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Fine-scale Weather Patterns Drive Reproductive Success in the Brown Pelican

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Abstract.—In the northern Gulf of Mexico, island restoration and creation have been used to mitigate potential negative effects of anthropogenic and environmental stressors to breeding seabirds. The long-term success of such projects can be enhanced when data are available to elucidate how site-specific and larger-scale factors may contribute to reproductive success. Nest-specific daily survival rate (DSR) of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) during incubation (i.e., pre-hatch; $n = 245$) and brood-rearing (i.e., post-hatch; $n = 185$) were measured at two breeding islands in the northern Gulf of Mexico USA in 2017 and 2018 in relation to macro- and micro- scale habitat and environmental measurements. DSR of nests during incubation ranged from 91-99%, and the DSR during brood-rearing exceeded 99% each year. Regional weather variables occurred in top-performing models more often and with more significance compared to microhabitat variables. Results suggest that reproductive success of Brown Pelicans may respond at least in part to weather factors that occur outside of the scope of habitat structure as it is typically incorporated into the restoration or creation of breeding habitat, indicating that climate conditions are likely an important factor in the success of restoration efforts. *Received 14 April 2020, accepted 25 November 2020.*

Key words.—Brown Pelican, daily survival rate, Gulf of Mexico, *Pelecanus occidentalis carolinensis,* weather.

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The reproductive success of seabirds, whether pelagic or nearshore, is affected by a variety of transboundary factors of both natural and anthropogenic origin. For example, mechanisms that commonly drive reproductive success of seabirds at the local scale include nest predation, quality of nesting habitat, and microclimate (Bried *et al.* 2008; Robinson and Dindo 2011; Brooks *et al.* 2013). At the regional scale, prey availability, diet quantity and quality, and regional weather patterns can influence reproductive success (Jodice *et al.* 2006; Frederiksen *et al.* 2008; Lamb *et al.* 2017). Regional drivers may further interact in complex ways with large-scale climate patterns and changes (Ramos *et al.* 2002; Sherley *et al.* 2011; Sovada *et al.* 2014). Local, regional, and global factors driving nest success may also differ within the breeding season. For example, for Least Terns (*Sternula antillarum*) breeding on natural shell mounds and barrier islands in coastal South Carolina, USA, predation was the primary cause of nest loss but tidal overwash the primary cause of chick loss (Brooks *et al.* 2013). Thus, identifying management actions to increase breeding success requires understanding potential sources of reproductive failure at a variety of spatial and temporal scales. Without such detailed data the success or failure of such efforts can be easily misinterpreted, and reproductive failure may be misassigned to manageable factors when in fact non-manageable factors may be relevant (Brooks *et al.* 2013).

The northern Gulf of Mexico of the USA (hereafter, Gulf) supports a rich assemblage of breeding waterbirds including shorebirds, marsh birds. wading birds, and nearshore seabirds (Wilson *et al.* 2019). Among the nearshore seabirds, Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis;* hereafter Brown Pelicans) have been identified as a high-priority species for monitoring and restoration (Jodice *et al.* 2019). The species breeds throughout the northern Gulf in colonies ranging from less than 100 to ~5,000 pairs (Robinson and Dindo 2011; Walter *et al.* 2014; Lamb 2016). The estimated breeding population in the Gulf is ~25k pair, making it the most populous breeding region for the subspecies in North America (Shields 2014). The species is prone to injury from oil spills including direct mortality and sublethal effects (Haney et al. 2014; Fallon *et al.* 2018). To offset these effects, restoration plans have been developed with the goal of enhancing and creating breeding habitat for Brown Pelicans and other nearshore seabirds (Deepwater Horizon Natural Resource Damage Assessment Trustees 2017; Louisiana Trustee Implementation Group 2019). Such restoration efforts require a breadth of highly detailed data to be fully successful. For many coastal birds; however, detailed measures of reproductive success and the identification of environmental drivers such as weather and climate that might affect reproductive success are lacking (Jodice *et al.* 2019; Wilson *et al.* 2019). These data gaps are likely to inhibit the success of restoration and management projects (Wilson *et al.* 2019). Given their reliance on robust forage fish populations during breeding, as well as their broad distribution across the region, Brown Pelicans can serve as a useful proxy for assessing breeding habitat quality for other co-occurring waterbirds with similar habitat needs (Lamb *et al.* 2017). However, given the wide range of colony conditions (e.g., xeric to mangrove (Rhizophora *spp.*)), sizes (e.g., nest counts from ~100 to ~5,000), and characteristics (e.g., ground, shrub, and tree-nesting) for Brown Pelicans and other waterbirds in the Gulf, plans for restoration and management will require a suite of site-specific studies across a range of conditions from which to develop plans and interpret results of their actions.

To inform restoration of coastal habitat for breeding birds in the Gulf, we examined factors affecting the reproductive success of Brown Pelicans at the largest breeding colony in the region. We focused our attention on a suite of nest-based variables and broader environmental measurements, including variables that have been or are often found to be impactful to reproductive success of coastal nesting birds during either incubation or chick-rearing (Table 1). We modeled the relationship between these variables and the daily survival (DSR) of nests and broods of Brown Pelicans during 2017 and 2018 to determine how both island-specific habitat features and external environmental conditions affect reproductive success. Studies such as ours, that simultaneously evaluate effects of local and regional conditions throughout the breeding season, can provide context needed for decision-makers (Wilson *et al.* 2019).

METHODS

Study Area

All research occurred along the Gulf of Mexico coast of Alabama, USA on Gaillard and Cat islands (Fig. 1). Gaillard Island (30° 30′ N, 88° 02′ W) is in Mobile Bay and was constructed by the Army Corps of Engineers in 1979 and currently supports the largest Brown Pelican colony in the Gulf of Mexico. The island's perimeter is protected by a rock-enforced earthen berm. Along the southern berm where Brown Pelicans nest (roughly 20% of the total island area), the dominant vegetation species are cogon grass (*Imperata clindrica*), Chinese tallow (*Sapium sebiferum*), phragmites cane (*Phragmities australis*), and *Sesbania* sp. (Robinson and Dindo 2008; Streker 2019). Cat Island (30° 19′ N, 88° 12′ W) in Portersville Bay is a shell-midden island and vegetation includes marsh elder (*Iva frutescens*) and baccharis (*Baccharis hamilifolia*; Robinson and Dindo 2008). Gaillard Island supported a breeding population of ~3,000-4,000 nesting pairs of Brown Pelicans during the study period. Cat Island supported a breeding population of ~200 nesting pairs of Brown Pelicans in 2017 but no nesting pairs in 2018.

Nest and Brood Monitoring

We established productivity plots within Brown Pelican colonies on Cat Island (2017: n = 2 plots) and Gaillard Island (2017: n = 4 plots; 2018: n = 7 plots). Each plot contained 10-30 nests, depending on nest configuration and proximity of nests to each other. All plots were spaced based on natural contours and aspects of the islands, resulting in a distance between plots ranging from 60-260 m. Plots were visited every 2-11 days depending upon weather conditions and logistics.

Table 1. Environmental and nest-based variables collected at nests of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) on Gaillard and Cat islands, Alabama, 2017 and 2018. Terms in italics are used as abbreviated descriptions in the text.

Variable	Range (continuous variables) or categories (discrete variables)	Relationship to reproductive success (previous studies)	Predicted relationship to reproductive success in our study
Local			
Height of nest base above ground	0-156 cm	- Reproductive success increases with nest height (Ranglack *et al.* 1991; Walter *et al.* 2013). - Reproductive success highest in ground nests (Robinson and Dindo 2011).	Positive relationship
Island (2017 only)	Gaillard or Cat	- Reproductive success rates differ among colonies for Brown Pelicans in Louisiana due to differences in island size, colony size and substrate (Walter *et al.* 2013).	Differs among sites
Location on island (2018 only)	Interior or Exterior	- Lower success at exterior nests due to exposure to storms and flooding (Sherley *et al.* 2011; Bonter *et al.* 2014).	Higher at interior than exterior nests
Substrate material under and supporting the nest	Shrub or Rock/Ground	- Chicks in shrub nests had higher apparent fledging success than chicks on ground nests (Lamb 2016).	Higher with shrub substrate than rock/ground substrate.
Elevation of nest location above sea level	Incubation: low (0-0.59 m), medium (0.60-0.75 m), high (0.76-1.0 m), or berm (> 1.0 m). Chick-rearing: low (0-0.75 m) or high (> 0.75 m)	- Wave activity and flooding decrease reproductive success of low-lying nests (Sherley *et al.* 2011; Walter *et al.* 2013; Bonter *et al.* 2014).	Positive relationship
Distance from the nest to the closest water's edge	1.5-127.7 m	- Proximity to water decreased reproductive success and recruitment by increasing exposure to wave activity, precipitation, and flooding from storm events (Sherley *et al.* 2011; Walter *et al.* 2013; Bonter *et al.* 2014).	Positive relationship
% *Vegetation cover* directly above nest	0-100%	- Hatching success was highest at moderate vegetation densities, allowing nest access while still providing cover (Robinson and Dindo 2011).	Parabolic relationship

Table 1. (Continued) Environmental and nest-based variables collected at nests of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) on Gaillard and Cat islands, Alabama, 2017 and 2018. Terms in italics are used as abbreviated descriptions in the text.

Variable	Range (continuous variables) or categories (discrete variables)	Relationship to reproductive success (previous studies)	Predicted relationship to reproductive success in our study
Nest temperature	24.09-32.29 °C	- Reproductive success increases with temperature in cold climates (Murphey *et al.* 1991; Dickey *et al.* 2008). - Heat exposure also reduces reproductive success, particularly for eggs (Sherley *et al.* 2011; Oswald and Arnold 2012).	Parabolic relationship; strongest during incubation
Regional			
Ambient *humidity*	70.31-90.22%	- High or low humidity decrease hatch success by affecting water loss rates in eggs (Walsberg and Schmidt 1992). - High humidity and precipitation decrease chick survival via exposure (Guttery *et al.* 2013).	Parabolic relationship
Ambient *barometric pressure*	100.772-102.225 kPa	- Barometric pressure decreases with severe weather or storms (Breuner *et al.* 2013). - Storms and severe weather negatively affect reproductive success at all stages (Sherley *et al.* 2011; Walter *et al.* 2013; Bonter *et al.* 2014).	Positive relationship

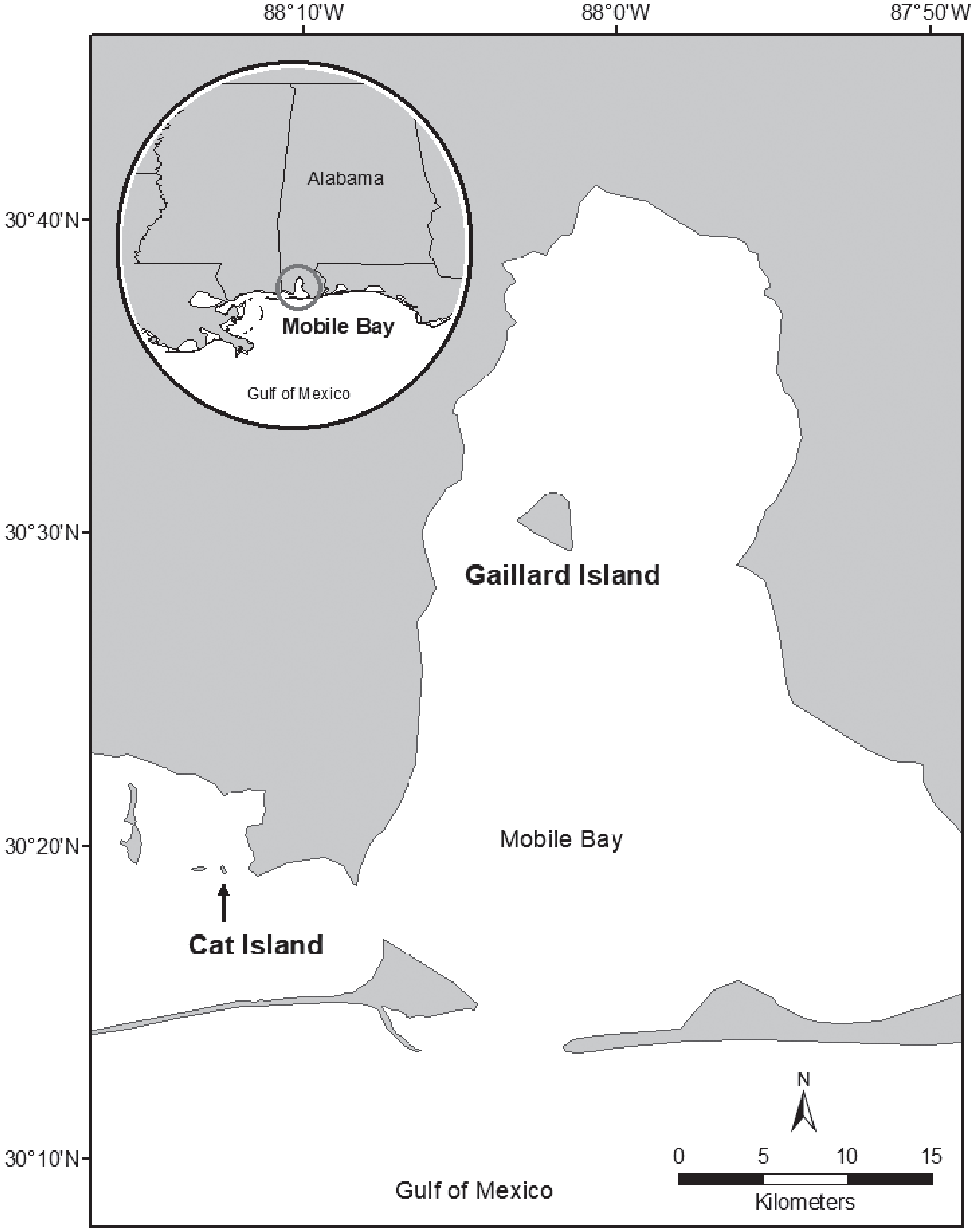

Figure 1. Location of Gaillard Island and Cat Island, Alabama, USA. Daily survival rates of nests and broods of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) were measured on each island in relation to habitat and environmental variables.

We enumerated and recorded nest contents during each visit. When chicks became mobile (~21 days post hatch) they were banded with both a Bird Banding Lab metal band and a plastic, field-readable, 3-letter leg band (2017: $n = 145$; 2018: $n = 156$). During subsequent visits, we searched for banded chicks on colony and via observations from a small power boat within 70 m of shore until all banded chicks were located and identified. Both binoculars (10 × 42 mm) and spotting scopes (20-60 x) were used to continuously scan for chicks during these observations. We maintained a distance of ≥ 15 m between observer and chicks to limit disturbance. The interval between resighting each chick was < 5 days in all cases. We continued re-sighting efforts until ≥ 80% of the banded chicks were > 65 days post hatch, which we defined as 'fledged' (Schreiber 1979). All monitored clutches were assigned a final fate of either successful (≥ 1 egg hatched) or failed (0 eggs hatched) and all broods were assigned a final fate of either successful (≥ 1 chick fledged) or failed (0 chicks fledged). We determined fate for all clutches and all broods (i.e., no nests or broods had an unknown fate). We refer to these fates as clutch success and brood success, respectively.

We measured habitat and environmental variables (Table 1) during the same period in which we monitored DSR. Nest-based variables that remained fixed throughout the breeding season were recorded at the establishment of plots and included substrate beneath nest, elevation at the base of the nest above sea level and distance from nest to water's edge. Nest-based variables that could change during the breeding season were measured at the establishment of plots and every 2-4 weeks thereafter and included nest height above ground and vegetation cover directly above the nest. We used the average value of the dynamic variables in subsequent analyses. We measured nest height above ground level by placing a level across the nest, then measuring the distance from the ground to the edge of the level (i.e., the rim of the nest). We measured vegetation cover using a photograph taken from the center of the nest, with the lens facing the sky; subsequently, we overlaid a grid of 100 squares on each photo in Adobe Photoshop CC 2019 and enumerated the grids that contained vegetation to establish percent cover.

We measured nest-specific temperature using an Onset HOBO Tidbit v2 temperature datalogger (Fotronic Corporation, Woburn, Massachusetts, USA). Not all nests received loggers and we therefore stratified placement of loggers ($n = 28$ nests in 2017, $n = 31$ nests in 2018) by nest height to produce equal sample sizes within each 10 cm interval from 0-140 cm. Dataloggers recorded the temperature hourly throughout each 24-hour period for the entirety of the breeding stage or until failure, and we subsequently calculated the average and maximum temperatures for each interval between nest visits. We measured regional weather by downloading hourly measures of barometric pressure and humidity from the Mobile Downtown Airport weather station (National Weather Service 2019) which is located approximately 12 km from Gaillard Island and 36 km from Cat Island. We calculated average values for each of these parameters for each interval between nest visits.

Statistical Analysis

To calculate DSR of nests and broods during the incubation and brood-rearing stages, we used the nest survival module in Program Mark (White and Burnham 1999) via the RMark package (Laake and Rexstad 2014) in program R (R Core Team 2016). The nest survival module models the survival probability (i.e., DSR) over the course of each breeding stage as a function of user-specified covariates using generalized linear models with a logit-link function and binomial errors. Prior to analyses we compared the DSR of clutches and broods between Gaillard and Cat islands and, finding no difference ($P > 0.10$ for each), pooled data from both islands in subsequent analyses.

We modeled the relationships of the independent variables with DSR separately for incubation and brood rearing. We also included as independent variables Julian date, nest age (clutch success models), and age of first chick hatched (brood success models). The latter two variables are created by RMark using the variables 'AgeFound' (age of nest in days the day the nest was found) and 'AgeDay1' (age of nest at beginning of study). We calculated all age parameters in RMark based on the date and age of the nest at first check. We tested both linear and quadratic terms for the age and time covariates and used the best-performing term for each variable (quadratic for age covariates in all breeding stages except for 2017 brood-rearing; linear for all time covariates in all models) in subsequent models (Streker 2019). We developed a suite of 14 models to assess the relationship between the independent variables and DSR including global and null models. Variables that were highly correlated ($|r| \geq 0.5$) were not included in the same model. For each year of incubation data we reran the top performing models on the subset of nests within which temperature was recorded to assess whether the addition of nest-specific temperature variables substantially improved model fit. Temperature variables were not tested during brood-rearing due to the small sample size of broods that failed that also had temperature loggers (2017: $n = 1$ nest with temperature logger + brood failure; 2018: $n = 7$ nests with temperature logger + brood failures).

We used Akaike's information criterion (AIC) to rank the models and evaluated the strength of the models using normalized weights (Burnham and Anderson 2002). There were significant differences in fate between years and breeding stages ($P < 0.003$ for each); therefore, we ran models separately by year (2017, 2018) and breeding stage (incubation, brood-rearing). We report models that were within $\Delta\text{AIC} \leq 2$ of the lowest-scoring model. To avoid potential biases associated with model-averaging, we report coefficient estimates ± SE from top-performing models only (Fieberg and Johnson 2015). Daily survival rates were calculated from top performing models for each year and breeding stage. We also conducted a post-hoc analysis to determine if the fit of DSR models for nests or broods were improved by including a quadratic term for distance to water. The quadratic term never out-performed the linear term in any breeding stage or year based on AICc values and weights (AICc weight for quadratic terms ≤ 0.39 in all cases) and we therefore report model results from the linear models only. We reported incubation and brooding success as the total number of observed clutches and broods, respectively, divided by the number of successful clutches and brood at the end of their respective breeding stage.

Results

During 2017 - 2018, we monitored 245 clutches during incubation (2017: *n* = 97; 2018: *n* = 148) and 185 broods containing 279 chicks during brood-rearing (2017: *n* = 85 broods, *n* = 128 chicks; 2018: *n* = 100 broods, *n* = 151 chicks). The DSR (± SE) of clutches during incubation in 2017 and 2018 was 0.9940 ± 0.002 and 0.9138 ± 0.002, respectively, and overall clutch success was 0.86 and 0.67, respectively. The DSR (± SE) of broods in 2017 and 2018 was 0.9998 ± 0.0003 and 0.9952 ± 0.006, respectively, and overall brood success was 0.94 and 0.78, respectively. We counted 142 fledged chicks from our sample of banded birds in 2017, and 155 fledged chicks from our banded sample in 2018.

In 2017, three models best predicted DSR during incubation (Table 2). The top-ranked model was approximately 1.6 times as likely to be the best model compared to the second-ranked model, and approximately 2.6 times as likely to be the best model compared to the third-ranked models. Average barometric pressure appeared in all top models, average humidity appeared in two of the top models, and distance from nest to water appeared in one top model. There was a negative relationship between barometric pressure (-0.98 ± 0.28) and DSR (Fig. 2a) and between humidity (-0.73 ± 0.38) and DSR (Fig. 2b) during incubation in 2017.

In 2018, the global model best predicted DSR during incubation (Table 2). The global model carried 99% of the model weight and included significant terms for date (-0.08 ± 0.01), distance from nest to water (-0.73 ± 0.35), nest elevation (-1.05 ± 0.47), average barometric pressure (-1.11 ± 0.27), average humidity (-1.23 ± 0.24), and maximum temperature at the nest (-3.92 ± 1.44). The three weather variables had stronger negative effects on DSR of nests during 2018 compared to time or microhabitat variables (Fig. 3).

In 2017, two models best predicted DSR during brood-rearing (Table 2). The top ranked model was 1.75 times more likely to be the best model than the second ranked model. Average barometric pressure and average humidity appeared in both top models, and distance from nest to water appeared in one top model. There was a negative relationship between barometric pressure (-0.69 ± 0.21) and DSR (Fig. 4a), and a positive relationship between humidity (2.47 ± 0.51) and DSR during brood-rearing (Fig. 4b) in 2017.

In 2018 a single model with 9 of the 10 variables available (average barometric pressure not included) best predicted DSR during brood-rearing and carried 99% cumulative weight (Table 2). There was a positive

Table 2. Top-performing models of daily survival rate of nests and chicks of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) breeding on Gaillard Island and Cat Island, Alabama, USA, 2017 and 2018. Only models within ΔAIC ≤ 2.0 included.

Model terms	ΔAIC	AIC weight
2017 Incubation		
Average humidity + average barometric pressure	0.00	0.36
Average barometric pressure	0.93	0.22
Average humidity + average barometric pressure + distance to water	1.90	0.14
2018 Incubation		
Nest height + vegetation cover + average humidity + average barometric pressure + Julian date (linear) + distance to water + elevation + substrate + location	0.00	0.99
2017 Brood-rearing		
Average humidity + average barometric pressure	0.00	0.63
Average humidity + average barometric pressure + distance to water	1.14	0.36
2018 Brood-rearing		
Chick age^2 + nest height + vegetation cover + average humidity average + Julian date (linear) + distance to water + elevation + substrate + location	0.00	0.99

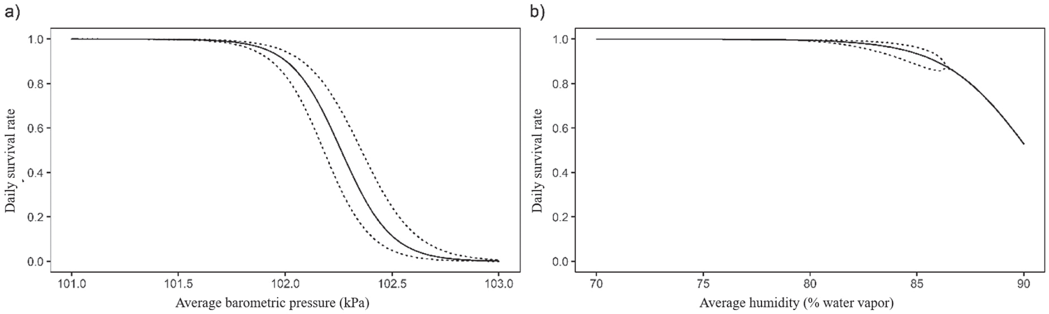

Figure 2. Relationships of daily survival rate of clutches with: (a) barometric pressure (range 101.30-102.20 kPa); and (b) humidity (range 79.5%-86.5%) during incubation in 2017 for Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) breeding on Gaillard Island and Cat Island, Alabama, USA. Dashed lines represent 95% confidence intervals.

relationship between DSR and both humidity (1.53 ± 0.29) and chick age^2 (0.09 ± 0.02), and a negative relationship between DSR and Julian date (-0.22 ± 0.11) during brood-rearing in 2018 (Fig. 5). The odds of a brood surviving an additional day increased by 4.6 times for each 1% increase in average humidity and decreased by 0.8 times for each 1 day increase in date of hatching.

Across the incubation period, clutch success rates in our study ranged from 0.67 to 0.86. During brood-rearing, brood success ranged from 0.78 to 0.94, with 1.02 to 1.29 chicks fledged per nest. These results are comparable to previous estimates from Gaillard Island and other colonies in the region (Table 3).

Discussion

Several variables consistently appeared in top performing models for DSR of Brown Pelican clutches and broods in both years of the study. Regional weather variables occurred more often and with greater significance in the top performing models compared to microhabitat variables. Previous studies on Brown Pelican nest selection at breeding sites in the Gulf, including Gaillard Island, found that reproductive success of Brown Pelicans was related to habitat variables including vegetation cover, nest height, and substrate beneath the nest (Ranglack *et al.* 1991; Robinson and Dindo 2011; Walter *et al.* 2013; Lamb *et al.* 2016). Our results differed from these previous studies in that we did not find significant relationships between most nest-based variables and survival of nests or broods. These differences could result from differences in the response variables being measured: previous studies focused on nest site selection, chick condition, or individual fledging success rather than DSR. The differences could also be due to the addition of weather variables in our modeling, which were not included in the previous studies. Our results suggest that the effects of habitat on reproductive success may be overwhelmed by the importance of weather variables at least in some years, as has been observed for Roseate Terns (*Sterna dougallii*) nesting on tropical islands and American White Pelicans (*P. erythrorhynchos*) nesting in North America (Ramos *et al.* 2002; Sovada *et al.* 2014).

Average barometric pressure consistently appeared in top models for both clutch and brood survival and negatively influenced daily survival rates of clutches and broods, despite different requirements during these breeding stages. We originally posited that barometric pressure would have a positive relationship with DSR, assuming lower values of barometric pressure would be indicative of severe weather or storms resulting in decreased survival (Breuner *et al.* 2013). The negative relationship we observed may have occurred because the lower values of barometric pressure measured during our study were primarily an indicator of cloudy days with occasional rain as opposed to more in-

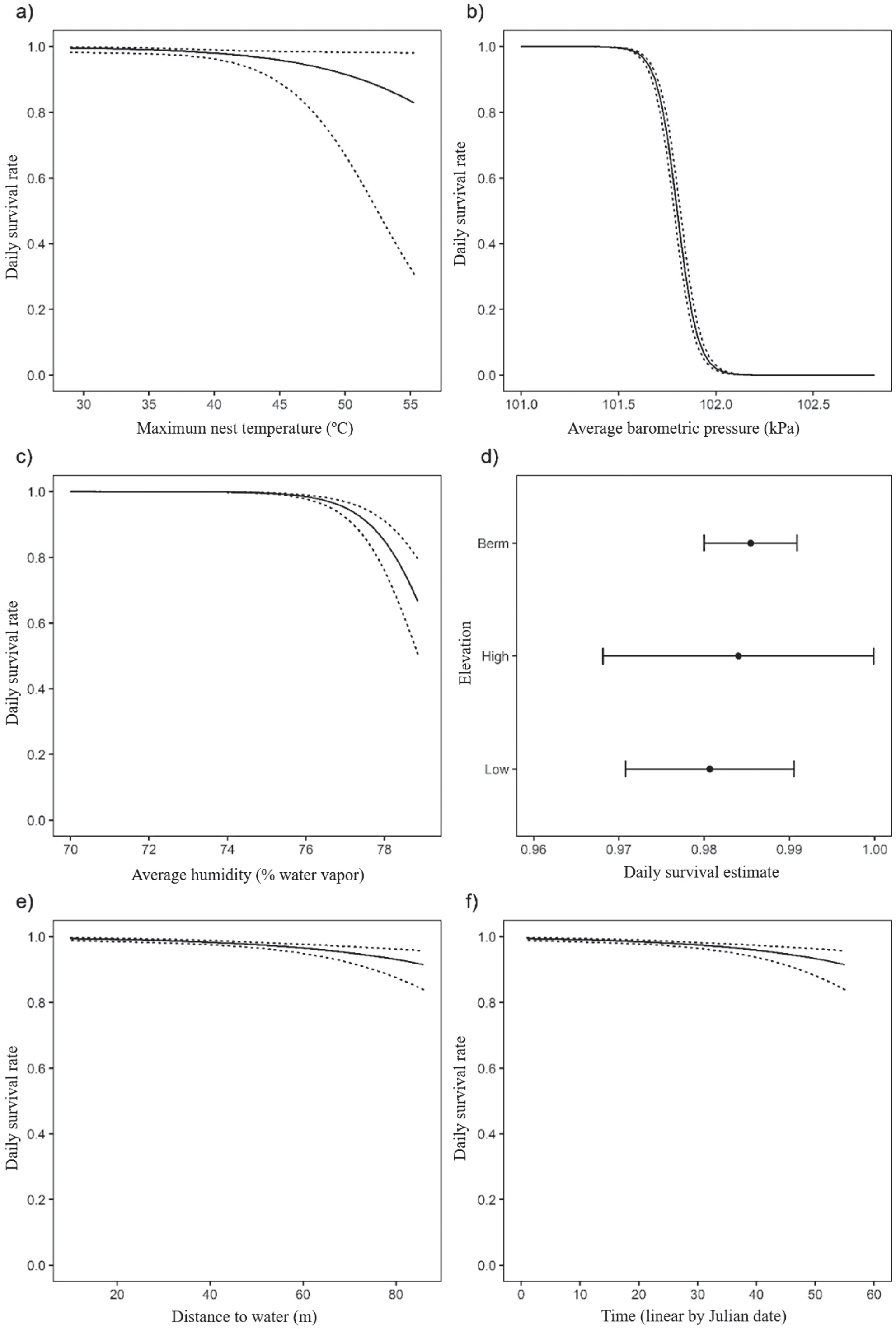

Figure 3. Relationships of daily survival rate of clutches with: (a) maximum nest temperature (29.64-57.66 °C); (b) average barometric pressure (range 101.53-101.66 kPa); (c) average humidity (range 75.09%-79.96%); (d) elevation category (low, high, berm); (e) distance to water (range 8.84-127.74 m); and (f) date (10 April-5 June 2018) during incubation in 2018 for Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) breeding on Gaillard Island and Cat Island, Alabama, USA. Dashed lines represent 95% confidence intervals.

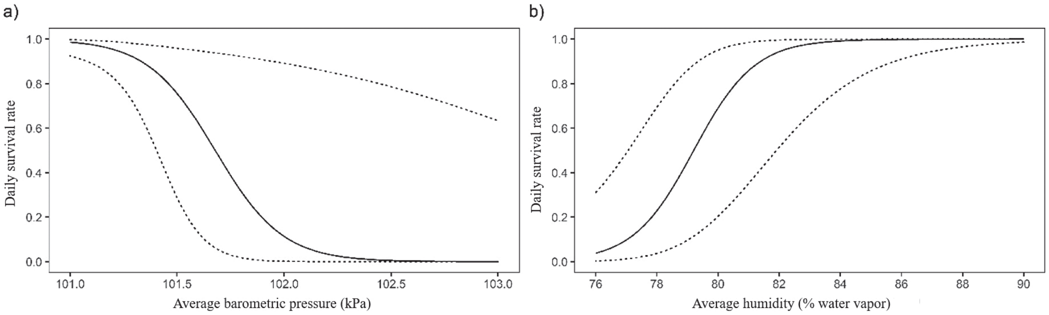

Figure 4. Relationships of daily survival rate of broods with: (a) average barometric pressure (range 101.17-102.13 kPa); and (b) average humidity (range 76.37%-90.22%) during brood-rearing of 2017 for Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) breeding on Gaillard Island and Cat Island, Alabama, USA. Dashed lines represent 95% confidence intervals.

tense weather patterns such as storms. The barometric pressure range for storms is commonly considered to be 98.21-98.88 kPa (Breuner *et al.* 2013). The minimum average barometric pressure we recorded from local weather data was 100.77 kPa, much higher than the storm range. It appears, therefore, that the relationship that we observed between DSR and barometric pressure could be a result of cloudy, but not stormy, days having a positive effect on DSR until a threshold in barometric pressure is reached beyond which conditions (e.g., sun and heat associated with higher kPa) may negatively affect survival. For example, the shading effect of clouds could reduce temperature and sun exposure of eggs and chicks during the summer breeding season and therefore in-

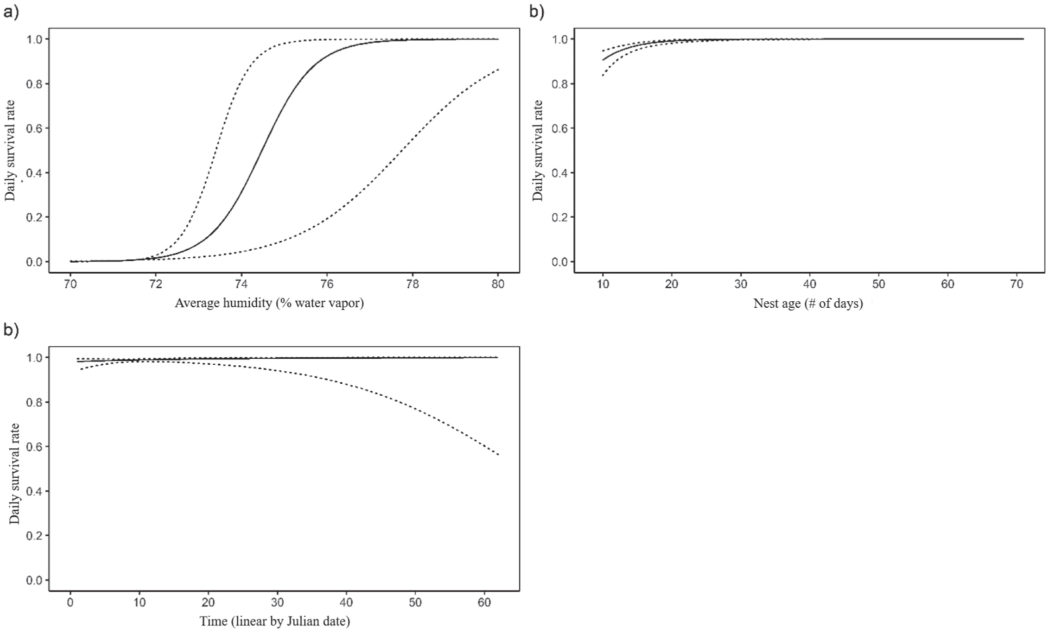

Figure 5. Relationships of daily survival rate of broods with: (a) average humidity (range 71.31%-85.65%); (b) nest age (1-41 days post-hatch); and (c) date (12 June-23 July 2018) during brood-rearing of 2018 for Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) breeding on Gaillard Island and Cat Island, Alabama, USA. Dashed lines represent 95% confidence intervals.

Table 3. Summary of metrics of reproductive success from published studies or reports of Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) in the Gulf of Mexico and the South Atlantic Bight, USA.

Stage/Location	Years	Description of parameter	Range or mean ± SE	Source
Incubation				
Gaillard Island, Alabama	2007 - 2008	Chicks hatched per egg laid	0.00-0.70	Robinson and Dindo, 2011
Marsh Island, South Carolina	1969 - 1975	Apparent nest success	0.68	Blus and Keahy 1978
Boca Ciega Bay, Florida	1969- 1976	Apparent nest success	0.53 - 0.89	Schreiber 1979
Gaillard Island, Alabama	2017 - 2018	Nest success	0.67-0.86	This study
Chick-rearing				
Boca Ciega Bay, Florida	1969 - 1976	Chick survival	0.16-0.77	Schreiber 1979
Various islands, Louisiana	1971 - 1984	Average number of chicks fledged per nest	0.00-1.80	Mcnease *et al.* 1984
Texas, Louisiana, Florida panhandle	2013 - 2015	Average number of chicks fledged per nest	0.30 - 1.64	Lamb 2016
Gaillard Island, Alabama	2015	Average number of chicks fledged per nest	1.06 ± 0.85	Lamb 2016
Racoon and Wine Islands, Louisiana	2008 - 2010	Average number of chicks fledged per nest	0.00-1.60	Walter *et al.* 2013
Gaillard Island, Alabama	2017 - 2018	Brood success	0.78-0.94	This study
Gaillard Island, Alabama	2017 - 2018	Average number of chicks fledged per nest	1.02-1.29	This study

crease their daily survival (Amat and Masero 2004; Robinson and Dindo 2011; Muzaffar *et al.* 2012).

Average humidity also consistently appeared in top performing models for DSR of clutches and broods; however, the relationship differed between clutch (nonlinear and negative) and brood (nonlinear and positive) stages. We found that humidity recorded from a local weather station often performed better in our models than nest-specific temperature variables. Humidity and temperature can be combined in a temperature-humidity index (El-Tarabany 2015; Young *et al.* 2018) which may reflect the heat stress experienced by an organism. During incubation, a negative relationship of nest survival with temperature and/or humidity could be caused by decreased survival of eggs due to heat stress (Sherley *et al.* 2011; Oswald and Arnold 2012), and our results suggest this occurred primarily above a specific threshold for Brown Pelicans during this study. In contrast, the significant positive relationship we observed between brood success and humidity in both years could occur if chicks can demonstrate an increased resilience to heat as they become capable of thermoregulation or if higher air temperatures are associated with higher humidity and these conditions promote chicks remaining drier and warmer during the frequent rainstorms in the region (Konarzewski and Taylor 1989; Hart et al. 2017).

Variables related to timing of breeding and to microhabitat structure of nests rarely had a significant effect on DSR during incubation or brood-rearing. Our observation of a decrease in DSR over time during brood-rearing and Julian date is consistent with previous studies (Antolos *et al.* 2006; Svagelj and Quintana 2011). However, we observed this relationship only in 2018, possibly due to the overall high reproductive success across all nests in 2017. Distance to water had a weak negative effect on DSR during incubation in 2018. Many studies of seabirds nesting on islands have found that proximity to water decreased reproductive success and recruitment, as wave activity, precipitation, and flooding from storm events increased the mortalities in nests closer to water sources (Sherley *et al.* 2011; Walter *et al.* 2013; Bonter *et al.* 2014). However, most Brown Pelican nests on Gaillard Island occur between the armored island perimeter and the berm, and thus appear to be relatively protected from over-wash events. For example, following Tropical Storm Cindy and Hurricanes Harvey, Irma, and Nate in 2018, we observed that vegetation and nesting material/substrate were reduced on the low-lying Cat Island and Brown Pelicans did not nest there; however, vegetation and nesting material/substrate did not appear to be similarly impacted on Gaillard Island and Brown Pelicans continued to nest there (Streker 2019).Our data suggest that the enhanced elevation, armored shoreline, and abundant shrub and nesting material on Gaillard Island may serve to reduce the effect of nest microhabitat on breeding success.

Although our study site is a regionally important colony and supports the largest number of breeding Brown Pelicans in the Gulf, extrapolation of results from any single colony is complicated by the broad nesting range of Brown Pelicans in the northern Gulf. Measures of apparent success during our study were within the range reported by Schreiber (1979) and Blus and Keahy (1978). Similarly, fledging rates from our study were also within the ranges of previous studies (Mendenhall and Prouty 1979; Mcnease *et al.* 1984; Walter *et al.* 2013; Lamb *et al.* 2016, Lamb *et al.* 2020). Thus, our data appear to represent relatively typical levels of breeding success for the region, suggesting that our results may be relevant to colonies outside the explicit study area. No single study, however, is likely to encompass the full range of factors affecting reproductive success, as factors are likely to vary among sites as well as within sites among years. Moreover, Brown Pelicans occupy a range of habitats including but not limited to xeric barrier islands in the southwest, complex estuaries in the central coast, and mangrove systems in the southeast, which likely respond differently to environmental drivers. For those reasons, and because the species continues to be a focus in the region, long-term monitoring of the species across a variety of habitats could help to improve understanding of how reproductive success responds to acute and chronic stressors (Jodice *et al.* 2019).

Our results suggest that DSR of clutches and broods of Brown Pelicans during our study responded more strongly to regional weather than to microhabitat features. Habitat variables that may act in synergy with storms, such as distance to water and nest elevation, improved model fit in some cases but were minimally significant, suggesting that modifying or creating islands to be more resilient to storms may enhance reproductive success of Brown Pelicans. Our data therefore indicate that the reproductive success of Brown Pelicans may be driven in whole or in part by environmental factors that operate at non-local scales and that are not within the control of management or restoration efforts. This is not to say that manageable factors (e.g., nesting habitat, elevation) should be ignored, but rather that stakeholders may want to consider the success of a management action through a broad lens that also includes the potential for unmeasured or unmanageable factors to play a role.

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