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Source: Waterbirds, 36(1):1-10. 2013.
Published By: The Waterbird Society
URL: http://www.bioone.org/doi/full/10.1675/063.036.0101

Waterbirds

Journal of the Waterbird Society

Vol. 36, No. 1 | 2013 | Pages 1-120

Daily Survival Rate for Nests and Chicks of Least Terns (*Sternula antillarum*) at Natural Nest Sites in South Carolina

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Abstract.—Although a species of conservation concern, little is known about the reproductive success of Least Terns (*Sternula antillarum*) throughout the southeastern USA where availability of natural beaches for nesting is limited. Daily survival rate (DSR) of nests and chicks was examined at four natural nesting sites in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010. Measures of nest success ($n = 257$ nests) ranged from 0-93% among colony sites. The DSR of nests was primarily related to colony site, but year and estimates of predation risk also were related to DSR. Predation was the principal cause of identifiable nest loss, accounting for 47% of nest failures when the two years of data were pooled. The probability (± SE) of a chick surviving from hatching to fledging = 0.449 ± 0.01 ($n = 92$ chicks). DSR of chicks was negatively related to tide height and rainfall. Therefore, productivity of Least Terns is being lost during both the nesting and chick stage through a combination of biotic and abiotic factors that may prove difficult to fully mitigate or manage. Although natural nesting sites within Cape Romain National Wildlife Refuge intermittently produce successful nests, the consistency of productivity over the long term is still unknown. Given that the long term availability of anthropogenic nest sites (e.g., rooftops, dredge-spoil islands) for Least Terns is questionable, further research is required both locally and throughout the region to assess the extent to which natural sites act as population sources or sinks. *Received 24 April 2012, accepted 11 October 2012.*

Key words.—chick survival, Least Tern, nest predation, nest success, South Carolina, *Sternula antillarum*.

Waterbirds 36(1): 1-10, 2013

South Carolina, Georgia, and the northern portion of Atlantic Florida annually support > 30,000 breeding nearshore seabirds and shorebirds (Jodice *et al. in press*), which naturally nest on offshore, estuarine, and riverine islands. During the past few decades, however, as human presence has increased some species have vacated natural nest sites in favor of anthropogenic sites. For example, > 75% of nests of Least Terns (*Sternula antillarum*) in the southeastern USA now occur on dredge-spoil islands and rooftops (Savereno and Murphy 1995; Thompson *et al.* 1997; Krogh and Schweitzer 1999). Artificial sites do not, however, consistently provide high quality nesting habitat. For example, extreme temperatures on rooftops (1.6-67.6 °C) are lethal to eggs and chicks (Krogh and Schweitzer 1999) and dredge-material sites undergo succession and may be subject to erosion (Mallach and Leberg 1999). Also, nesting sites such as rooftops and dredge-spoil islands may not provide permanent replacements for natural sites. Gravel rooftops are being replaced with gravel-free roofing which terns will not use for nesting (Gore and Kinnison 1991; Cimbaro 1993) and the cost of building and maintaining dredge-spoil islands to prevent succession and erosion continues to rise (Bailey and Hatcher 2005). Therefore, the conservation value of natural sites cannot be dismissed and an assessment of threats to productivity at these sites is needed.

Although the reproductive ecology of Interior and California Least terns has received much research attention, Least Terns in the southeastern USA have not been thoroughly studied, particularly at natural nesting sites (Thompson *et al.* 1997). The Least Tern is currently listed as 'threatened' in South Carolina and Florida, and 'rare' in Georgia (Georgia Department of Natural Resources 2009; Florida Fish and Wildlife Commission 2011; South Carolina Department of Natural Resources 2012). Approximately 2,000 pairs of Least Terns currently nest on natural beaches in coastal South Carolina, Georgia, and north Florida (Jodice *et al. in press*) and in South Carolina there are typically 5-10 natural sites that host Least Tern colonies annually (South Carolina Department of Natural Resources, unpubl. data). Given that the shift in selection of nesting habitat by Least Terns appears to coincide with poor reproductive success at natural sites, we sought to determine which stressors contributed to nest and chick loss on some of the few remaining natural nesting sites within the region. Our objectives were to measure the daily survival rate (DSR) of nests and chicks of Least Terns at natural nesting areas and to identify factors that influenced DSR. Identifying these factors is an important first step in prioritizing conservation of high quality nesting sites and designing management strategies for increasing reproductive success.

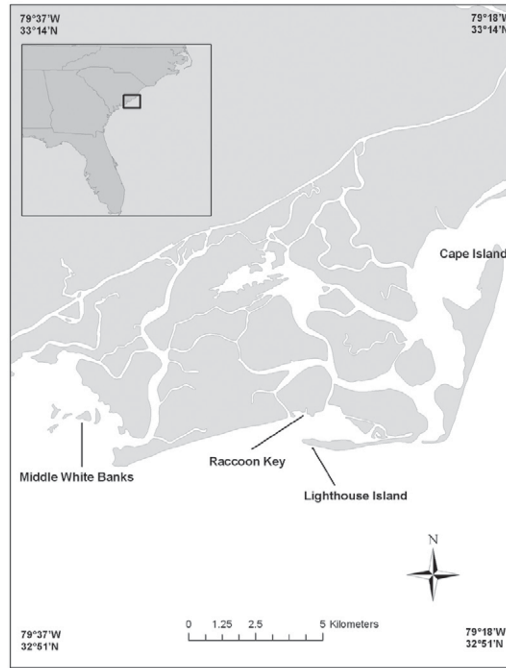

Figure 1. Location of colony sites of Least Terns (*Sternula antillarum*) within Cape Romain National Wildlife Refuge, South Carolina, 2009-2010.

METHODS

Study Area

Cape Romain National Wildlife Refuge (NWR) extends along 35 km of coastline in Charleston County, South Carolina. The refuge consists of barrier islands, saltmarsh, shell mounds, fresh and brackish water impoundments, mudflats, reefs (primarily oyster *Crassostrea virginica*), tidal creeks, bays, and maritime forest. Colonies of Least Terns were monitored at four sites within the refuge (Fig. 1). The area is strongly tidal with two cycles per day. Mean annual tidal range is 1.59 m and spring tidal range is 1.87 m. Middle White Banks, located in Bulls Bay, is an 11-ha island formed from the accretion of oyster and clam (*Mercenaria* sp.) shells. Raccoon Key is a 1,400-ha barrier island that consists primarily of sandy beach and salt marsh. Lighthouse Island and Cape Island are each 500-ha barrier islands comprised primarily of salt marshes, maritime forest, and sandy beaches. Lighthouse Island is located between Cape Romain Harbor and Key Inlet, while Cape Island is located in Cape Romain Harbor. Vegetation at study sites consisted primarily of seaside panicum (*Panicum amarum*), sea purslane (*Sesuvium portulacastrum*), seaside spurge (*Euphorbia polygonifolia*), wild bean (*Strophostyles helvola*), and cordgrass (*Spartina* spp.).

Each island monitored during this study is used regularly for nesting by nearshore seabirds and shorebirds. Cape Romain NWR receives about 160,000 visitors annually (U.S. Fish and Wildlife Service 2009). Public access to Middle White Banks is prohibited from February through September. Raccoon Key, Lighthouse Island, and Cape Island are open to the public year-round, except for colony areas that are closed to the public during April-August.

Nest and Chick Monitoring

Historical and potential nesting areas within Cape Romain NWR were searched intensively for active Least Tern colonies from late April through late June 2009 and 2010. A sample of nests was selected to monitor from each active colony. Numbers of monitored nests within colonies were not constant within a nesting season but increased as new nests were found. Nests were individually marked and number of eggs and location were recorded. Initiation dates of nests were estimated based on egg floatation (Hayes and LeCroy 1971). Each egg was marked with permanent nontoxic marker to indicate egg and nest number. To record flooding or overwash events at colonies, plastic cups (ca. 0.5 L) were positioned adjacent to nests located along colony edges. Cups were secured to the ground by affixing nails to the base. Cups had holes set along the upper circumference to allow inflow of water from horizontal movement (e.g., flooding), and lids which restricted water flow from vertical movement (e.g., rain).

Nests were monitored approximately every 3 days (Range 1-10 days) beginning in early May and continuing until nest fate was determined. Colony visits were ≤45 min in duration and occurred before 10:30 or after 16:30 to minimize heat stress. Colonies were not entered during heavy rain, high wind, or extreme temperatures. During each visit the number and condition of eggs or young within each nest were recorded. The fate of each nest was defined as successful, failed, or undetermined. We considered a nest successful if ≥1 egg hatched; i.e., if a recently hatched chick was found in the nest scrape, or if a recently hatched chick was found within close proximity (~0.25 m) to the nest scrape on visits occurring close to the estimated hatch date. For failed nests, cause of failure was classified as abandoned (eggs were cold and/or moisture was seen on the eggshell), depredated (signs of predation such as broken eggshells and yolk stains and/or evident predator tracks leading to the nest scrape), overwashed (cup next to a study nest contained saltwater, marked eggs found in wrack debris that was recently deposited), failure to hatch (hatching never occurred although parents continued to incubate through subsequent nest observation intervals), or unknown (empty scrapes were observed before estimated hatch date and no sign of predation or overwash were evident). All other causes of nest loss (i.e., nesting substrate such as a shell rake collapsed and human error) were defined as 'other'. Nest fate was recorded as undetermined for nests where there was no clear evidence of success or failure.

Daily survival rate of chicks was estimated through banding and re-sighting efforts but was restricted to Middle White Banks due to logistical constraints at other colony sites. We banded 1-2 day old chicks at Middle White Banks with a unique color-band combination (2009: n = 35; 2010: n = 57). After the first day of banding, 2-hr observations were conducted every 2-5 days to re-sight banded chicks. In 2009, re-sight surveys were conducted by one or two observers simultaneously, and in 2010 two or three observers conducted re-sight surveys simultaneously. Re-sight surveys were conducted either before 10:30 or after 16:30 when chicks appeared to be most active. Re-sighting was conducted throughout Middle White Banks with a spotting scope from a portable blind. Banded chicks that were re-sighted (i.e., survived) 18 days post-hatch were considered fledged. Re-sight surveys were conducted until no Least Tern fledglings (banded or unbanded) were observed at the study site for two consecutive visits.

Statistical Analysis

A suite of logistic-exposure models (Shaffer 2004) was used (SAS PROC GENMOD, binomial distribution and logit function; SAS Institute, Inc. 2008) to estimate DSR of nests and chicks and to identify factors that influenced DSR. The information-theoretic approach to model selection was followed (Burnham and Anderson 2002). A set of *a priori* models was constructed (Appendix), including a global model and a constant survival (intercept-only) model. Each model for nest survival included a subset of the following variables: year (2009 or 2010), colony site (Middle White Banks, Lighthouse Island, or Cape Island; data from the Raccoon Key colony were not included in this latter analysis because every nest monitored within the colony (n = 5) failed on the first observation interval), nest age (average for observation interval), date (average for observation interval; proxy for seasonal effect), clutch size, rainfall (cumulative rainfall during observation interval), ambient temperature (maximum during observation interval), tide height (maximum during observation interval), and predation risk (during the observation interval if ≥1 egg within the colony was preyed upon, if predator tracks were observed, or if a predation event was documented on video camera then predation risk = yes). For models of chick survival, independent variables included year (2009 or 2010), chick age (average for observation interval), chick age^2, day in nest season (average for observation interval), day^2, rainfall (cumulative rainfall during observation interval), ambient temperature (maximum during observation interval), and tide height (maximum during observation interval). Models were constructed such that correlated terms were not included in the same model. Daily rainfall and ambient temperature were obtained from records at the Charleston International Airport (69 km from study area) and reflect the general climate of the study area. Tide height was obtained from records at the South Carolina Port Authority, Charleston, South Carolina, and then adjusted with a tide correction factor specific to our study sites. The goodness-of-fit of the global model was evaluated by calculating c-hat (observed deviance/expected deviance), which determines the amount of over-dispersion of the original data (Allison 1999). Once run, models were ranked based on their Akaike Information Criteria (AIC) value (Burnham and Anderson 2002). Regression coefficients from the most-supported model were used to estimate DSR for various values of the explanatory variable(s). For each model, ΔAIC (difference in AIC value of the most-supported model and each other model tested) and AIC weights (w_i, a measure of the probability that model i is the best model tested, given the data collected and models assessed) were calculated. A set of candidate models was created where the cumulative sum of AIC weights, when models were ranked from most- to least-supported, equaled approximately 0.95. These models were used to calculate model-averaged coefficients, unconditional standard errors, and 85% confidence intervals for each variable. An 85% confidence interval was calculated because it allowed for more congruent model selection and model-evaluation criteria (Arnold 2010). For independent variables only occurring in one model from the 95% confidence set, the single coefficient and standard error estimate from that specific model were used. Model-averaged coefficients, standard errors, and 85% confidence intervals were used to interpret the effect of specific variables on daily nest survival. Coefficients were also converted to odds ratios to allow for additional interpretation. Nest success (the probability of a nest surviving from egg laying to hatch) and fledge success (the probability of a chick surviving from hatch to fledge) were calculated as the DSR from the most supported model raised to an exponent equal to the number of days in each reproductive stage (i.e., 21 day for incubation and 18 day for fledging)

RESULTS

We monitored 257 nests during 1,141 observation intervals at four colony sites during 2009 and 2010. Observation intervals ranged from 1-10 days, although 93% of intervals were 2-4 days. The fate of 18 nests was undetermined and these nests were not included in calculations of DSR. Three models were included in the 95% confidence set of nest-survival models and each contained the variables colony site, year, and predation risk (Table 1). The global model (which did achieve an adequate fit for the observed data: $\hat{c}$ = 0.73) and null model were not included in the 95% confidence set. The top-ranked model was nearly two and six times as likely to be the best model compared to the second- and third-ranked models, respectively.

Nest survival was most strongly related to colony site (Table 2). The odds of a nest surviving at Middle White Banks were 38 and 15 times the odds of a nest surviving at Lighthouse Island and Cape Island, respectively. Year and predation risk were important factors related to nest survival. The odds of a nest surviving in 2010 were three times the odds of a nest surviving in 2009, and the odds of a nest surviving when a predation event did not occur in the colony were two times the odds of a nest surviving when a predation event did occur in the colony. The influence of rainfall and tide height on nest survival was negligible (85% confidence interval overlapped 0; Table 2), although these two variables were not collected directly from colony sites. The probability of nest success calculated from the best model ranged from 0.157-0.926 (Table 3). Nest success was higher at Middle White Banks compared to the other two colonies, higher during 2010 compared to 2009, and higher when predation events were absent compared to present (Table 3). Complete colony failure occurred during 2009 at Lighthouse Island and in 2010 at Raccoon Key.

Nests failed primarily from predation (47%) although unknown causes and overwash also accounted for substantial levels of nest loss (Fig. 2). Physical signs, observations and/or remote documentation from video cameras (Brooks 2011) documented Black Vulture (*Coragyps atratus*) and American mink (*Neovison vison*) as definitive nest predators. Raccoons (*Procyon lotor*), Great-Horned Owls (*Bubo virginianus*), ghost crabs (*Ocepode quadrata*), and humans also were documented within colonies.

We monitored 92 chicks during 403 observation intervals in 2009 and 2010 at

Table 1. Model selection results for daily survival rate of Least Tern (*Sternula antillarum*) nests and chicks in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010. Models are ranked by ascending ΔAIC values, with the most-supported model at the top of the list. K = number of parameters in each model, ω_i = Akaike weight (probability of being the best model). Only models within the approximate 95% confidence set are included.

Model No.	Parameters	K	ΔAIC	ω_i	Cumulative sum of ω_i
Nest Survival					
N20	Colony site + Year + Predation	5	0.00	0.58	0.58
N19	Colony site + Year + Predation + Rainfall	6	1.36	0.29	0.87
N18	Colony site + Year + Predation + Rainfall + Tide	7	3.35	0.11	0.98
Chick Survival					
C10	Tide height + Rainfall + Temperature	4	0.00	0.54	0.54
C11	Tide height	2	0.40	0.44	0.98

Table 2. Average parameter estimates, unconditional standard errors and 85% confidence intervals for the parameter estimates for variables included in 95% confidence set of models predicting survival of Least Tern (*Sternula antillarum*) nests and chicks in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010.

Variable[a]	Coefficient Estimate	85% Confidence Interval
Nest Survival		
Intercept	-11.82 (0.45)	-10.85, -12.78
Colony - Lighthouse Island	-3.63 (0.44)	-2.67, -4.59
Colony - Cape Island	-1.14 (0.41)	-1.80, -3.65
Year - 2009	-1.14 (0.24)	-0.44, -1.84
Predation risk - No	0.88 (0.27)	1.62, 0.13
Rainfall	-0.03 (0.04)	0.24, -0.30
Tide Height	0.01 (0.07)	0.39, -0.37
Chick Survival		
Intercept	-0.97 (3.62)	-3.71, 1.76
Tide height	2.84 (0.78)	1.56, 4.11
Rainfall	-0.09 (0.04)	-0.38, 0.21
Temperature	-0.02 (0.09)	-0.46, 0.42

[a]Reference levels for categorical variables were Middle White Banks for colony, 2010 for year, and Predation Risk = Yes.

Middle White Banks. Observation intervals ranged from 2-4 days. We re-sighted 86% (*n* = 31) and 46% (*n* = 26) of banded Least Tern chicks at least once before fledging in 2009 and 2010, respectively. Two models were included in the 95% confidence set of chick-survival models and each contained the variable for tide height (Table 1). The probability of either of these two models being the best model was > 98%. DSR of chicks increased strongly with maximum tide height and decreased moderately with increased rainfall (Table 2, Fig. 3). The probability of a chick surviving (±SE) the entire interval from hatching to fledging was 0.449 ± 0.01.

Discussion

We present the first estimates of DSR for Least Tern nests and chicks from natural nest sites in South Carolina, and one of the few estimates for the region. Nest success for Least Terns within Cape Romain NWR varied nearly six-fold among colony sites and years. We observed a strong colony effect. DSR of nests was highest at Middle White Banks compared to colonies at Lighthouse and Cape Islands. Middle White Banks receives greater management protection from human disturbance compared to colonies at Lighthouse and Cape Islands (U.S. Fish and Wildlife Service 2009) and the lack of human disturbance may have partly contributed to higher success at Middle White Banks. Middle White Banks also contained a greater number of nests and the density of nests also appeared higher (although density was not measured due to logistical constraints) compared to Lighthouse and Cape Islands. A positive correlation between nest success and both colony size and density occurs in Least Terns (Lombard *et al.* 2010) as well as other colonial species (Birkhead 1977; Wittenberger and Hunt 1985) and thus may have contributed to the colony-effect we observed. Further, the colony at Middle White Banks also supported nesting Common Terns (*Sterna hirundo*), Gull-billed Terns (*Sterna nilotica*), and Laughing Gulls (*Luecophaeus atricilla*) while Lighthouse and Cape Islands did not. Shorebirds (e.g., Spotted Sandpiper, *Actitcis macularius*) and nearshore seabirds (e.g., Black Skimmer, *Rhynchops niger*) nesting in close proximity to Common Terns can experience enhanced nest protection due to the aggressive behavior of the latter species (Erwin 1979; Burger and Gochfeld 1990; Quinn and Ueta 2008). Thus, Least Terns nesting on Middle White Banks may have experienced enhanced nest protection and nest success due to the presence of an active Common Tern colony.

Predation accounted for 47% of nest loss during our 2-year study and has been identi-

Table 3. Daily survival rate (SE) and probability of success for Least Tern (*Sternula antillarum*) nests in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010. Probability of success is the daily survival rate raised to an exponent equal to 21 (incubation days). All estimates were calculated by using coefficients and standard errors of the most-supported model from Table 1.

Variable	Daily Nest Survival	Probability of Success
Colony site		
Lighthouse Island	0.916 (0.006)	0.157
Cape Island	0.930 (0.003)	0.218
Middle White Banks	0.996 (0.001)	0.926
Year		
2009	0.959 (0.003)	0.412
2010	0.977 (0.001)	0.613
Predation risk		
No	0.986 (0.001)	0.749
Yes	0.916 (0.004)	0.160

fied as a primary source of nest loss for Least Terns in the southeastern USA (Blus and Stafford 1980; Krogh and Schweitzer 1999; O'Connell and Beck 2003). We likely underestimated nest loss due to predation (particularly avian) because nests classified as 'unknown cause of loss' may have been depredated but not classified as such based on our strict guidelines for categorizing nests as predated. For example, nests for which the cause of failure was undetermined increased in 2010 coincident with observations of Black Vultures consuming Least Tern eggs during

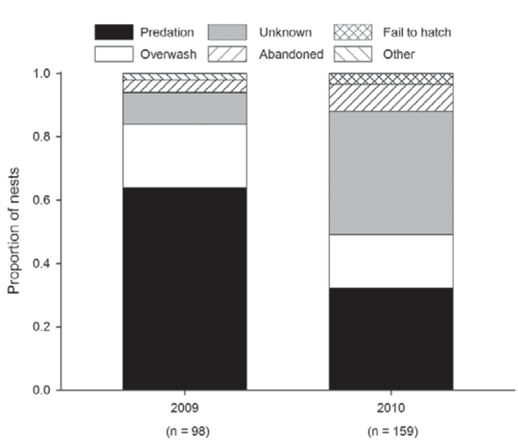

Figure 2. Cause of nest loss for Least Terns (*Sternula antillarum*) in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010.

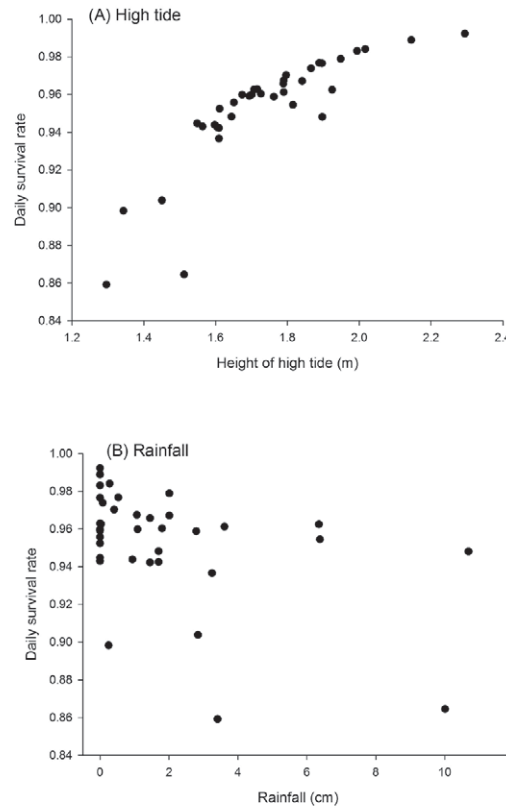

Figure 3. Daily survival rate (DSR) of Least Tern (*Sternula antillarum*) chicks in Cape Romain National Wildlife Refuge, South Carolina, 2009-2010.

daylight hours and with Great Horned Owls entering Least Tern colonies at night. Avian predators do not leave conspicuous tracks, making it difficult to positively identify them as the cause of nest loss (Nisbet and Welton 1984; Thibault 2008). American mink presence and predation were documented at all colonies located on barrier islands and the occurrence of mink was coincident with failure of the Least Tern colonies at Lighthouse Island in 2009 and Raccoon Key in 2010. Depredation of tern nests by mammals has been documented in Cape Romain NWR since at least the 1970s (Blus and Stafford 1980).

Overwash is a common cause of nest loss for Least Terns throughout their breeding range (Smith and Renken 1993; Krogh and Schweitzer 1999; Rounds *et al.* 2004). However, nests on Middle White Banks may not have been exposed to overwash events as frequently or in the same manner as nests elsewhere in this study. Water was never observed in washover cups at this site and we speculate this is due to the microtopography of this shell-mound island. The Least Tern colony at Middle White Banks was surrounded by trenches that formed as shells accreted. During high-water events these trenches channeled water away from the nests. In contrast, at Lighthouse and Cape Islands, the sand-substrate provided no opportunities to channel water and overwash cups within or along the Least Tern colony were observed containing water on three visits coincident with nest loss (e.g., during storm-driven high tides in late June 2009 and late May 2010). Although rainfall and tide height were not strong variables in the DSR models, overwash accounted for approximately 20% of nest loss through acute events such as a storm-driven tide.

The DSR of chicks increased with maximum tide height and decreased slightly with increasing rainfall. Chick survival in terns and gulls is often compromised by poor weather conditions such as rainfall (Becker and Specht 1991; Dugger *et al.* 2000; Thyen and Becker 2006). The positive relationship between tide height and survival is less clear. Tide height would be unlikely to have a negative effect on predation. Mammalian predators in the study area (e.g., American mink) would not be limited by higher tides and while avian predators (e.g., raptors) may not be directly affected by tide height it would appear that high tides might in fact concentrate chicks in smaller areas and hence be associated with decreased survival. We suggest that the positive relationship we observed between maximum tide height and DSR of chicks was due to enhanced foraging conditions for parent Least Terns during these conditions. In our study area, severe high tides are associated with severe low tides, the latter of which are often favored for foraging by estuarine and nearshore birds as they serve to trap prey more effectively (Becker and Specht 1991; Brenninkmeijer *et al.* 2002; Paiva *et al.* 2008). Periods of time associated with more extreme tides may therefore lead to increased DSR for chicks via enhanced food availability. Presently, there are no other published measures of DSR for Least Tern chicks on natural sites within the southeastern USA.

Our data demonstrated that nest success differed among proximal sites, and that local scale factors (e.g., predation, flooding) and unidentified island-specific attributes affected DSR of nests and chicks. Cape Romain NWR has trapped mammalian nest predators although to date these efforts have not occurred consistently across years or locations. Control of avian nest predators, if a desired approach of the Refuge, would prove far more difficult and likely require efforts to remove animals individually. Tide height and rainfall were not strongly related to DSR of nests yet overwash did account for a substantial proportion of nest loss each year, suggesting that acute and less predictable events such as tidal overwash from storms can influence nest success. However, management actions to protect Least Terns from flooding would be challenging to implement. Although Least Tern colonies in Cape Romain NWR can intermittently produce successful nests and fledglings, the consistency of productivity within colonies and over longer periods of time is unknown. Additional data are needed, therefore, on nest and chick survival throughout the region at both natural and artificial nesting areas to understand the meta-population dynamics of this species in a core area of its breeding range. Without such data conservation and management, actions cannot be prioritized and will be limited in scope to colony-centric activities. Nonetheless, management of stressors such as predation and flooding may need to be considered on a colony-by-colony basis to account for unique attributes at each site.

Acknowledgments

We thank M. Spinks, S. Dawsey, C. Wakefield, L. Eggert, M. Martin, L. Brooks, J. Tavano, and L. Barnhill as well as numerous interns and volunteers for support and assistance in the field. This research was funded by the U.S. Fish and Wildlife Service, South Carolina Department of Natural Resources, School of Agriculture, Forestry, and Environmental Sciences at Clemson University, and the U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit. Logistical support was provided by the U.S. Fish and Wildlife Service, South Carolina Department of Natural Resources, and the U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit. The manuscript benefitted from comments by R. Powell, J. Stucker, and anonymous reviewers. Permits for various phases of this research were provided by The U.S. Geological Survey Bird Banding Lab (Permit # 22408) and The Clemson University Institutional Animal Care and Use Committee (Protocol # 2009-018). The South Carolina Cooperative Fish and Wildlife Research Unit is supported by the South Carolina Department of Natural Resources, Clemson University, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey. Any mention of commercial products is for information purposes only and does not imply recommendation or endorsement by the U.S. Geological Survey.

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Appendix. Logistic-exposure candidate models used in analysis of factors influencing daily survival rates of Least Tern (*Sternula antillarum*) nests (N) and chicks (C), Cape Romain National Wildlife Refuge, South Carolina, 2009-2010.

Model No.	Parameters
N1	Age + Date + Date^2 + Clutch + Colony Site + Year + Date^2 x Year
N2	Age + Date + Date^2 + Clutch + Colony Site + Year + Date x Year
N3	Age + Date + Clutch + Colony Site + Year + Date x Year
N4	Age + Date^2 + Clutch + Colony Site + Year + Date^2 x Year
N5	Age + Date + Date^2 + Clutch + Year + Date^2 x Year
N6	Age + Date + Date^2 + Clutch + Year + Date x Year
N7	Age + Date + Clutch + Colony Site + Year
N8	Age + Date^2 + Clutch + Colony Site + Year
N9	Age + Date + Clutch + Year + Date x Year
N10	Age + Date^2 + Clutch + Year + Date^2 x Year
N11	Age + Date + Clutch + Colony Site
N12	Age + Date^2 + Clutch + Colony Site
N13	Age + Date + Clutch
N14	Age + Date^2 + Clutch
N15	Age
N16	Date
N17	Date^2
N18	Colony Site + Year + Predation + Rainfall + Tide
N19	Colony Site + Year + Predation + Rainfall
N20	Colony Site + Year + Predation
N21	Predation + Rainfall + Tide
N22	Predation + Rainfall
N23	Predation + Tide
N24	Predation
N25	Rainfall + Temp + Tide + Year
N26	Rainfall + Temp + Tide
N27	Rainfall + Temp
N28	Colony Site + Date + Year
N29	Colony Site + Date^2 + Year
N30	Colony Site + Year
N31	Colony Site
N32	Year
N33	Global
N34	Intercept-only
C1	Year + Age + Age^2 + Year x Age + Year x Age^2
C2	Year + Age + Year x Age
C3	Year + Day + Day^2 + Year x Day + Year x Day^2
C4	Year + Day + Year x Day
C5	Age + Age^2
C6	Day + Day^2
C7	Age
C8	Day
C9	Year
C10	Tide height + Rainfall + Temperature
C11	Tide height
C12	Rainfall
C13	Temperature