WINTERING REDDISH EGRET (*EGRETTA RUFESCENS*) FORAGING RESPONSE TO ENVIRONMENTAL VARIABILITY ON THE SOUTHERN TEXAS GULF COAST

by

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LIST OF ABBREVIATIONS

Abbreviation	**Description**
AICc	Akaike Information Criterion corrected for small sample sizes
ΔAICc	Difference between a model's AICc value and the AICc value of the best candidate model
AICcWt.	AICc weight. The proportion of explanatory power one model contains relative to all other models being compared.
Cum.Wt.	Cumulative AICc weight
L.L.	Log-Likelihood
S.D.	Standard Deviation
S.E.	Standard Error

ABSTRACT

The Reddish Egret (*Egretta rufescens)* is a rare species of heron due to its limited geographic range as well as its narrow habitat requirement, relying exclusively on coastal tidal flats throughout its yearly cycle. It is therefore vulnerable to stressors ranging from human coastal development to sea level rise due to climate change. While Reddish Egret breeding ecology has been well studied, little information is known about the wintering ecology of the species. With the goal of gaining more knowledge of its winter foraging habitat requirements, I conducted line transect surveys via boat of foraging Reddish Egrets from November 2019 to March 2021 in the Laguna Madre land cut of the Gulf Intracoastal Waterway, an area with a large portion of tidal flat habitat. Using negative binomial and logistic generalized linear mixed effect models of my count data and multiple environmental variables, I found increasing wind speed and an easterly wind direction had negative effect on the presence of foraging Reddish Egrets in the study area, while a westerly wind direction had a positive effect, suggesting that wind patterns influence the distribution of foraging individuals on the Texas coast. In comparison of light and dark plumage morph Reddish Egrets, higher air temperature and an increasing cloud cover was associated with a higher proportion of light morph to dark morph Reddish Egrets in the flats, indicating support for difference in foraging response between the two color morphs. This study will help in furthering knowledge of Reddish Egret winter foraging preferences and may help inform conservation actions including suitable habitat identification and protection in the future.

1. WINTERING REDDISH EGRET (*EGRETTA RUFESCENS*) FORAGING RESPONSE TO ENVIRONMENTAL VARIABILITY ON THE SOUTHERN TEXAS GULF COAST

Introduction

The Reddish Egret (*Egretta rufescens*) is one of the rarest and most habitat-restricted herons in North America. It is found exclusively in shallow coastal wetland habitat ranging from the northern Gulf Coast of the United States to the northern coast of South America, along the Pacific coast of Mexico, and throughout most of the Caribbean (Koczur et al., 2020). As a habitat specialist that relies on coastal tidal flats throughout its annual cycle, it is vulnerable to small changes in such habitat (e.g., water depth) (Bates et al., 2016), as well as to disturbance and degradation from human activities (Moulton et al., 1997). Much is known about the breeding ecology of Reddish Egrets, but more information is needed about their foraging habitat throughout the annual cycle, especially during winter when little research has been done (Koczur et al., 2020).

Although nesting and hatching success appears to be high in Reddish Egret colonies on the Texas coast (Holderby et al., 2012) juvenile survival in the non-breeding season is low (Geary et al., 2015), indicating there may be insufficient winter foraging habitat. Habitat quality experienced during the wintering portion of an animal's annual cycle, as well as the distance required to reach suitable winter habitat (Bregnballe et al., 2006), may have an impact on individuals' reproductive success for the following breeding season (Gunnarsson et al., 2005; Harrison et al., 2011; Norris, 2005; Sedinger & Alisauskas, 2014). Furthermore, if low quality winter habitat leads to increased mortality, a compensatory increase in reproductive rates due to density dependent factors may also occur (Norris, 2005); hence, a better understanding of the non-breeding ecology of Reddish Egrets is important.

The Laguna Madre of Texas is recognized as a population stronghold for the Reddish Egret, accounting for an estimated 45-65% of the Texas population (Koczur et al., 2020). Geary et al. (2015) found the majority of tagged juvenile Texas Reddish Egrets from the Laguna Madre remained either on the Texas coast or near the Texas/Mexico border in winter, suggesting a largely resident behavior. However, there is evidence of a seasonal decline in available habitat there during the winter (mainly due to an increase in water depth) with an estimated 50% decrease in foraging habitat compared to summer months (Bates et al., 2016).

As migration is a hazardous and energetically costly undertaking, an individual will only migrate when its current habitat quality declines below a certain threshold or when they must move to suitable breeding areas (Gauthreaux, 1982). Koczur et al., (2017) found that Reddish Egrets employ a partial winter migration strategy in the Laguna Madre, with approximately 40% of satellite-tagged individuals leaving the study area during the winter season, indicative of a response to a decline in winter foraging habitat (Bates et al., 2016). While species who are less habitat-constrained may be able to migrate to more suitable wintering grounds, Reddish Egrets are coastal habitat specialists and may find it more difficult to find alternative roosting and foraging areas if their normal wintering habitat declines further, potentially reducing fitness.

One of the distinguishing characteristics of the Reddish Egret is the presence of two color morphs: One dark grey and rusty red, the other pure white. Both morphs are reported as roughly equal in frequency on the Texas Gulf Coast (Green, 2005). The proportion of the two color morphs were found to follow a geographic east-west gradient, with Baja California containing only dark morph individuals, and the eastern portion of its range containing majority light morph individuals (Green et al., 2011; Howell & Pyle, 1997). Crypsis against prey and better thermotolerance are hypothesized advantages of light morph plumage in Reddish Egrets (Green & Leberg, 2005).

The aim of this study is to conduct an examination of Reddish Egret foraging response to environmental factors at a finer scale, considering both the species as a whole and differences between the two color morphs. To accomplish this, I chose to survey the Laguna Madre of Texas, specifically the "land cut" (Figure 1), an artificial shipping channel with shallow unvegetated tidal flats along the entirety of its western shoreline. Koczur et al. (2018) found that unconsolidated sediment, specifically wind-driven tidal flats, was the primary habitat type used by marked Reddish Egrets for both feeding and roosting, and Bates & Ballard (2014) found that Reddish Egrets were more successful when foraging in shallower areas with less seagrass coverage. My objective is to examine Reddish Egret abundance in relation to these and other environmental variables over two non-breeding seasons. I hypothesize that the broader scale seasonal habitat availability model proposed by Bates et al. (2016) will be further validated by these finer scale habitat and abundance measurements.

Methods

Study Site

The Upper and Lower Laguna Madre of Texas are connected by a manmade canal, dredged in 1949, to extend the Gulf Intracoastal Waterway. This canal is informally known as the "land cut", and averages about four meters in depth along its length to allow for barge traffic. This is in contrast to the rest of the Laguna Madre, which averages about one meter in depth (Tunnell & Judd, 2002). Along the length of the eastern shore of the land cut there are a series of dredge spoil islands, while the left shoreline contains a wind-driven tidal flats which have been identified as foraging habitat for Reddish Egrets (Bates et al., 2016). As much of the Laguna

Madre is too shallow for safely surveying via boat, the land cut serves as a convenient place to systematically survey Reddish Egret foraging response.

Surveys

Two series of monthly three-day winter survey counts of Reddish Egret abundance were conducted in the study area over two periods from November through February 2019-2020 and 2020-2021 (One survey was delayed until March 2021 due to the COVID-19 pandemic). The study area was delineated as a series of eight, two kilometer transects, spaced 2.5 kilometers apart to avoid counting individual birds more than once (Bibby et al., 1992). A handheld GPS unit (Garmin eTrex 20) was used to navigate by boat to the transects, which were marked on both ends with marked plastic piping. Transects were surveyed in series from a boat trolling at a constant speed (~8-10 km/h) through the land cut while foraging Reddish Egrets were counted. Foraging Reddish Egrets were defined as individuals residing in a body of water within the transect being surveyed (Rodgers, 1983). Observed individuals were further divided into counts of dark and light color morphs.

Each monthly field trip consisted of three consecutive daily surveys of all transects, with the direction of travel reversed each day to minimize temporal and directional bias. For example, on the first day of a field trip, transects one through eight were surveyed in order. On the second day, the survey direction was reversed, and transects eight through one were surveyed. On the third day, the direction was reversed again. Figure 1 shows the placement of transects in the study area.

Reddish Egrets were counted from the boat using 8x42 binoculars. Spotting scopes (Swarovski ATS65, 25x60x) were used to confirm bird sightings farther away and to opportunistically identify any birds with alphanumeric leg bands from ongoing mark-resight studies.

Environmental Data

In addition to Reddish Egret counts, a set of environmental variables were collected during surveys. At the beginning and end of every transect a Secchi disk was used to measure water clarity in meters and a meter stick was used to measure the water depth in meters. Cloud cover was estimated by sight as a percentage of cloudy sky overhead. A NOAA tidal gauge and weather station located approximately 3.5 kilometers from the southernmost transect provided the water level in meters, air and water temperature in degrees Celsius, wind speed in meters per second, and wind direction in degrees from North. I recorded these data at the start and end times of each transect survey and averaged them to get mean environmental values per transect survey.

Data obtained from the NOAA tidal gauge and weather station contained some missing data. To partially remedy this, I performed linear interpolation for single missing values only by imputing the mean of the values directly before and after the missing value in the time series, and only when both values were from the same transect survey. The remainder of rows with missing data were removed from the data set.

Wind direction is a circular variable, with 0 and 360 degrees treated as equivalent, and is incompatible with standard linear regression methods. To include wind direction in a linear model, I calculated its sine and cosine components and added both to my models as two explanatory variables, the sine value representing the east-west component of wind direction and the cosine value representing the north-south component (Cox, 2006; Hribar et al., 2010).

Statistical Analyses

To examine the effects of my environmental variables on total Reddish Egret counts in the survey area, I constructed a series of negative binomial generalized linear mixed effect models in R (R Core Team, 2022) using the R package glmmtmb (Brooks et al., 2017). The total foraging Reddish Egret count per transect survey was the response variable and transect was specified as a random variable. Models were compared using Akaike's Information Criterion for small sample sizes (AICc), a relative measure of model quality that attempts to balance model fit and complexity (Burnham et al., 2011). The effects of the best model were estimated with 95% confidence intervals generated through bootstrapping the parameters of the model 1,000 times using the R package parameters (Lüdecke et al., 2020).

To examine possible differences in environmental effects on dark and light morph Reddish Egrets in the study area, I constructed a series of logistic generalized linear mixed models with a binomial proportion as the response using the R package glmmtmb (Brooks et al., 2017). The proportion of foraging light morph Reddish Egrets to the total count of foraging light and dark morph birds per transect survey was the response variable. Transect was again specified as a random variable. Models were compared using Akaike's Information Criterion for small sample sizes (AICc). The effects of the best model were estimated with 95% confidence intervals generated through bootstrapping the parameters of the model 1,000 times using the R package parameters (Lüdecke et al., 2020). I also investigated a relationship between the proportion of light morph individuals per transect survey and an interaction between air temperature and cloud cover, under the hypothesis that light morph individuals would tolerate higher temperatures as well as use cloud cover as a form of crypsis against prey.

Results

From 8 November 2019 to 7 March 2021, a total of 157 transect surveys were conducted in the Laguna Madre study area. After removing surveys with missing data, 134 transect surveys were available for analysis. A total of 778 Reddish Egrets were observed foraging in the study area with 253 and 552 dark and light morphs respectively. Table 1 shows the mean, minimum, maximum, standard deviation, and standard error of Reddish Egret counts across all transects. Figure 2 shows the mean proportion of color morphs per transect survey at each transect. Transects two and three had higher mean counts than the remaining transects, and all transects showed a higher mean proportion of light morphs compared to dark morphs.

For my examination of the environmental effects on total foraging Reddish Egret counts, the model that included wind speed and the sine (east-west) and cosine (north-south) components of wind direction best explained the variation in total counts of Reddish Egrets in the survey area out of all candidate models. Wind speed had a negative effect on Reddish Egret counts (β = -0.23, 95% CI = [-0.43, -0.03]. The sine component of wind direction had a negative effect on Reddish Egret counts as it shifted from West (sine of -1) to East (sine of 1) (β = -0.26, 95% CI = [-0.44, -0.02]). The cosine component of wind direction did not have a significant effect on Reddish Egret counts (β = 0.03, 95% CI = [-0.17, 0.23]). Figure 3 shows the plotted effects. Table 2 shows all models ranked best to worst using AICc as the criterion.

In my examination of possible differences in environmental effects on foraging dark and light morph Reddish Egrets, the model that included a combination of wind speed, the sine (east-west) and cosine (north-south) components of wind direction, air temperature, cloud cover, and a significant interaction between air temperature and cloud cover ($\chi2(7,8) = 6.12$, $p = 0.01$) provided the best explanation for the variation in the observed ratio of light morph to total

Reddish Egrets per transect survey out of all candidate models. Wind speed (β = 0.62, 95% CI = [0.27, 0.96]), the cosine component of wind direction (shifting from south to north) (β = 0.52, 95% CI = [0.26, 0.81]), air temperature (β = 0.56, 95% CI = [0.28, 0.81]), cloud cover (β = 0.26, 95% CI = [0.01, 0.51]) all had a positive effect. The sine component of wind direction did not have a significant effect on Reddish Egret counts (β = -0.01, 95% CI = [-0.25, 0.25]). The interaction between air temperature and cloud cover also had a positive effect on the proportion of light morph individuals, with the effect of more white morphed birds increasing with air temperature and cloud cover (β = 0.34 [0.04, 0.60]). Figure 5 shows the plotted main effects and interaction effect. Table 3 shows all models ranked best to worst using AICc as the criterion.

Discussion

Among the environmental factors examined for their effect on Reddish Egret foraging response, the most significant variables in my models were wind speed and direction. I found that as wind speed increased the total counts of Reddish Egrets per surveyed transect decreased. This may be explained by wave action generated by higher wind speeds obscuring prey. Rodgers (1983) found that higher wind speeds increased wave action, leading to a lower success rate in foraging herons. The east-west (sine) component of wind direction was also found to be significantly correlated with Reddish Egret counts. Westerly winds were associated with more individuals in the foraging area and easterly wind with less. Bates & Ballard (2014) found that environmental variables, including wind speed (moderated by light intensity), were correlated with Reddish Egret foraging success (specifically strike efficiency). However, wind direction was not examined in their study.

Wind-driven tidal flats are a key component of Reddish Egret foraging habitat throughout the annual cycle (L. M. Koczur et al., 2020; Tunnell & Judd, 2002). My findings that wind direction perpendicular to the study site was correlated with the number of individuals sighted in surveys may reflect this wind-driven mechanism present in the Laguna Madre. The tidal flats of the land cut contain little if any seagrass, an important habitat for prey species of the Reddish Egret. However, the surrounding deeper waters of the laguna contain 80% of all seagrass beds on the Texas coast (Tunnell & Judd, 2002). Easterly winds blow water, and potentially prey, from these regions onto the tidal flats of the land cut where they may be more accessible to Reddish Egrets. However, easterly winds may also raise the water level of these flats above what is ideal for a foraging Reddish Egret to hunt efficiently. A westerly wind may counteract this by lowering the water level and leaving remaining prey in the flats more vulnerable to predation. The Laguna Madre experiences water level fluctuations of 0.6-0.9 meters due to these wind-driven tides (Tunnell & Judd, 2002), while Reddish Egrets can tolerate a maximum water depth of 0.25 cm and still forage effectively (Green, 2005; Green et al., 2022). My findings provide evidence that wind exerts a notable influence on Reddish Egret foraging response.

From a spatial perspective, my finding that transects two and three were the most active out of all the transects surveyed agrees with the spatial model put forth by Bates et al., 2016, which predicted that the section of the land cut these two transects reside in contain almost all the suitable Reddish Egret foraging habitat in the land cut portion of the Laguna Madre. This study therefore helps to validate the accuracy of the spatial aspect of that model.

Differences between color morphs

When examining the proportion of light and dark morph Reddish Egrets counted in the study, wind speed and the north-south (“cosine”) component of wind direction had a significant effect on the proportion of light morphs counted. As wind speed increased and as the wind direction changed from south to north, a higher proportion of light morph individuals were counted per transect survey. Green (2005) found that light morph individuals were more likely to actively forage in intermediate and deep water than dark morph individuals. Wind speed and direction play a role in water depth on tidal flats of the Laguna Madre and may therefore influence the proportion of light morph individuals seen foraging. A wind direction parallel to the shoreline might induce an intermediate water depth, favoring the light morph.

Cloud cover had a significant positive effect on the proportion of white morph individuals per transect survey. Green & Leberg (2005) found evidence that herons with white plumage are afforded a degree of crypsis when hunting for prey in open water, while Gotmark (1987) found that gulls with darkened underwings were less successful in hunting aquatic prey than gulls with white underwings. The effect of cloud cover may improve crypsis of foraging white morph Reddish Egrets further by reducing their outline against the sky or by reducing their shadow. While shadow can be a cue for the presence of a predator overhead, the more diffuse sunlight on cloudy days may minimize its appearance and help to prevent this form of predator detection (Green & Leberg, 2005).

Ambient air temperature also had a significant positive effect on the proportion of white morphs counted during surveys. White plumage may be a factor as lighter colors absorb less solar radiation than darker colors (Mock, 1980). Galván et al. (2018) found a relationship between preferred air temperature and reflectance of feather pigment of 96 bird species. The positive interaction between cloud cover and air temperature in the model indicates both factors are beneficial to lighter morph Reddish Egrets. Cloud cover may improve crypsis of lighter morphs, and higher air temperatures may be more tolerable to them even on cloudy days, as cloud cover does not completely block solar radiation. For example, in complete cloud cover, UV-B radiation still penetrates high altitude clouds completely, and low altitude clouds at a rate of 53% (Calbó et al., 2005).

Study Limitations

One possible point of concern regarding this study is the higher-than-expected proportion of light morph to dark morph Reddish Egrets recorded over the course of my surveys compared to previous published findings. The total count consisted of an approximate ratio of 2:1 light to dark morphs, with mean proportional counts in each transect also skewed toward light morph individuals (Figure 2). This disagrees with previous findings suggesting a roughly 1:1 ratio in this portion of the Reddish Egret's range (Green et al., 2011; Holderby et al., 2012; Howell & Pyle, 1997). One potential explanation for this discrepancy is that there may be a differential propensity between the two color morphs to migrate during winter. In an examination of juvenile dispersal in Reddish Egrets hatched in Texas, Geary et al. (2015) reported 3 out of 14 dark morphs (and 0 out of 11 white morphs) dispersed outside of Texas. With breeding adults in Texas however, Koczur et al. (2017) found no difference between color morphs in adults that migrated versus adults that remained residents (i.e. over-wintered) in Texas.

The two color morphs may also have a differential contrast with the surrounding habitat, leading to missed counts of dark morph individuals. We conducted surveys from a boat, with surveyors looking across the tidal flats with binoculars. Background terrain and vegetation may have obscured darker colored birds while lighter colored birds may have been seen more easily due to greater contrast.

Ecological Implications

The Reddish Egret is a uniquely vulnerable species as it inhabits both a narrow geographic range and relies on specific habitat characteristics. Sea level rise, human development, and human disturbance are factors threatening the availability of an already scarce habitat niche (Green et al., 2022; L. M. Koczur et al., 2020). One of the goals of the Reddish Egret International Working Group (Green et al., 2022) is to identify important breeding and winter foraging areas and knowledge from studies like this may aid in that effort. This study adds to the knowledge of Reddish Egret winter foraging ecology in these areas, specifically how individuals respond to environmental variation in foraging habitat and the differences in response between color morphs. It also provides evidence to support the spatial model of foraging habitat availability in the land cut of the Laguna Madre put forth by Bates et al., (2016).

Tables

Transect	# Surveys	Mean Count	S.D.	Min Count	Max Count	S.E.
1	18	1.67	1.78	0	6	0.42
2	16	15.69	28.98	0	110	7.24
3	16	12.13	10.46	2	41	2.61
4	17	2.18	1.88	0	6	0.46
5	17	2.35	4.34	0	18	1.05
6	17	2.88	3.14	0	10	0.76
7	17	2.35	2.21	0	7	0.54
8	16	2.38	1.86	0	6	0.46

Table 1. Summary of mean, minimum, maximum (and standard deviation and standard error) total Reddish Egret (*Egretta rufescens*) counts across all surveys from November 2019 – February 2020 and November 2020 – March 2021 in the Laguna Madre Land Cut, Texas, USA.

Models	**K**	**AICc**	**ΔAICc**	**AICcWt.**	**Cum. Wt.**	**LL**
Wind sp.+sin(wind dir.)+cos(wind dir.)	6	672.61	0.00	0.23	0.23	-329.98
Wind sp.+sin(wind dir.)+cos(wind dir.)+water clarity	7	672.90	0.28	0.20	0.42	-329.00
Wind sp.+water clarity	5	673.68	1.07	0.13	0.56	-331.61
Wind sp.	4	673.77	1.15	0.13	0.68	-332.73
Wind sp.+sin(wind dir.)+cos(wind dir.)+cloud cover	7	674.70	2.08	0.08	0.76	-329.90
Water clarity	4	674.94	2.33	0.07	0.84	-333.32
wind Sp.+sin(wind dir.)+cos(wind dir.)+water clarity+cloud cover	8	674.97	2.36	0.07	0.91	-328.91
Null Model	3	675.67	3.06	0.05	0.95	-334.74
Water temp.+water clarity+water depth	6	676.57	3.96	0.03	0.99	-331.95
Water temp.+air temp.	5	678.84	6.23	0.01	1.00	-334.19
Full Model	11	680.65	8.03	0.00	1.00	-328.24

Table 2. Ranked generalized linear mixed negative binomial model comparison table for Total Reddish Egret (*Egretta rufescens*) counts per transect survey using data collected from 8 November 2019 to 7 March 2021 in the Laguna Madre Land Cut, Texas, USA.

Models	K	AICc	ΔAICc	AICcWt.	Cum.Wt.	LL
Wind sp.+sin(wind dir.)+ cos(wind dir.)+air temp*cloud cover	8	283.29	0.00	0.83	0.83	-133.07
Wind sp.+sin(wind dir.)+ cos(wind dir.)+air temp+cloud cover	7	287.15	3.86	0.12	0.95	-136.13
Full Model	10	289.21	5.92	0.04	1.00	-133.71
Air temp+cloud cover	4	296.17	12.88	0.00	1.00	-143.93
Air temp	3	297.07	13.78	0.00	1.00	-145.44
Air temp*cloud cover	5	297.63	14.34	0.00	1.00	-143.58
Wind sp.+cloud cover	4	301.37	18.08	0.00	1.00	-146.53
Cloud cover	3	302.94	19.65	0.00	1.00	-148.38
Null model	2	304.79	21.50	0.00	1.00	-150.35

Table 3. Ranked generalized linear mixed logistic model comparison table for light morph Reddish Egret (*Egretta rufescens*) proportions per transect survey count using data collected from 8 November 2019 to 7 March 2021 in the Laguna Madre Land Cut, Texas, USA.

Figures

Fig.1 Location of the Laguna Madre Land Cut, Texas, USA. Transects are indicated by black lines. Arrows indicate survey effort focus on the west side of the transects. Location of NOAA tidal gauge and weather station is labeled.

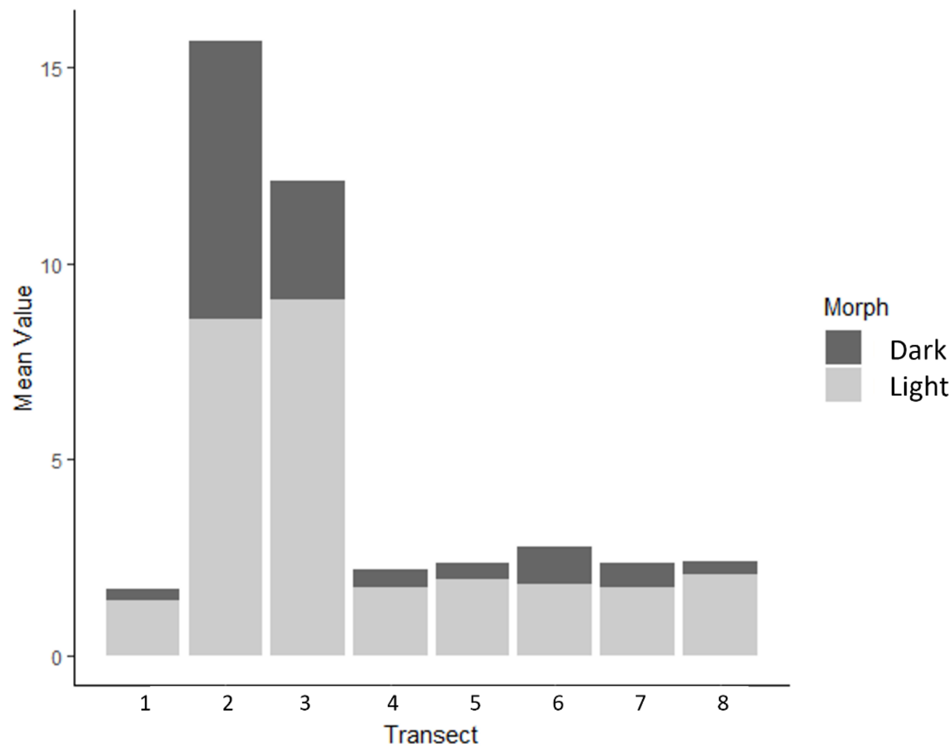

Fig.2. Stacked bar plot showing mean transect counts of Dark and Light Reddish Egrets (*Egretta rufescens*) for each transect in the Laguna Madre Land Cut, Texas, USA.

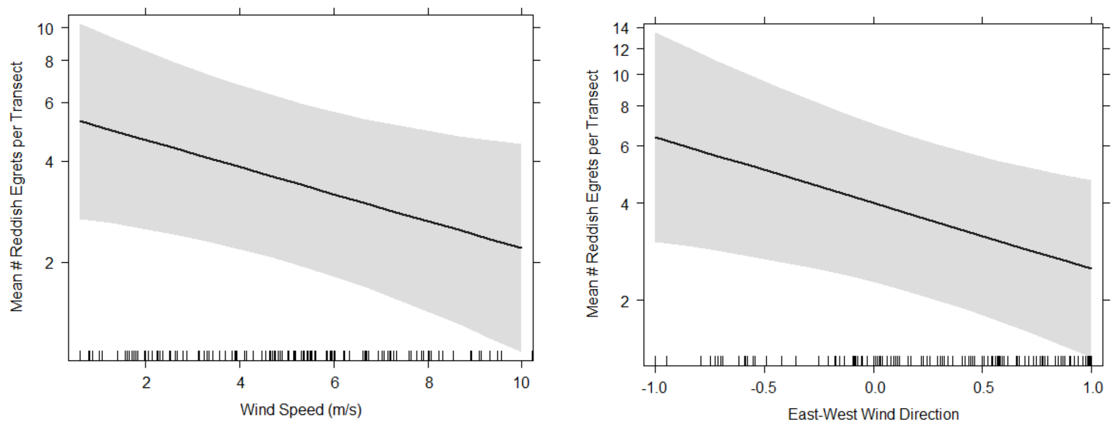

Fig.3. Effect plots of the main effects (wind speed in m/s and sine (west to east) of wind direction) for the top ranked generalized linear mixed negative binomial model of Total Reddish Egret (*Egretta rufescens*) counts per transect survey.

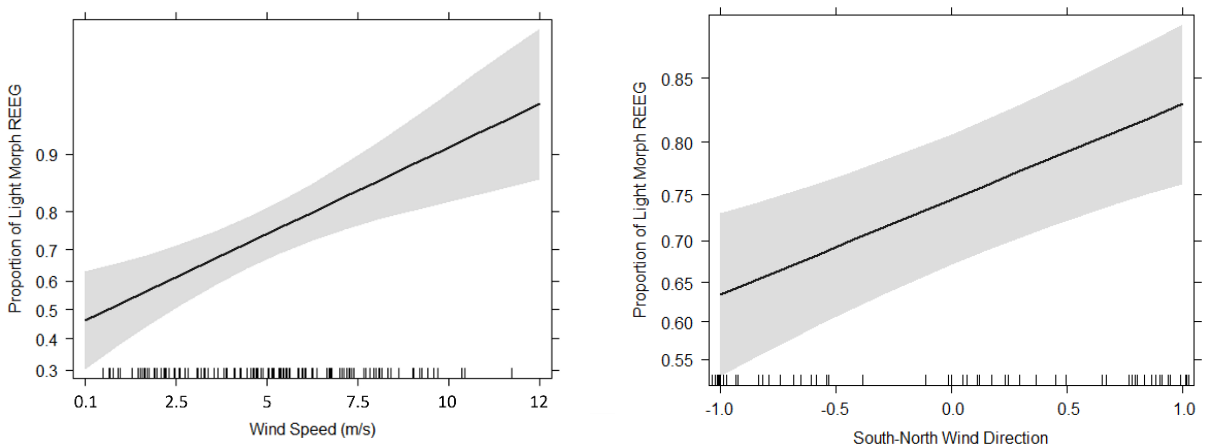

Fig.4. Effect plots of the two main effects (wind speed and cosine (north to south) of wind direction) in the top ranked generalized linear mixed logistic model of the proportion of total Reddish Egret (*Egretta rufescens*) counts per transect survey that were light morphs. (The x axis of the wind speed plot was manually rescaled to reflect the scale of the original data rather than the scaled data used in the model).

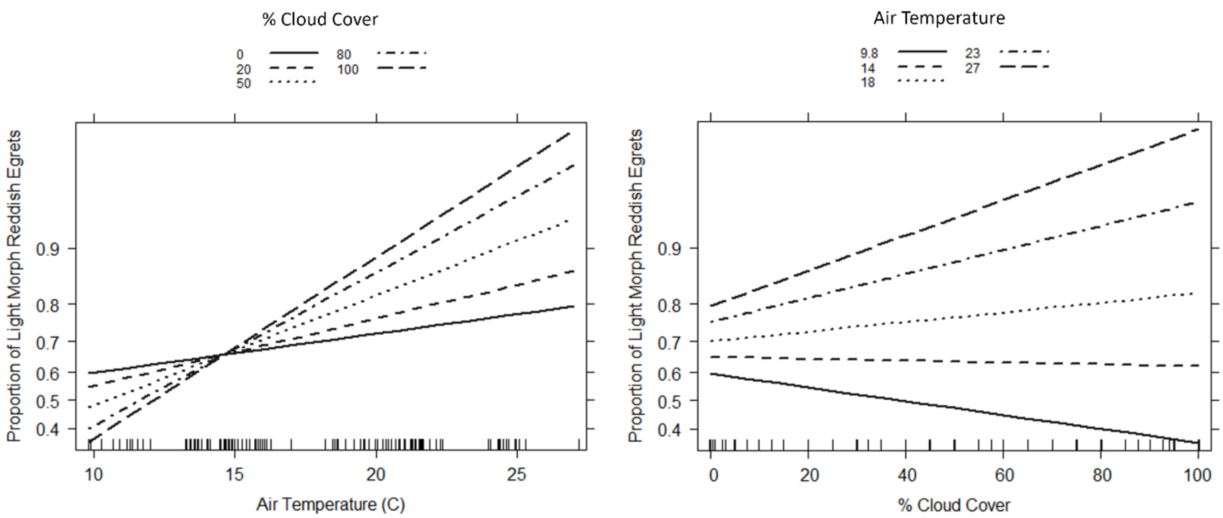

Fig.5. Plots of the two interacting variables (air temperature and percent cloud cover) for the top ranked generalized linear mixed logistic model of the proportion of total Reddish Egret (*Egretta rufescens*) counts per transect survey that were light morphs.

LITERATURE CITED

Bates, E. M., & Ballard, B. M. (2014). Factors Influencing Behavior and Success of Foraging Reddish Egrets (*Egretta rufescens*). *Waterbirds*, *37*(2), 191–202. https://doi.org/10.1675/063.037.0213

Bates, E. M., Koczur, L. M., Krainyk, A., Ballard, B. M., & Kasner, A. C. (2016). Spatial and temporal dynamics of foraging habitat availability for reddish egrets in the Laguna Madre, Texas. *International Journal of Biodiversity and Conservation*, *8*(10), 251–258. https://doi.org/10.5897/IJBC2016.1025

Bibby, C. J., Burgess, N. D., & Hill, D. A. (1992). *Bird Census Techniques*. Elsevier Science. https://books.google.com/books?id=5TqfwEHCVuoC

Bregnballe, T., Frederiksen, M., & Gregersen, J. (2006). Effects of distance to wintering area on arrival date and breeding performance in Great Cormorants. *Ardea*, *94*(3), 619–630.

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., & Bolker, B., M. (2017). GlmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378. https://doi.org/10.32614/RJ-2017-066

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Calbó, J., Pagès, D., & González, J.-A. (2005). Empirical studies of cloud effects on UV radiation: A review. *Reviews of Geophysics*, *43*, RG2002. https://doi.org/10.1029/2004RG000155

Cox, N. J. (2006). Speaking Stata: In Praise of Trigonometric Predictors. *The Stata Journal*, *6*(4), 561–579. https://doi.org/10.1177/1536867X0600600408

Galván, I., Rodríguez-Martínez, S., & Carrascal, L. M. (2018). Dark pigmentation limits thermal niche position in birds. *Functional Ecology*, *32*, 1531–1540. https://doi.org/10.1111/1365-2435.13094

Gauthreaux, S. A. (1982). The Ecology and Evolution of Avian Migration Systems. In *Avian Biology* (pp. 93–168). Elsevier. https://doi.org/10.1016/B978-0-12-249406-2.50011-3

Geary, B., Green, M. C., & Ballard, B. M. (2015). Movements and survival of juvenile reddish egrets Egretta rufescens on the Gulf of Mexico coast. *Endangered Species Research*, *28*, 123–134. https://doi.org/10.3354/esr00682

Gotmark, F. (1987). White underparts in gulls function as hunting camouflage. *Animal Behaviour*, *35*(6), 1786–1792.

Green, M. C. (2005). Plumage Dimorphism in the Reddish Egret: Does Plumage Coloration Influence Foraging Habitat Use and Tactics? *Waterbirds*, *28*(4), 519–524. https://doi.org/10.1675/1524-4695(2005)28[519:PDITRE]2.0.CO;2

Green, M. C., Demarest, D. W., Tarbox, B. C., Cox, W. A., Franco, J. G., Narváez-Torres, S., Stone, K. L., & Vermillion, W. G. (2022). *Reddish Egret Conservation Action Plan. Unpublished report*.

Green, M. C., Hill, A., Troy, J. R., Holderby, Z., & Geary, B. (2011). Status of Breeding Reddish Egrets on Great Inagua, Bahamas with Comments on Breeding Territoriality and the Effects of Hurricanes. *Waterbirds*, *34*(2), 213–217. https://doi.org/10.1675/063.034.0210

Green, M. C., & Leberg, P. L. (2005). Influence of plumage colour on prey response: Does habitat alter heron crypsis to prey? *Animal Behaviour*, *70*(5), 1203–1208. https://doi.org/10.1016/j.anbehav.2005.03.003

Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M., & Sutherland, W. J. (2005). Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1578), 2319–2323. https://doi.org/10.1098/rspb.2005.3214

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, *80*, 4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Holderby, Z., Simper, W., Geary, B., & Green, M. C. (2012). Potential Factors Affecting Nest Initiation Date, Clutch Size and Nest Success in the Plumage Dimorphic Reddish Egret. *Waterbirds*, *35*(3), 437–442. https://doi.org/10.1675/063.035.0308

Howell, S. N. G., & Pyle, P. (1997). Twentieth Report of the California Bird Records Committee: 1994 Records. *Western Birds*, *28*(3), 124.

Hribar, L. J., DeMay, D. J., & Lund, U. J. (2010). The association between meteorological variables and the abundance of Aedes taeniorhynchus in the Florida Keys. *Journal of Vector Ecology*, *35*(2), 339–346. https://doi.org/10.1111/j.1948-7134.2010.00092.x

Koczur, L., Ballard, B., & Green, M. (2017). Survival of adult reddish egrets Egretta rufescens marked with satellite transmitters. *Endangered Species Research*, *34*, 103–107. https://doi.org/10.3354/esr00846

Koczur, L. M., Green, M. C., Ballard, B. M., Lowther, P. E., & Paul, R. T. (2020). *Reddish Egret—Distribution, Migration, and Habitat | Birds of North America Online*. https://birdsna-org.libproxy.txstate.edu/Species-Account/bna/species/redegr/distribution

Koczur, L. M., Kent, G. M., Ballard, B. M., Meyer, K. D., & Green, M. C. (2018). Space Use and Movements of Adult Reddish Egrets (*Egretta rufescens*) During Winter. *Waterbirds*, *41*(1), 1–15. https://doi.org/10.1675/063.041.0102

Lüdecke, D., Ben-Shachar, M., Patil, I., & Makowski, D. (2020). Extracting, Computing and Exploring the Parameters of Statistical Models using R. *Journal of Open Source Software*, *5*(53), 2445. https://doi.org/10.21105/joss.02445

Mock, D. W. (1980). White-dark polymorphism in herons. *Proceedings of the First Welder Wildlife Foundation Symposium*, *1*, 145–161.

Moulton, D., Dahl, T., & Dall, D. (1997). Texas coastal wetlands: Status and trends, mid-1950s to early 1990s. *U.S. Department of the Interior, Fish and Wildlife Service, Southwestern Region, Albuqerque, New Mexico*.

Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. *Oikos, 109*(1), 178–186. https://doi.org/10.1111/j.0030-1299.2005.13671.x

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rodgers, J. A. (1983). Foraging Behavior of Seven Species of Herons in Tampa Bay, Florida. *Colonial Waterbirds*, *6*, 11–23. https://doi.org/10.2307/1520962

Sedinger, J. S., & Alisauskas, R. T. (2014). Cross-seasonal effects and the dynamics of waterfowl populations. *Wildfowl, S.I.*, 277–304.

Tunnell, J. W., & Judd, F. W. (2002). *The Laguna Madre of Texas and Tamaulipas*. Texas A&M University Press.