bird movements at least in two ways. First, anthropogenic disturbances may fragment avian habitat (including inland freshwater wetlands—AWPE foraging habitat), breaking habitat up into small patches and thus increasing distance between habitat or food patches. The resource dispersion hypothesis predicts that movement distances and home ranges increase with increasing habitat or resource fragmentation [69]. For instance, eastern wild turkeys move longer distances on more fragmented habitat [70]. Second, birds may fly longer with more intensified human disturbances. Lilleyman et al. (2016) found that human disturbances at the roost sites increased the flight times and distance of shorebirds (*Calidris* spp. and *Charadrius* spp.) during winter [29]. Increases in movements induced by human disturbances reduce the energy reserve during winter, likely bearing demographic consequences in migratory birds [71]. Increases in human disturbances during the non-breeding period are likely to be a driver of overall declines of the eastern populations of Canada warblers (*Cardellina canadensis*) [71]. However, human disturbances increased the movement distance of roosting Eurasian Oystercatchers (*Haematopus ostralegus*) but marginally affected their daily energy budget [72]. Future studies are needed to investigate the effects of anthropogenic disturbances on the movement, daily energy budget, and demography of migratory birds at the non-breeding grounds using biologging and demographic modeling [73].

Inverse relationships between population abundance and home range size are well established in mammals [27]. Reduced home range size and daily movement distance have been ascribed to increased aggression toward conspecifics. Intensified social fence and territoriality with increasing population density have been invoked as a behavioral mechanism of density dependence and population regulation of mammalian populations. Previous studies have commonly used the resource availability or amount to explain home range or territory sizes of birds [74, 75]. Few studies have used population density to explain bird home range sizes. Home range size of male Swainson's Warblers (*Limnothlypis swainsonii*) is inversely related to the number of competing male warblers [76]. In addition to intensified competition for resource with increased densities, social interactions such as increased aggression may affect bird movement and spacing behavior. Papageorgiou and Farine (2020) have found that social group size reduced home ranges of vulturine guineafowl (*Acryllium vulturinum*) when group size exceeded a threshold [77]. We found that home range size and hourly movement distance decreased with increasing AWPE relative abundance. This study used the Christmas Bird Count index as relative abundance index of AWPEs given that estimates of AWPE winter abundance and densities with rigorous survey methods were not available for a large area such as the Northern and Southern GOM. However, we caution that the

Christmas Bird Count index may not accurately measure temporal variation in AWPE population abundance.

Conclusions

American white pelicans exhibited seasonal variation in hourly flying speed with hourly flying speed during spring and autumn migration being greater than those during summer and winter. Furthermore, AWPE hourly flying speed differed between the Northern and Southern GOM, demonstrating regional difference, during winter. However, winter regional differences in movement and spacing did not carry over to the breeding grounds during summer. Anthropogenic disturbances increased hourly flying speed and home range size on the non-breeding grounds during winter. Exogenous factors may be the primary factors determining the movement pattern and spacing behavior of soaring birds.

Abbreviations

AIC: Akaike Information Criterion; AWPE: American white pelican; CI: Confidence interval; DBBMM: Dynamic Brownian bridge movement model; GLMM: Generalized linear mixed model; GOM: Gulf of Mexico; GPS: Global positioning system; hfp: human footprint index; IACUC: Institutional Animal Care and Use Committee; LMM: Linear mixed model; USDA: United States Department of Agriculture

Declarations

Ethics approval and consent to participate

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) for AWPEs captured in the Northern GOM and by Northern Prairie Wildlife Research Center's Animal Care and Use Committee (Project Number: NN00.0LLX3) for 19 AWPEs captured in the Northern Great Plains.

Consent for publication

All authors have read the manuscript before submission.

Availability of data and materials

The data used in this work will be available in a public repository after the manuscript is accepted for publication.

Competing interests

There are not conflicts of interests.

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Author's contributions

GW and RO conceived the idea. DTK and MAS collected GPS location data. RO carried out statistical analysis. RO led manuscript writing. LWB, JBD, BKS, FLC, and GW supervised the study. LWB, JBD, BKS, FLC, DTK, GW, and MAS participated in writing and editing the manuscript.

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Figures

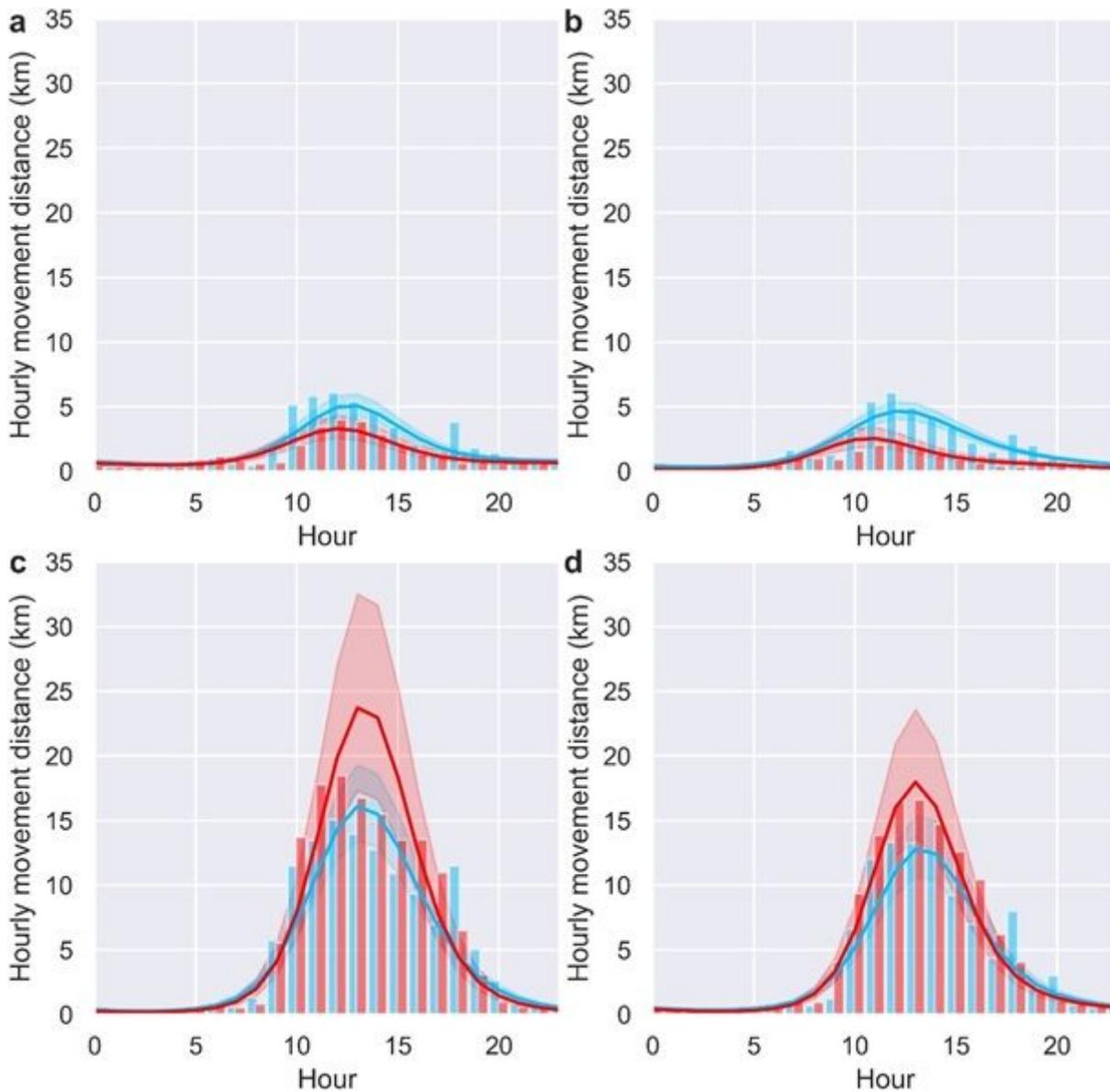


Figure 1

Average hourly movement distances of American white pelicans with circadian hours. Blue and red colors represent wintering populations at Northern and Southern Gulf of Mexico, respectively. Panels represent a) summer, b) winter, c) spring migration, and d) autumn migration. Bars show observed average hourly movement distances. Lines indicate the estimated average hourly movement distances based on the best model. Polygons represent 95 confidence intervals of the average hourly movement distances.

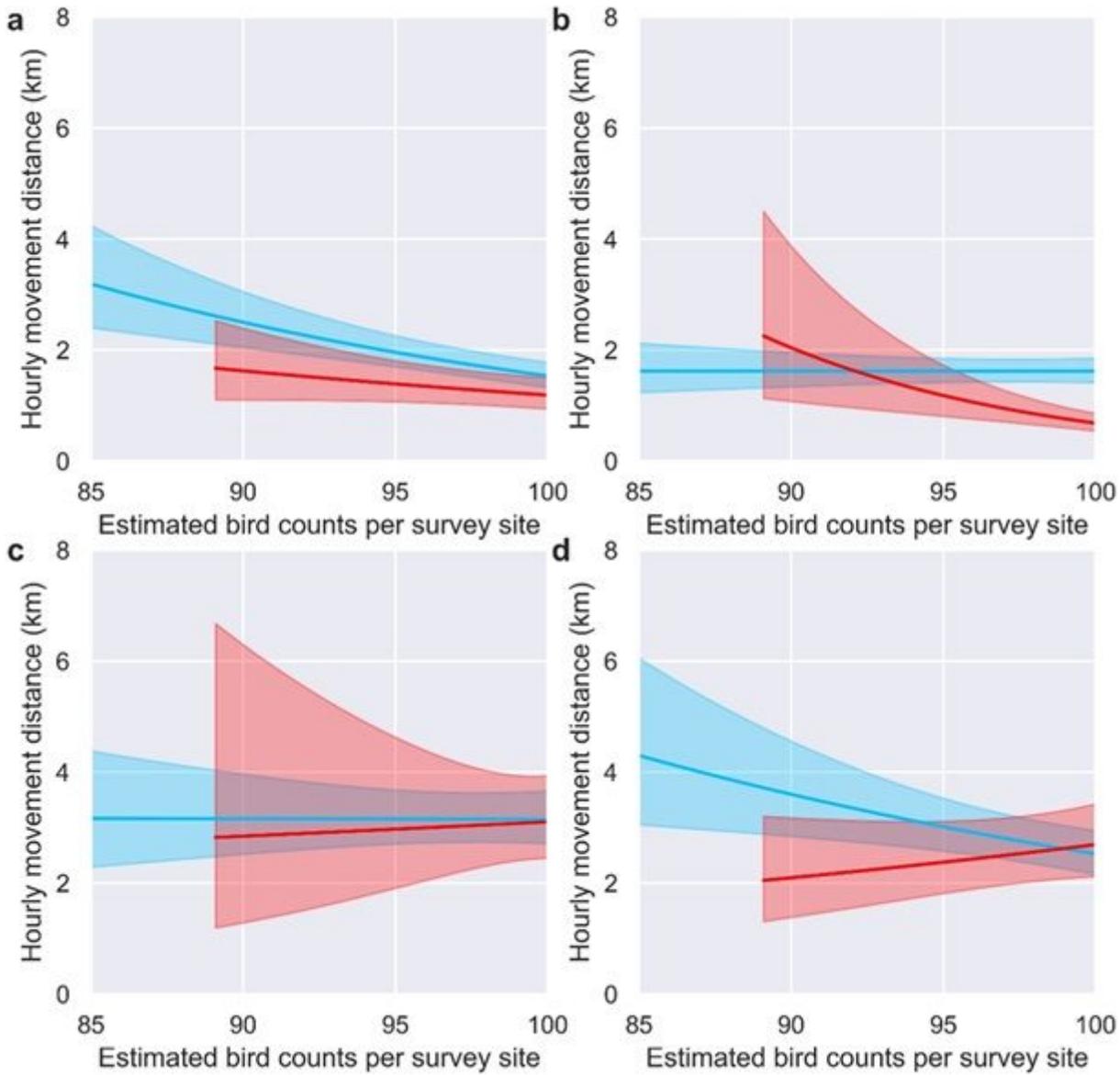


Figure 2

Effects of migration phases and relative population abundance on average hourly movement distances of American white pelicans. Panels show a) summer, b) winter, c) spring migration, and d) autumn migration. Blue and red colors represent wintering populations at Northern and Southern Gulf of Mexico, respectively. Polygons represent 95% confidence intervals of the average hourly movement distances.

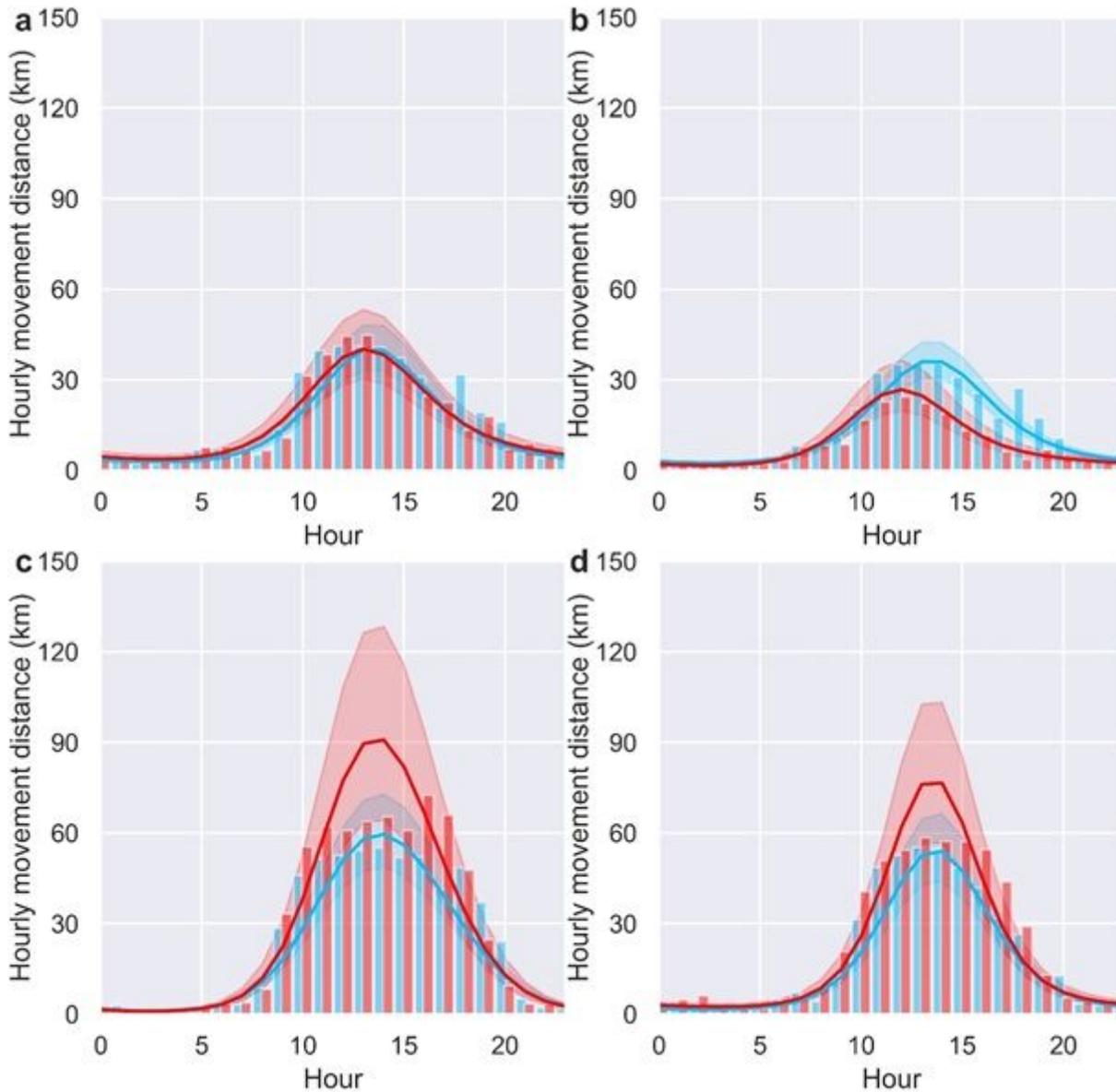


Figure 3

Maximum Hourly movement distances of American white pelicans with circadian hours. Blue and red colors represent wintering populations at Northern and Southern Gulf of Mexico, respectively. Panels represent a) summer, b) winter, c) spring migration, and d) autumn migration. Bars show observed maximum hourly movement distances. Lines indicate the estimated maximum hourly movement distances based on the best model. Polygons represent 95% confidence intervals of the maximum hourly movement distances.

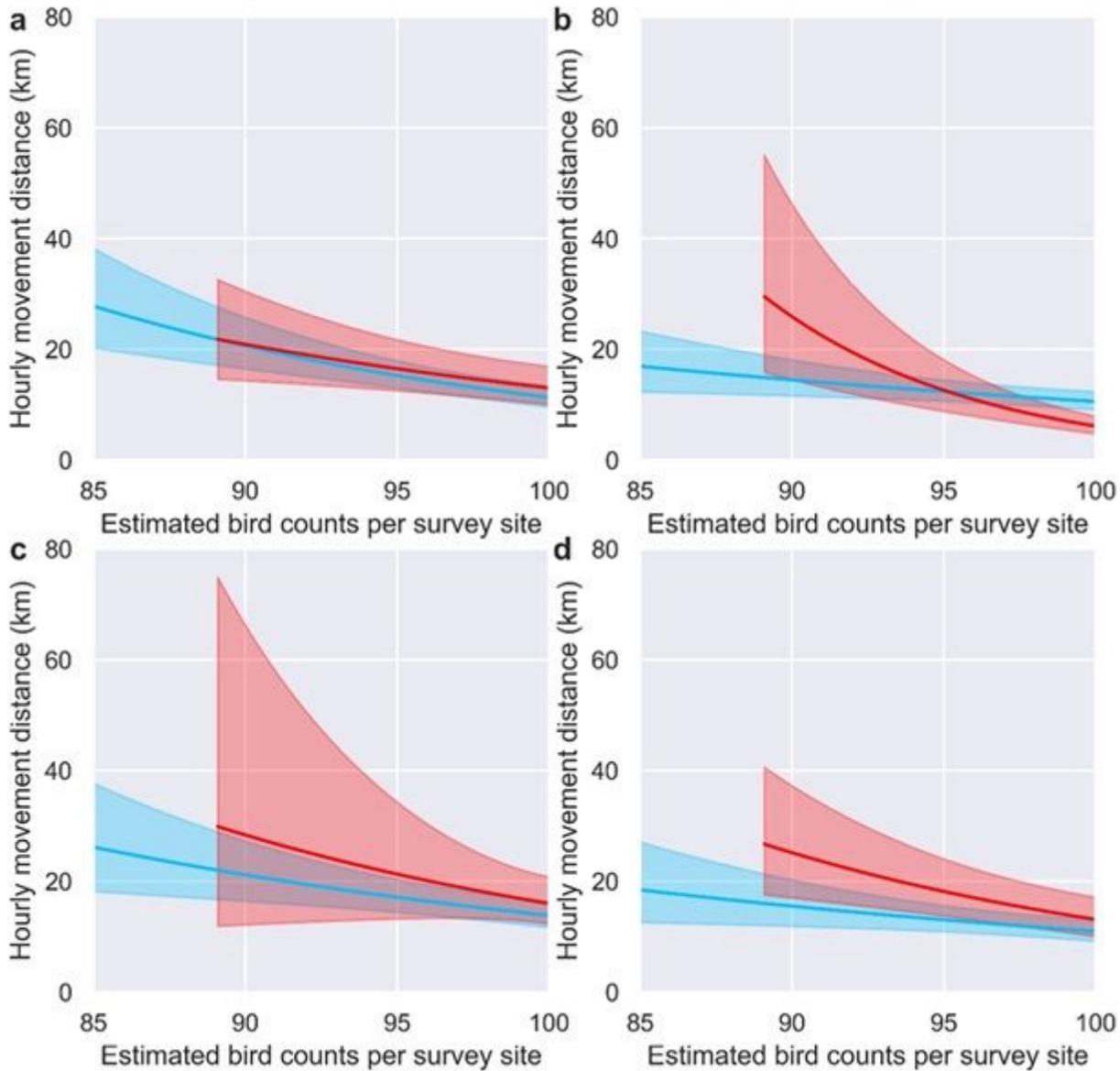


Figure 4

Effects of migration phases and relative population abundance on maximum hourly movement distances of American white pelicans. Panels show a) summer, b) winter, c) spring migration, and d) autumn migration. Blue and red colors represent wintering populations at Northern and Southern Gulf of Mexico, respectively. Polygons represent 95% confidence intervals of the maximum hourly movement distances.

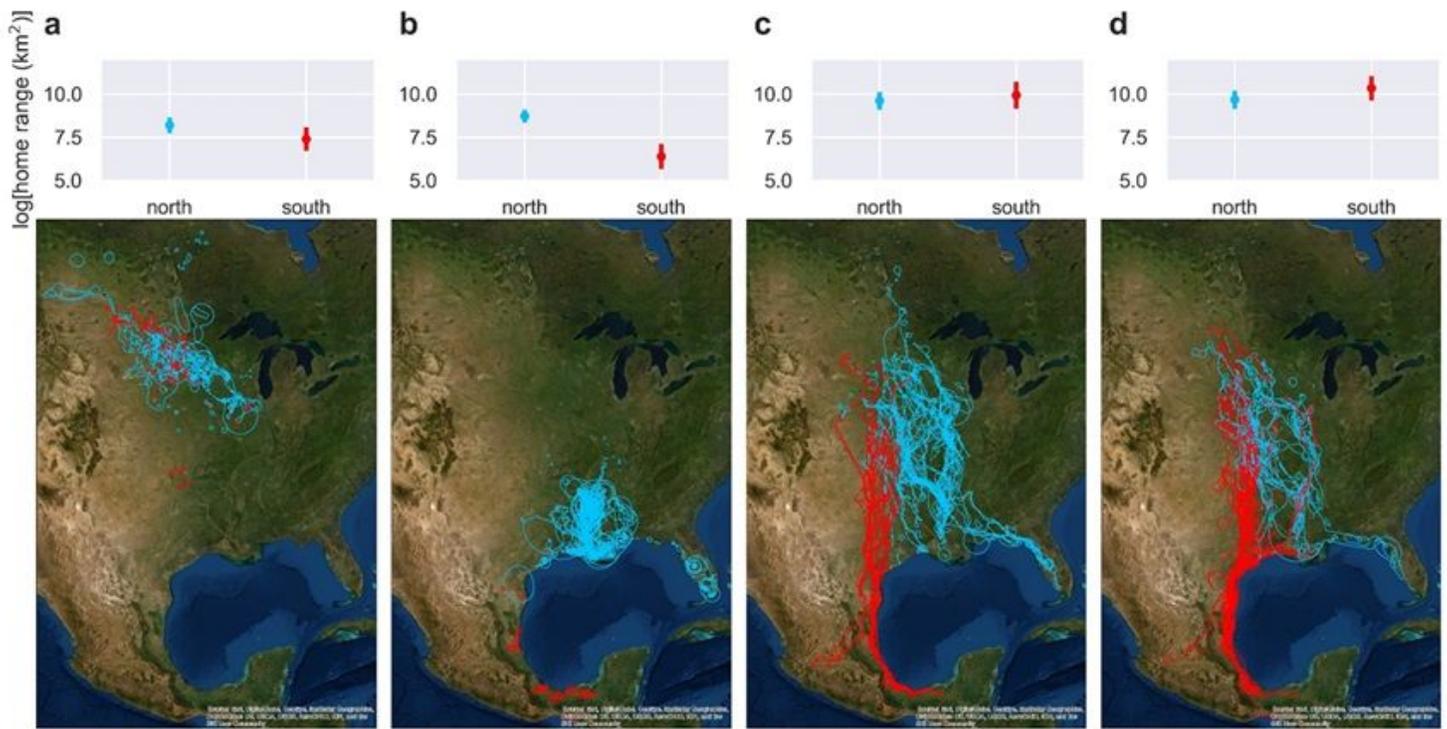


Figure 5

Seasonal home ranges of American white pelicans estimated by dynamic Brownian bridge movement models. Panels show a) summer, b) winter, c) spring migration, and d) autumn migration. Blue and red polygons represent seasonal home ranges of pelicans wintering in the Northern and Southern Gulf of Mexico, respectively. Upper subpanels show the estimates and 95% confidence intervals of log-transformed home ranges at each wintering population.

Supplementary Files

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