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Abstract.—The Reddish Egret (*Egretta rufescens*) is considered a species of conservation concern throughout its range, primarily due to high rates of coastal land loss at key nesting locations. Nest and brood survival, causes and timing of nest failures, as well as nest site characteristics and site selection were studied for three breeding seasons (2016-2018) on a natural marsh island in southwestern Louisiana, USA. Of 110 nesting attempts, 58.2% hatched at least one egg. During incubation, overall daily survival rate was 0.979 (± 0.003 SE), corresponding to 56.4% success from egg laying to hatching. For broods, daily survival rate was 0.993 (± 0.002 SE), or 72.9% success from hatching to fledging. Overwash was identified as the primary cause of known nest and brood loss, accounting for 48.9% and 27.8% of all nest and brood failures, respectively. Overall productivity for breeding pairs within the study area was 1.06 chicks/pair for all years. Data suggests that overwash from extreme high tides and wind can significantly contribute to lower reproductive success of breeding pairs but the lack of mammalian predators on the island may contribute to increased nest success, especially in years that do not experience high water levels. *Received 7 February 2020, accepted 30 August 2020.*

Key words.—Egretta rufescens, *daily survival rate, Louisiana, nesting, overwash, Reddish Egret, reproductive success, wading bird*

The Reddish Egret (*Egretta rufescens*) is listed as a Bird of Conservation Concern in the USA (Kushlan *et al.* 2002), has been identified as being of continental and regional concern (Wilson *et al.* 2014), and is in need of immediate management (Hunter *et al.* 2006). The nesting range for the species is inclusive of the USA (Texas, Louisiana, Alabama, Florida and South Carolina states), Mexico (Baja California, Baja California Sur, Sonora, Sinaloa, Oaxaca, Chiapas, Yucatan, Quintana Roo, and Tamaulipas states), Belize, Cuba, the Bahamas (Great Inagua, Grand Bahama, Bimini Islands, and New Providence Islands), Turks and Caicos, the Dominican Republic, Colombia, and Venezuela (Wilson *et al.* 2014; Koczur *et al.* 2020).

Despite its relatively large breeding range, the global population is estimated to be less than 5,000-7,000 individuals (Wilson *et al.* 2014). The International Union for Conservation of Nature and Natural Resources (IUCN) (BirdLife International 2016) classifies the Reddish Egret as Near Threatened, primarily because it occupies a restricted habitat, it is patchily distributed throughout its wide range, and is believed to have a moderately small and declining global population. It is considered the rarest and least known of the egrets and herons of North America (Wilson *et al.* 2014), although recent studies have reported important aspects of their biology, behavior, habitat use, genetic diversity, and population structure (Bates

et al. 2009; Bates and Ballard 2014; Geary *et al.* 2015; Bates *et al.* 2016; Koczur *et al.* 2018).

Three management units (Eastern, Central, and Western) have been established across the Reddish Egret range to further assist in conservation planning for this species (Wilson *et al.* 2014). The Central Management Unit (CMU) includes the Gulf coasts of Mexico and the USA east to Florida, as well as the Yucatan Peninsula and south into Central America, while the Eastern Management Unit (EMU) includes peninsular Florida, USA, the Caribbean, and the northern coast of South America. The CMU has the largest population of Reddish Egrets with estimates of 2,750 breeding pairs (Wilson *et al.* 2014). With limited records of breeding pairs in Alabama and Mississippi, it is critically important to identify and protect habitats utilized by Reddish Egrets throughout Louisiana, because nesting areas throughout this region of the Gulf of Mexico may serve as a link between the EMU and CMU based on the physical movement of birds (Geary et al. 2015) and estimates of gene flow (Shahrokhi et al. 2020).

Coastal land loss in Louisiana has negatively impacted many coastal nesting islands for birds (Selman *et al.* 2016), and this is a result of a combination of factors including anthropogenic activities (canal dredging, channelization of streams, levee construction, and hydrocarbon extraction), subsidence, storm-induced wave erosion, sea level rise, and sub-surface geological control (Penland *et al.* 1990). Historically, shifting courses of the Mississippi River led to deposition and erosion cycles along the Deltaic Plain (southeast) and the Chenier Plain (southwest) of coastal Louisiana. However, with the containment of the Mississippi River through levees and other flood mitigation measures, sediment deposition has been significantly altered over the past 200 years (Latuso *et al.* 2017). Land loss mapping indicates that the location and magnitude of land loss is highly variable along the Louisiana coastline (Britsch and Dunbar 1993). With increased loss of important coastal nesting islands, there is an urgent need for conservation actions to restore and enhance nesting areas for sensitive species like the Reddish Egret.

Within the Gulf Coast region, the Reddish Egret is considered a priority species by the Gulf Coast Joint Venture (Vermillion and Wilson 2009) and identified as a Species of Greatest Conservation Need (SGCN) in Louisiana, ranked as critically imperiled (S1; Holcomb *et al.* 2015). Within Louisiana, the number of breeding Reddish Egrets has declined over the past decade, primarily due to limited suitable habitat and the Deepwater Horizon oil spill (Remsen *et al.* 2019). Currently, there are ~130 breeding birds in Louisiana, ~4% of the estimated USA breeding population of Reddish Egrets (Remsen *et al.* 2019). Statewide surveys conducted in 1990-2005 indicated that nesting pairs of Reddish Egrets were confined in their breeding range to the southeastern Deltaic Plain region of the state (M. Seymour, unpubl. data). It was not until 2013 that Reddish Egrets were confirmed nesting on a single marsh island, Rabbit Island, in the southwestern Chenier Plain of Louisiana (Selman and Davis 2015). Selman and Davis (2015) indicated that this nesting colony was an important geographical connection between colonies in Texas and other nesting colonies located in southeastern Louisiana.

The goal for this study was to conduct a detailed investigation into the reproductive success and nesting ecology of Reddish Egrets in southwestern Louisiana. Our objectives were to: (1) measure daily survival rates during incubation and chick rearing; (2) assess nest site selection and nest site characteristics that may influence nest success; and (3) determine causes and timing of nest failure.

METHODS

Study Area

Rabbit Island (29° 50′ 54″ N, 93° 22′ 58″ W) is an 85-ha salt marsh island located in the middle of West Cove of Calcasieu Lake in Cameron Parish, Louisiana, USA. Island elevation ranges from 0.3-0.5 m above mean sea level (maximum elevation: 0.57; Selman and Davis 2015) but slightly higher elevation exists along the outer rim (within 35 m of the edge of the island)

than within the interior portion of the island (K. Ritenour, unpubl. data). Along with elevation differences, there are a diverse number of habitats throughout the island, including completely vegetated marsh areas, vegetated marsh areas interspersed with shallow, open tidal ponds, and the island rim that consists primarily of saltgrass (*Distichlis spicata*) flats and/or shell substrate. Consequently, different wetland vegetation communities occupy different flooding regimes along an elevational gradient. The lower elevations of the island interior are dominated by smooth cordgrass (*Spartina alterniflora*). Slightly higher elevations of the interior and exterior of the island are dominated by saltgrass, saltmeadow cordgrass (*S. patens*), and black needlerush (*Juncus roemarianus*). Big cordgrass (*S. cynosuroides)* and Jesuit's bark (*Iva frutescens)* occur at the highest elevation marshes along the rim of the island. A small inlet is located on the eastern side of the island, which permits tidal exchange to multiple ponds of varying sizes on the interior of the island. Recently, the rim of the island has been breached on the northwestern and southern end of the island because of continued wave action, and this made two smaller tidal inlets.

Surrounding Rabbit Island is the shallow bottom estuary of West Cove of Calcasieu Lake. It averages ≤1.82 m (Selman and Davis 2015) and is surrounded by brackish and salt marshes owned by both public (Sabine National Wildlife Refuge) and private land owners. Prior to the initial creation of Calcasieu Pass in 1874 by the U.S. Army Corps of Engineers (Quinn 1897), a ≤1.5 m deep shoal at the mouth of Calcasieu Pass likely limited excessive saltwater intrusion (Louisiana Coastal Wetlands Conservation and Restoration Task Force 2002). Following the widening and deepening of the Calcasieu Ship Channel in 1937 (Louisiana Coastal Wetlands Conservation and Restoration Task Force 2002), greater tidal exchange and increased salinities occurred throughout the region. Thus, the Calcasieu Lake estuary and marshes surrounding Rabbit Island have converted from a low salinity environment to a moderate to seasonally high salinity environment.

Along with being a regionally important nesting colony for Reddish Egrets, Rabbit Island is also a regionally important island for at least 13 other nesting coastal waterbird species (W. Selman, unpubl. data), including six species identified as SGCN in Louisiana (Holcomb *et al.* 2015). Further, thousands of other wading birds (primarily Tricolored Herons (*E. tricolor*) and Snowy Egrets (*E. thula*)) nest on the island, as well as thousands of Laughing Gulls (*Leucophaeus atricilla*), who are known predators of colonial-nesting waterbird species (Donehower *et al.* 2007).

Nest and Chick Monitoring

During the months of February and March each year, we surveyed Rabbit Island for signs of nesting Reddish Egrets. We monitored breeding pairs from late March until late August in 2016 and from late March until late July in 2017 and 2018; the difference in monitoring time was due to renesting attempts in 2016 that extended the nesting season. Reddish Egrets

were visible at nest locations during perimeter surveys conducted by motorboat because of the relatively small size of the island, low marsh vegetation height, and distinguishable external characteristics of the species. Despite exhaustive search efforts, it seems likely that nests or breeding pairs were occasionally missed during surveys due to the challenges of detecting all Reddish Egrets nesting in a colony (Cox *et al.* 2017). Hence, our estimates of nesting pairs and total number of nests annually should be viewed somewhat conservatively.

We trapped territorial adults at nest sites when possible using noose carpets (McGowan and Simons 2005) and a modified version of a self-tripping cage trap (Frederick 1986). Captured adults were banded with a U.S. Bird Banding Lab aluminum band on one leg and a colored alphanumeric band on the other leg; the latter allowed us to identify each individual by the unique code. Along with identification, banding efforts also allowed us to assess nest site fidelity, pair bonds, and identify renesting attempts by banded pairs monitored within the study area. For a related project, we outfitted several adults ($n = 14$) with 17 g solar-powered GPS transmitter (Platform Terminal Transmitter [PTT-100], Microwave Telemetry, Inc.) attached via a backpack harness to study their survival, movements, and habitat use. The transmitter data also allowed observers to remotely determine these individuals' nesting locations, as well as pair bonds and renesting attempts.

When a nest was discovered, we recorded its location using a handheld GPS (accurate to ± 3 m). We also recorded the number of eggs or chicks present, the nesting substrate (i.e., the dominant vegetation within 1-m of the nest), the vegetation composition of the nest (i.e., the vegetation used to construct the nest), and the band combinations of any adults observed at the nest. Nest measurements included nest height (i.e., the height from the soil surface to the top of the nest), nest diameter, and nest bowl depth (i.e., the difference between the top of the nest and the bottom of the interior of the nest). We only collected these measurements when we were certain that nest building was complete and adults were incubating eggs. We monitored nests at weekly intervals until the eggs hatched or until the nest failed. A nest was considered successful if at least one egg hatched. Causes of nest failure were classified into five categories: abandoned (eggs cold and/or moisture was seen on the eggshells), avian depredation (exhibited signs of predation such as broken eggshells, disturbed nest, or yolk stains in nest), nest collapse (construction of the nest deteriorated since previous check and eggs missing or found below the nest), unknown (nest was found empty prior to the estimated hatching date with no evident signs of failure), or overwash. We identified the latter as the cause for nest failure when eggs were no longer in the nest or when we found cold/wet eggs in or around the nest along with observation of wrack debris accumulated near the nest or high water levels at the nest. We continued to monitor all nesting areas within the study site throughout the study period for signs of renesting by pairs whose nest had failed. Following hatching of eggs, we continued to monitor ter-

ritories with successful nests at weekly intervals to assess brood survival. We considered a brood successful if at least one chick reached fledging age at 45 days or when observed in flight (Koczur *et al.* 2020). Where possible we identified causes of chick loss based on field signs such as avian predation (chick observed with visible wounds to head or body) and overwash (chicks cold/wet with no visible wounds in or near nest and visible signs of flooding at nest site).

Statistical Analyses

We used the Program MARK nest-survival module (Rotella *et al.* 2004; White and Burnham 1999) to evaluate daily survival rates (DSR) and identify what ecological and environmental factors best explained variation in DSR. We also modelled brood survival using the nest survival model (Dinsmore *et al.* 2002) in Program MARK (White and Burnham 1999). When examining specific model effects (e.g., covariates), we inferred strong effects in models in which 95% confidence intervals did not include zero. Nest success (the probability of a nest surviving from egg laying to hatching) and brood success (the probability of at least one chick surviving from hatching to fledging) was calculated as the DSR from the most-supported model raised to an exponent equal to the number of days in each reproductive stage (27 days for incubation and 45 days for fledging; Koczur *et al.* 2020).

In our survival analyses, we were interested in understanding the possible influence of several factors on nest and brood survival. Because of a complete island overwash event that occurred during the 2016 season, we conducted separate nest success analyses on DSR of nests within and between years because of differences in nest initiation timing, location, and nesting substrate. Models tested various hypotheses, including but not limited to, environmental variation, nest location in relation to potential disturbance factors, and temporal variation of success within nesting seasons. All analyses included a global model and a constant survival (intercept-only) model. We investigated the effect of maximum water level (maximum MLLW) during the interval between visits (National Oceanic and Atmospheric Administration (NOAA) 2018)) and nest height to document the effect of overwash on DSR for all active nests monitored during the 2016-2018 study period. We considered the following explanatory variables for DSR of nests initiated after the overwash event for the 2016 season: nest location (i.e., north or south side of island), nesting substrate (black needlerush or smooth cordgrass), edge distance, and interactions between nest location and these variables. Nest height was confounded with nesting location and was not included in this analysis, and water level was not included because of limited variability in maximum water level during this nesting period. We conducted t-tests to investigate differences in nest height before and after the overwash event and between nesting locations after the overwash event in 2016 using JMP v. 14.0 statistical software (SAS Institute 2017). We investigated DSR for all nests initiated in the 2017 and 2018 seasons because pairs within these seasons nested in similar locations and did not experience a complete overwash event early in the nesting season. Location and nesting substrate were not included as explanatory variables for DSR for these analyses, as pairs primarily nested in smooth cordgrass and selected nesting areas almost exclusively on the south side of the island (Fig. 1). We considered the following explanatory variables for DSR of nests in the 2017 and 2018 seasons: maximum water level, nest height, edge distance, day of the nesting season, year, and interactions between water level and these variables.

We also conducted separate analyses for broods in 2016 and 2017-2018 because of temporal and locational differences that may be related to brood survival. Maximum water level, brood age, edge distance, and interactions of these terms were included as explanatory variables in all brood survival analyses conducted. We additionally investigated island location (north or south) as an explanatory variable for broods in 2016. Year and day in season were included as explanatory variables for DSR of broods in 2017 and 2018. For all analyses, we present parameter estimates and standard errors (SE). Means and coefficient estimates are also presented ± 1 SE unless stated otherwise.

RESULTS

Nesting Ecology and Habitat

Rabbit Island annually hosted between 25-30 pairs of Reddish Egrets between 2016 and 2018. Within these years, we made 906 observations of 110 nesting attempts at a mean frequency of one nest check every 6.77 ± 0.34 days (Table 1). The duration of nesting activity (i.e., the time from when the first egg in the population was laid until the last chick fledged) was 145 days in 2016, 91 days in 2017, and 123 days in 2018. The earliest nest initiation date was 22 March (2017) and the latest nest initiation was 28 June (2016). Mean clutch size was 3.54 ± 0.06 eggs (range: 2-5 eggs).

The mean nest height for all nests monitored was 45.88 ± 0.77 cm (range: 26-71 cm). Following an extreme overwash event in 2016, pairs appeared to construct nests higher than before the event. Mean nest height after the overwash event was 47.64 ± 1.64 cm (range: 35-52 cm), and nests constructed before the overwash event was 43.8 ± 1.95 cm (range: 34-71 cm). However, nest heights before and after the overwash event were not significantly different ($t_{46} = 1.51$, $p = 0.14$). We also found that pairs
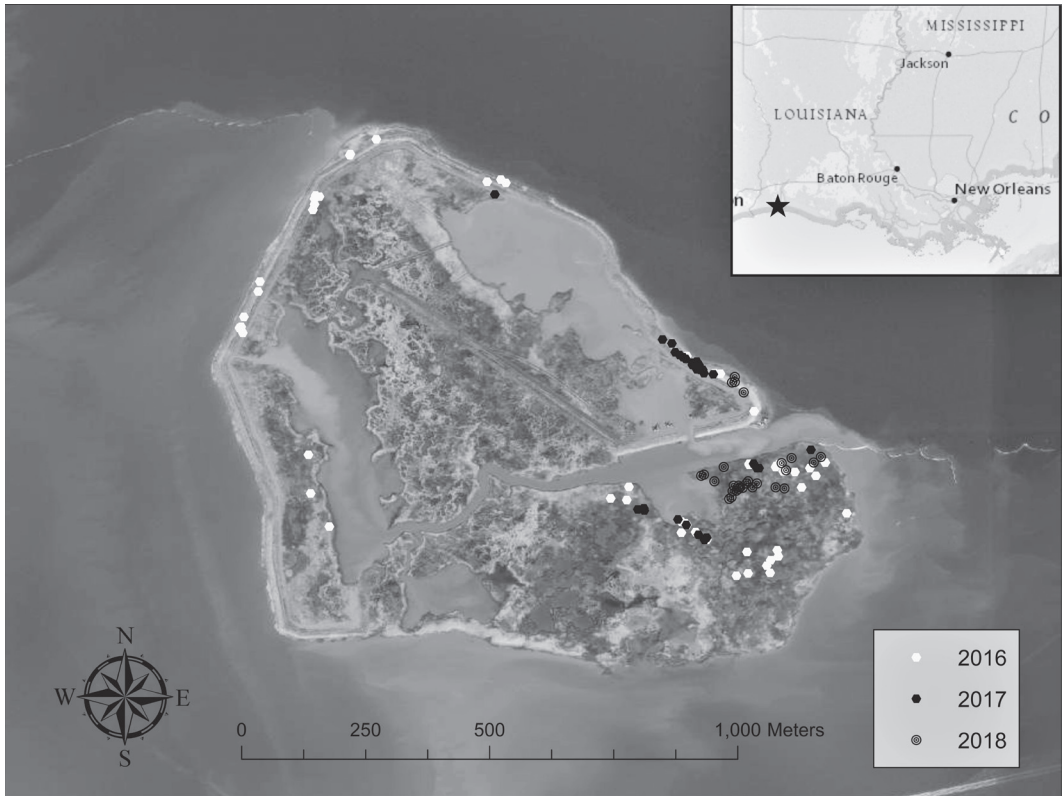
Figure 1. Distribution of Reddish Egret (*Egretta rufescens*) nests on Rabbit Island, Louisiana, USA March-June 2016-2018.

nesting after the overwash event appeared to construct nests higher on the north side of the island (52.27 ± 3.2 cm) compared to pairs nesting on the south side after the overwash event (44.38 ± 2.94 cm). Comparison of nest height between nesting locations on the island was not significantly different (t_{22} = -1.82, P = 0.08). Approximately 70% of all nests monitored during this study were constructed in marsh areas dominated by smooth cordgrass (n = 77), while the remainder were constructed in black needlerush (n = 29) or a mix of both types of vegetation (n = 4). Nest composition also appeared to be primarily smooth cordgrass (80.37 ± 2.22%), regardless of the marsh type immediately surrounding the nest site, but also consisted of saltgrass (14.37 ± 1.84%), black needlerush (3.37 ± 0.79%), saltwort (*Batis maritima*; 1.02 ± 0.60%), saltmeadow cordgrass (0.24 ± 0.14%), and other substrates (i.e., unidentified woody vegetation, rope or string; 0.26 ± 0.13%).

Table 1. Reproductive effort and success of Reddish Egret (*Egretta rufescens*) on Rabbit Island, Louisiana, USA, 2016-2018. Nests and broods were considered successful if ≥ 1 egg hatched and ≥ 1 chick fledged, respectively.

Year	No. pairs	No. nests	Nest success (%)	Brood success (%)	No. fledglings	Productivity estimate[1]
2016	30	54	22 (40.7)	17 (77.3)	24	0.8
2017	25	29	22 (75.8)	14 (63.6)	29	1.16
2018	25	27	21 (77.8)	15 (71.4)	32	1.28
TOTAL	80	110	65 (59.1)	46 (70.8)	85	1.06

[1]Number of young fledged/ number of pairs

We documented five pairs where both adults were banded during the 2016 nesting season. We confirmed banded adults from two of these pairs nesting together in 2017 and 2018. One of the banded pairs from 2016 was observed nesting together for the 2017 season, but these adults were observed with different mates during the 2018 season. Banded adults comprising three additional pairs were confirmed nesting together during the 2017 season, but were confirmed with different mates during the 2018 season.

Nest Success and Daily Nest Survival

Of the 110 nesting attempts that we monitored, 65 nests (59.1%) hatched at least one egg (Table 1). The major identifiable cause of nest loss for all nests was overwash, accounting for 48.9% of all nest failures ($n = 22$). An extreme overwash event occurred on 18 April 2016 that resulted in 100% nest failure of all active nests ($n = 19$). Along with overwash, avian predation appeared to be another significant cause of nest loss, accounting for 20.0% ($n = 9$) of all nest failures. Nest collapse and abandonment were observed infrequently and resulted in 8.9% ($n = 4$) and 4.4% ($n = 2$) of nest loss, respectively. We often would not observe any sign of nest loss at failed nests and listed the cause of nest loss as unknown for 17.8% ($n = 8$) of failed nests. We found no evidence of mammalian predation on the island, and only observed evidence of muskrat (*Ondatra zibethicus*; vegetated nest mounds and visual observation of individuals on the island), which is the only documented mammal inhabiting the island.

We investigated DSR in relation to water level, nest height, and distance to edge for all nests in all years and found that maximum water level best explained variability ($w_i = 0.97$; Table 2). The DSR estimate for all nests based on the top competing model was 0.979 (95% CI: 0.972-0.984). We found that DSR for all nests declined as water level increased ($\beta_0 = 9.72 \pm 1.79$; $\beta_1 = -5.47 \pm 1.61$; Fig. 2). After the overwash event in 2016, we found that location of nests best explained variability in nest survival for this nesting period ($w_i = 0.36$; Table 2). DSR was higher for nests located on the north side of the island 0.991 (95% CI: 0.976-0.997) compared to nests located on the south side of the island 0.973 (95% CI: 0.945-0.987). We found the best-supported model for all nests initiated in 2017 and 2018 included the day in season ($w_i = 0.60$; Table 2). DSR declined as the nesting season progressed ($\beta_0 = 5.38 \pm 0.56$; $\beta_1 = -0.03 \pm 0.01$; Fig. 3) with higher DSR estimates for nests at the start of the season at

Table 2. Model selection results for daily survival rate of Reddish Egret (*Egretta rufescens*) nests on Rabbit Island, Louisiana, USA 2016–2018. Models are ranked by ascending value of difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), with the most-supported model at the top of the list. K = the number of parameters in each model, ΔAIC_c is the AIC_c value relative to the highest-ranked model, w_i = Akaike weight (likelihood of being the best model). Only models with $w_i > 0.10$ are presented.

Breeding stage and model parameters	K	Dev	ΔAIC_c	w_i
All Nests				
Maximum water level[a]	2	229.34	0.00	0.97
2016 nests (after overwash event)				
Location[b]	2	67.73	0.00	0.36
Intercept	1	70.86	1.11	0.21
Location + Edge distance	3	67.34	1.62	0.16
Nesting substrate	2	70.19	2.45	0.11
Edge distance	2	70.20	2.46	0.11
2017 and 2018 nests				
Day in season[c]	2	99.34	0.00	0.60
Intercept	1	104.73	3.39	0.11

[a]The AIC_c value of the best model (Maximum water level) = 233.35
[b]The AIC_c value of the best model (Location) = 71.75
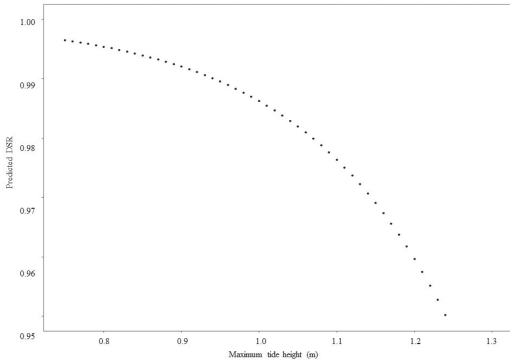[c]The AIC_c value of the best model (Day in season) = 103.35

Figure 2. Daily survival rates (DSR) of Reddish Egret (*Egretta rufescens*) nests on Rabbit Island, Louisiana, USA in relation to water level 2016-2018.

0.995 (95% CI: 0.986-0.998) compared to lower estimates at the end of the season at 0.952 (95% CI: 0.867-0.983).

Brood Success and Daily Brood Survival

Of the 65 successful nests, 47 (72%) fledged at least one young and ultimately produced 85 chicks (Table 1). Pooling across all years, 81 pairs fledged 85 chicks from 110 nest attempts, resulting in a productivity estimate for the study period of 1.06 chicks per pair. Of the 47 successful broods, 19 (40%) fledged one chick, 19 (40%) fledged two chicks, eight (17%) fledged three chicks, and one (2 %) fledged four chicks. We estimated that 49% of hatched chicks died before they reached fledging age (45 days).
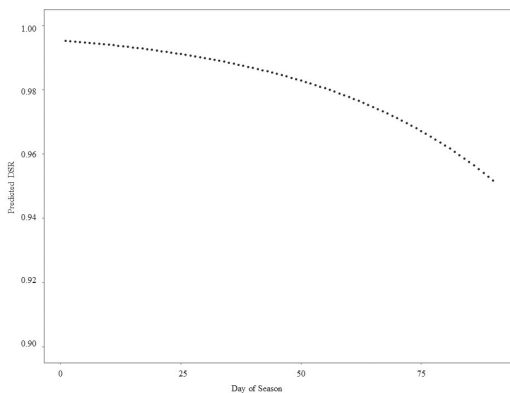

Figure 3. Daily survival rates (DSR) of Reddish Egret (*Egretta rufescens*) nests on Rabbit Island, Louisiana, USA in relation to the day in the nesting season 2017-2018.

For individual chicks that did not survive to fledge, 66% died within 21 days of hatching, while 34% died > 21 days post-hatching. Overwash appeared to be a cause for chick loss during early developmental stages in 2017, and we identified overwash as the primary cause of brood loss (28%, *n* = 5). Field observations also suggested that avian predation may contribute to chick loss, but evidence of the cause of chick loss was infrequently observed on the island.

Constant DSR for all broods was 0.993 (95% CI: 0.989-0.996). We investigated DSR for broods after the overwash in 2016 and found that maximum water level best explained variability (w_i = 0.49; Table 3), with lower DSR for increased water levels (β_0 = 22.62 ± 5.42; β_1 = -18.60 ± 5.51). Estimated DSR for broods following the overwash event in 2016 based on the top competing model was 0.997 (95% CI: 0.989-0.999). Brood age was the top competing model for DSR of broods in 2017 and 2018 (w_i = 0.29; Table 3). Survival of broods increased with age (β_0 = 4.06 ± 0.42; β_1 = 0.04 ± 0.02), with DSR as low as 0.902 (95% CI: 0.373-0.993) for newly hatched broods and as high as 0.999 (95% CI: 0.985-1.000) for broods near fledging.

DISCUSSION

Nesting ecology studies have been identified as a research priority to inform conservation plans for Reddish Egret range-wide, and in Louisiana specifically (Wilson *et al.* 2014; Holcomb *et al.* 2015; Koczur *et al.* 2020). This is the first study to investigate the nesting ecology of Reddish Egrets within the eastern portion of the CMU for the species. Mean dates of nest initiation (20 April), hatching (16 May), and fledging (30 June), as well as mean clutch size (3.5 eggs) for Reddish Egret pairs on Rabbit Island were similar to pairs nesting in Texas and Florida (Toland 1999; Holderby *et al.* 2012). However, we observed pairs nesting in different substrates than previously published descriptions, which is notable given that nesting substrate of Reddish Egrets is extremely varied across the species' range. Reddish Egret pairs nesting on Rabbit Island

Table 3. Model selection results for daily survival rate of Reddish Egret (*Egretta rufescens*) broods on Rabbit Island, Louisiana, USA 2016–2018. Models are ranked by ascending value of difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), with the most-supported model at the top of the list. K = the number of parameters in each model, ΔAIC_c is the AIC_c value relative to the highest-ranked model, w_i = Akaike weight (likelihood of being the best model). Only models with $w_i > 0.10$ are presented.

Breeding stage and model parameters	K	Dev	ΔAIC_c	w_i
2016 broods (after overwash event)				
Maximum water level[a]	2	27.75	0.00	0.49
Maximum water level + location	3	27.32	1.59	0.22
Maximum water level + edge distance + chick age + location	4	25.33	1.61	0.22
2017 and 2018 broods				
Brood age[b]	2	71.75	0.00	0.29
Maximum water level + brood age	1	72.87	1.34	0.15
Intercept	3	73.37	1.40	0.15
Maximum water level	2	74.21	1.53	0.14

[a]The AIC_c value of the best model (Maximum water level) = 31.76
[b]The AIC_c value of the best model (Brood age) = 103.70

typically selected nesting areas in smooth cordgrass on the south side of the island in all years. However, following the overwash event in 2016 pairs selected nesting areas in black needlerush on the north and west side of the island. For comparison, nesting pairs in Texas have been reported to primarily nest in low-lying vegetation like seaside tansy (*Borricha* spp.) and prickly pear cactus (*Opuntia* spp.; Holderby and Green 2013; Geary *et al.* 2015), while pairs nesting in the EMU (i.e., Florida) typically nest higher off the ground (usually 2-10 m) in red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), or Brazilian pepper (*Schinus terebinthifolius*; Koczur *et al.* 2020). Interestingly, in southeastern Louisiana, where black mangrove is present, Reddish Egrets prefer this nesting habitat, although we observed different nesting strategies on these islands with nests primarily located on the ground under black mangrove trees (S. Collins, pers. obs.). Thus, our observations at Rabbit Island are unique and are further evidence that Reddish Egrets may be generalists when choosing a nesting substrate.

Limited information is available for Reddish Egret pair bonds between years, but studies have investigated extra-pair copulation within nesting colonies. We only confirmed one occasion of a pair switching mates during the breeding season, which suggests that pairs are primarily socially monogamous within a breeding season at Rabbit Island. Previous research documented low extra pair copulations within multiple colonies range-wide and reported that multiple paternity predominantly occurred at colonies where breeding densities were high (Hill and Green 2016). Therefore, it is likely that most pairs at Rabbit Island remain monogamous throughout the nesting season because of lower breeding density. Of the eight pairs with two banded adults, we documented two pairs (25%) nesting together in subsequent years. It is suggested that breeding pairs are not likely maintained from year to year, but low density of nesting pairs and the persistence of territories by pairs that are permanent residents suggest that some pair bonds may be renewed from year to year and may persist over several years (Koczur *et al.* 2020).

Research that provides estimates on nest survival rates and identifies causes of nest loss for Reddish Egret pairs is needed to further inform conservation plans (Wilson *et al.* 2014). Nest success was ~58% over the duration of our study, but a complete island overwash event that occurred in 2016 resulted in failure of all active nests and contributed to higher rates of nest failure overall. In the absence of this overwash event, apparent nest success for all nests was ~70%, which is comparable to nest success reported for breeding pairs in Florida (60 to 75%; Toland 1999). However, nest success for this study was lower than nest success for a one-

year study conducted on breeding pairs in Texas that reported ~93% of nests survived to hatch (Holderby *et al.* 2012). Results from this study indicate the extreme variability in environmental conditions that can influence reproductive success for species nesting on a low-lying marsh island. Species like Reddish Egret that select nest sites on a low-lying island like Rabbit Island are able to adapt nesting strategies, such as early nest initiation and selection of nesting location, to enhance reproductive success to compensate for occasional overwash events or competition with other nesting species. Early occurrence of an extreme overwash event may result in lower nest success, but pairs are able to renest and produce young. Alternatively, the absence of an extreme overwash early in the nesting season may result in high nest success, but an extreme overwash event later in the season may contribute to lower brood success. Protection and management of these important nesting islands may be necessary to enhance sensitive nesting populations with increases in the occurrence of extreme overwash events and sea level rise.

No documentation of nest failure was available for nesting studies of Reddish Egrets conducted in Florida or Texas, USA making this study the first to document causes of nest failure for Reddish Egrets range-wide. It is likely that nesting areas in Texas and Florida were not as vulnerable to overwash, which was a significant cause of nest failure on Rabbit Island. While Reddish Egrets are reported to nest in low-lying vegetation in Texas (Holderby and Green 2013; Geary *et al.* 2015), island elevation is typically higher for colonies within this area (Chaney and Blacklock 2003). Further, pairs in Florida typically nest higher off the ground (2-10 m), where they are less prone to overwash events (Koczur *et al.* 2020). Water level had the strongest effect on the DSR of all nests on Rabbit Island, and its negative influence on DSR of nests is consistent with the identification of overwash as the primary identifiable cause of nest loss (14-68% of nest failures in any year). Storms during early spring, as well as tropical storms during the summer, can enhance tide heights substantially and

result in overwash of the island during the nesting season. We noted a significant decline in DSR, particularly when water levels were above 1.1 m MAMSL (Fig. 2). Elevation for Rabbit Island is between 0.3 and 0.5 m MAMSL, and the low-lying vegetation on the island makes nests particularly vulnerable to rising water levels that flood the marsh. Selman *et al.* (2016) observed lower nest success in Brown Pelicans in Louisiana associated with strong, early spring storms that overwashed portions of pelican colonies on barrier islands. Because most offshore barrier islands and marsh islands in Louisiana have low elevations, it seems likely that these natural events may diminish nesting success of coastal nesting birds like Reddish Egrets in a stochastic and unpredictable fashion.

After the overwash event in 2016, breeding pairs selected nesting territories that were dispersed throughout the island (Fig. 1). We found that nesting location best explained variability in DSR for these nests; nests on the north side of the island were more successful than nests located on the south side. Island elevation is higher on the north side of the island (K. Ritenour, unpubl. data), and pairs appeared to also constructed nests higher on this side of the island, although the differences were not significantly different. Thus, one hypothesis was that pairs renested in this area to reduce risk of failure due to overwash. However, we did not observe significant fluctuations in water level that would result in overwash during this period, so it is unlikely that differences in DSR between location was related to water level. Based on this result, it seems likely that differences in DSR between nesting locations on the island following the overwash event was related to avian predation. Nesting areas in smooth cordgrass and saltgrass flats on the south side of the island also appeared to be preferred nesting areas for thousands of Laughing Gulls. Laughing Gull nest predation and flooding have been documented to significantly contribute to nest loss for other nesting avian species in Louisiana (Leberg *et al.* 1995; Hervey 2001; Leumas 2010; Owen and Pierce 2013). In a similar study in Texas, Reddish Egrets initi-

ated nests on high quality nesting habitat earlier in the season prior to the nesting islands becoming saturated with other species as the season progressed (Holderby *et al.* 2012). Reddish Egrets were also among the first species to initiate nests on Rabbit Island early in the breeding season when competition with other avian nesting species was limited. Our data suggest that Reddish Egrets may modify nesting strategies later in the season when there is increased competition with other nesting species.

Results from this study also supported date of nest initiation as a significant factor related to DSR of nests in 2017 and 2018. Nests initiated early in the nesting season had higher DSR than nests initiated later in the nesting season. Highest water levels recorded between visits did not exceed 1.1 m MAMSL during the 2017 and 2018 nesting seasons; therefore, in the event of lower water levels, it appears that there are other factors related to nest initiation timing that may contribute to lower nest survival. We suspect the differences in DSR based on nest initiation may be associated with the increased presence of other avian nesting species, particularly Laughing Gulls, that may cause disturbance or nest failure. We documented avian predation as the cause of nest failure for 10-43% of nests that did not survive to hatch in any year of the study.

Brood success (~72%) for pairs during this study was lower than previously reported for pairs in Florida and Texas (92-94%; Toland 1999; Holderby *et al.* 2012). However, fledging success estimates from Texas were based on a cutoff of three weeks when parents continuously attend young nestlings and chicks may be more vulnerable to predators or exposure (Koczur *et al.* 2020). If this same cutoff was applied to our data, brood success would be 86.2%. These results indicate that there are other factors on this island that may limit brood survival compared to nesting areas in Florida and Texas. Analyses indicated that water level had the strongest effect on the DSR of broods during the 2016 season. We observed complete brood failure when water levels exceeded 1.1 m. Although water level was not the top-ranking model

for broods in 2017 and 2018, lowest brood success was observed during the 2017 season (Table 1). We documented failure of three broods with young chicks following Tropical Storm Cindy (22 June 2017). Chick age best explained variability in DSR for broods during these nesting seasons with older broods having higher DSR. Chick age, vis-à-vis earlier nest initiation dates, is therefore related to vulnerability of chicks to avian predation or flooding events. More direct measures of chick predation as well as parental provisioning and attendance rates within nesting areas would be valuable to better understand factors influencing chick and brood survival.

Threats to Reddish Egret populations in Louisiana include, but are not limited to, anthropogenic and natural habitat alterations from sea level rise and subsidence (Wilson *et al.* 2014). Because of changes in nest site suitability associated with coastal land loss and erosion, breeding pairs may shift nesting locations throughout the region. Rabbit Island provides the only suitable nesting area for Reddish Egret pairs in southwestern Louisiana and is a relatively new nest site for breeding pairs (Selman and Davis 2015). Based on survey efforts to estimate breeding pairs and identify nesting locations statewide, it is likely that Rabbit Island holds the largest concentration of nesting pairs in Louisiana (S. Collins, unpubl. data). However, storms occurring in the winter and early spring accelerate erosion rates for this small island because of its low elevation. Nesting locations for Reddish Egrets during the 2013 breeding season appeared to be more dispersed out throughout the island, as well as concentrated in the southeastern area of the island as observed in this study (Selman and Davis 2015). Differences in nest site selection on the island may be associated with a narrowing of areas of marsh surrounding the larger tidal ponds that have subsided and are no longer suitable for nesting birds because of frequent flooding.

There is an urgent need for protection and enhancement of Reddish Egret nesting habitat on this important marsh island and others throughout the northern Gulf of Mexico. Future restoration plans of nest-

ing islands should consider nesting habitat requirements, such as vegetation composition and cover, for this vulnerable species. Restoration plans for these nesting islands should also consider the distance to the mainland when determining the target for island elevation as higher elevations following restoration may promote the presence of mammalian predators for islands close to the mainland (Ritenour 2019). Establishment of mammalian predators on nesting islands can be a significant cause of nest failure, and abandonment of nesting colonies appears to be greater in areas subjected to mammalian predation pressures than those subjected to flooding (Burger 1982; Post 1990; Erwin *et al.* 2001). Because of high rates of nesting island erosion/loss and subsequent nomadic nature of rookeries, periodic surveys are needed to document colony persistence, locate additional Reddish Egret nest sites, update wading bird population assessments, and initiate appropriate protective measures throughout the CMU. Furthermore, additional reproductive ecology studies throughout the range of the Reddish Egret are needed to better inform management and conservation planning, and efficacy of population viability models that may enhance the conservation measures provided to the species.

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