APPARENT SURVIVAL OF ROYAL TERN *THALASSEUS MAXIMUS* AND SANDWICH TERN *T. SANDVICENSIS* AT ISLES DERNIERES BARRIER ISLANDS REFUGE, LOUISIANA, USA

JEFF S. LIECHTY[1], ASHLEE K. MINOR[1,2], MEGAN NEPSHINSKY[1] & AARON R. PIERCE[1]

[1] *Nicholls State University, 906 E. 1st Street, Thibodaux, Louisiana 70310, USA (aaron.pierce@nicholls.edu)*
[2] *Current address: Southern Illinois University, 1263 Lincoln Drive, Carbondale, Illinois 62901, USA*

ABSTRACT

LIECHTY, J.S., MINOR, A.K., NEPSHINSKY, M. & PIERCE A.R. 2017. Apparent survival of Royal Tern *Thalasseus maximus* and Sandwich Tern *T. sandvicensis* at Isles Dernieres Barrier Islands Refuge, Louisiana, USA. *Marine Ornithology* 45: 83–88.

The Isles Dernieres Barrier Island Refuge (IDBIR) in Louisiana constitutes a major colonial waterbird breeding site but is also subject to tremendous rates of land loss and habitat degradation. Restoration projects have been undertaken to sustain breeding waterbird populations on IDBIR, including Royal Terns *Thalasseus maximus* and Sandwich Terns *T. sandvicensis*. However, very little is known about the population dynamics of these species in the Gulf of Mexico. The objective of this study was to determine the apparent survival rate and breeding-site fidelity for Royal and Sandwich terns at IDBIR. A capture-mark-resight experiment of breeding adult terns was conducted during 2012–2016, and adult survival rates were estimated using the Cormack–Jolly–Seber model in program MARK. Adult Royal Terns (*n* = 283) and adult Sandwich Terns (*n* = 285) were color-banded over a four-year period, with 36% percent of Royal Terns and 23% of Sandwich Terns observed as returnees to IDBIR at least once in a subsequent breeding season. Apparent annual adult survival estimates were 0.68 for both Royal and Sandwich terns, indicating some breeding-site fidelity but also a degree of emigration or higher-than-expected mortality rates. Given that populations at IDBIR increased during the study period, we suspect emigration rather than high mortality rates as the reason for our low apparent survival estimates. These results support the hypothesis that waterbirds breeding in unstable habitats typically demonstrate weaker breeding-site fidelity, but further research is needed to determine factors affecting dispersal.

Key words: adult survival, breeding-site fidelity, capture-mark-recapture, Gulf of Mexico, Sternidae

INTRODUCTION

Louisiana's barrier islands are important breeding grounds for many species of waterbirds, including Royal Terns *Thalasseus maximus* and Sandwich Terns *T. sandvicensis* (Spendelow & Patton 1988, Visser & Peterson 1994, Raynor *et al.* 2013). Although all barrier islands are highly dynamic environments, coastal Louisiana is experiencing greater rates of land loss than any other marine coastline in the United States (Penland *et al.* 2005). Rapid deterioration of barrier islands in Louisiana has negatively impacted waterbird populations through declines in breeding-habitat quality (Walter *et al.* 2013), breeding success (Walter *et al.* 2013), and breeding-bird abundance (Raynor *et al.* 2013). Many restoration projects have been undertaken to stabilize barrier islands (Khalil & Lee 2006, Khalil *et al.* 2013), and the majority of seabird breeding colonies in Louisiana now depend on restoration efforts (Visser & Peterson 1994). In addition to habitat restoration, conservation of waterbirds also depends on understanding their breeding ecology and population dynamics.

Historically, coastal Louisiana supported 16% of the US breeding population of Royal Tern and 77% of Sandwich Tern (Spendelow & Patton 1988), with both species being of conservation concern in Louisiana (Lester *et al.* 2005). In the United States, Royal and Sandwich terns breed in densely packed, mixed-species colonies on barrier islands of the Atlantic Coast and Gulf of Mexico. Relative to other terns (e.g., Common Terns *Sterna hirundo*, and Roseate Terns *Sterna dougallii*), very little is known

about the demographics of these species, including breeding-site fidelity, natal dispersal, and survival rates, particularly in the Gulf of Mexico (Shealer *et al.* 2016, Buckley & Buckley 2002). Information on adult survival in Royal Terns is limited to one study in California (Collins & Doherty 2006); Sandwich Tern survival has been studied only in Europe (Møller 1983, Green *et al.* 1990, Robinson 2010). The long-lived nature of these species makes demographic studies paramount in understanding population trends and viability (Weimerskirch 2002).

Colonial waterbirds often demonstrate breeding-site fidelity, returning to a location at which they had previously bred. Breeders returning to previous colonies are thought to gain an advantage through familiarity with local resources and threats (McNicholl 1975, Greenwood & Harvey 1982). Populations of birds breeding in unstable habitats, such as barrier islands, typically show weaker site fidelity (McNicholl 1975, Switzer 1993, Renken & Smith 1995). In Louisiana, suitable breeding sites are limited (Visser & Peterson 1994), which may influence site fidelity. Understanding the degree of breeding-site fidelity demonstrated by waterbirds in coastal Gulf of Mexico is vital to population management at a regional level and has important consequences for prioritizing restoration sites.

Apparent survival is a useful metric for determining site fidelity, as it identifies the percentage of breeders that are retained in the population and the percentage that are lost (either to emigration or mortality). Understanding apparent survival rates of Royal and Sandwich terns in the Gulf of Mexico will help to anticipate how

populations may respond to changes to breeding-habitat quality and to develop which conservation strategies are appropriate. The objective of this study was to determine apparent adult annual survival and breeding-site fidelity for Royal and Sandwich terns breeding in Louisiana.

METHODS

Study area

The Isles Dernieres Barrier Island Refuge (IDBIR) is a chain of barrier islands in Terrebonne Parish, Louisiana (29°03′N, 90°57′W to 29°05′N, 90°36′W; Fig. 1). A product of Mississippi River deltaic processes, IDBIR forms a barrier between the Barataria-Terrebonne Estuary to the north and the Gulf of Mexico to the south. IDBIR comprises low-elevation islands that are subject to wash-over and has experienced rapid rates of land loss (McBride & Byrnes 1997). To stabilize the islands, restoration projects such as sediment applications, rock breakwaters, sand fences, and plantings have been implemented. IDBIR hosts over 20 species of breeding waterbirds, including thousands of Royal and Sandwich terns (Fontenot *et al.* 2012, Raynor *et al.* 2013). Royal and Sandwich terns nested on East Raccoon Island throughout the study period (2012–2016). Additionally, both species nested on West Raccoon Island in 2012, 2014, and 2015, and on Trinity Island in 2016; as well, Royal Terns nested on Wine Island in 2014.

Banding and resighting

Adult Royal and Sandwich terns were captured from breeding colonies on East and West Raccoon Islands by hand or using dip nets, during late incubation and early chick-brooding (between 21 May and 18 June), when they strongly defend their young chicks. All terns were banded with a US Geological Survey aluminum band and three plastic color bands in unique combinations to create field-readable marks. Plastic color bands were sealed with acetone and heat-sealed with a portable battery-powered soldering iron. Field-readable color band combinations eliminated the need for physical recapture; and we refer to recaptures and resightings collectively as "re-encounters." All breeding colonies on IDBIR were surveyed approximately once per week during the breeding season (April through July) in 2013–2016 to locate previously banded individuals. Using 8 × 42 binoculars and 20–60× spotting scopes, observers surveyed terns loafing near colonies, brooding eggs in colonies, and feeding and guarding chicks in crèches. Due to the difficulty of spotting banded terns within the large, densely packed colonies, many resightings were of birds loafing near the periphery of the colony area. These individuals were assumed to be local breeders.

Statistical analysis

Adult annual survival was modeled using program MARK version 8.0 (White & Burnham 1999). The Cormack–Jolly–Seber (CJS)
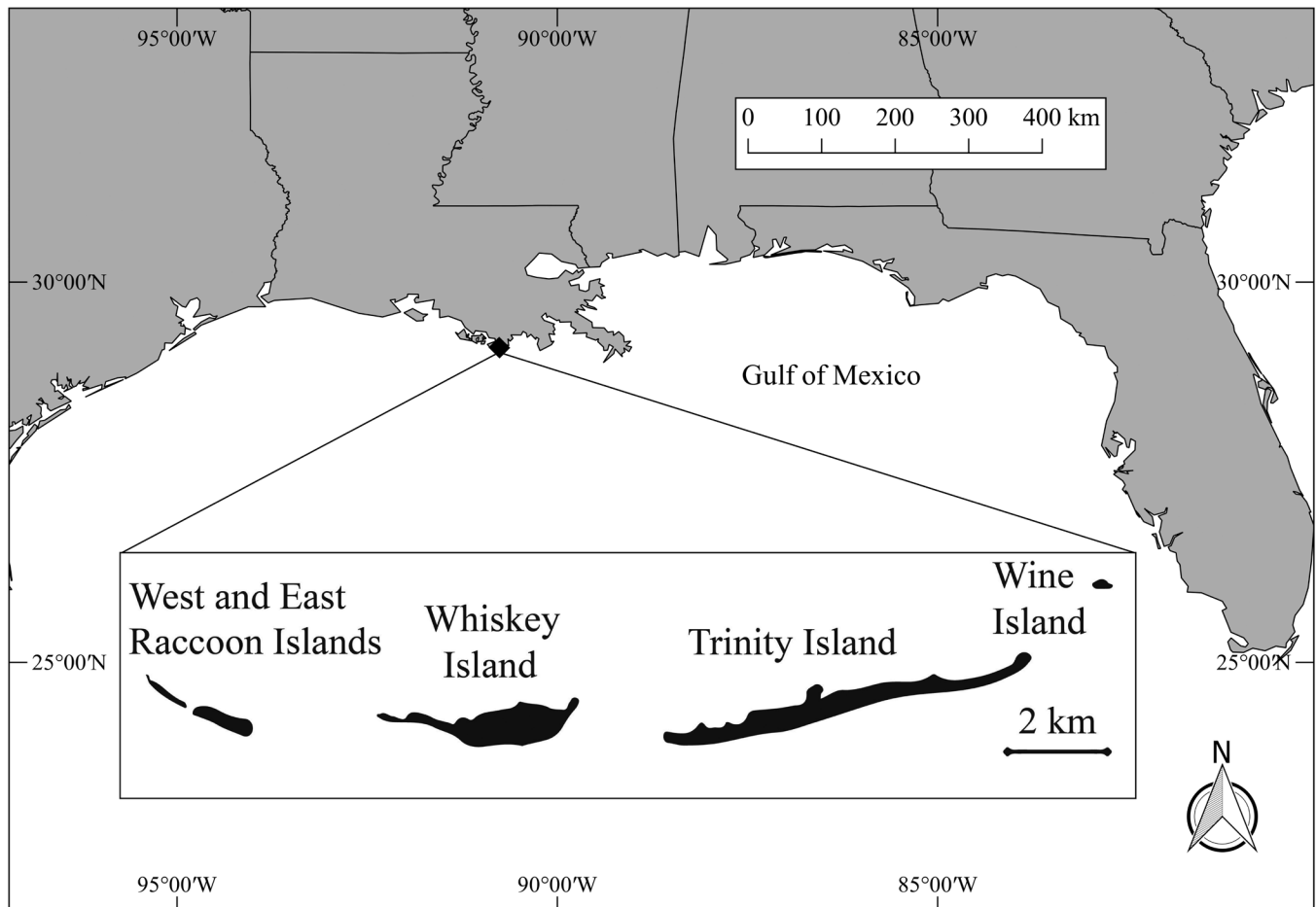

Fig. 1. Location of Isles Dernieres Barrier Island Refuge, Louisiana.

model for open populations was used to estimate apparent survival and re-encounter probability (Lebreton *et al* 1992). The CJS model estimates survivorship better than simple return rates because it estimates detection probabilities, thus accounting for unobserved individuals. CJS results cannot distinguish between mortality and emigration out of the study site, thus it is termed "apparent" or "local" survival. During the study period, colonies were established on East Raccoon Island and West Raccoon Island. As these colonies were close to each other (~2 km), and many of the observations were of birds loafing near colonies, they were treated as one site for modeling purposes.

This study had five encounter occasions (each breeding season from 2012–2016), including the initial year of banding with four intervening periods. Model parameters included apparent survival (Φ) and detection probability (p). Both parameters were allowed to vary across time (t) or remain constant (.), resulting in four models for each tern species. The variance inflation factor ($\hat{c}$) was used to indicate overdispersion and was identified using the median $\hat{c}$ function in MARK. Akaike's Information Criteria corrected for small sample size with quasi-likelihood adjustment (QAICc) was

used for model selection (Burnham & Anderson 2002). Models with a ΔQAICc > 2 were considered to have minimal support and were excluded (Burnham & Anderson 2002).

RESULTS

A total of 568 breeding adult Royal and Sandwich terns were banded during 2012–2015, with 167 individuals re-encountered at IDBIR during a subsequent breeding season (Table 1). Observed return rates were 36% for Royal Terns and 23% for Sandwich Terns. Tern encounter data used to model apparent survivorship of adults demonstrated moderate overdispersion (Royal Tern $\hat{c}$ = 1.51, Sandwich Tern $\hat{c}$ = 1.76), and the adjusted $\hat{c}$ values were used in model selection and estimates of variance.

The top-supported model for Royal Terns held survival constant, with detection probability varying among years (Φ(.) $p(t)$; Table 2). Estimated apparent annual survival was 0.68 (95% confidence interval [CI] 0.54–0.80), and annual detection probability ranged from 0.13 to 0.54 (Table 3). The second model ($\Phi(t)$ $p(.)$) had a ΔQAICc of 0.985 but Φ *2014* was poorly estimated (1.00 ± 0.00 standard error [SE]), so we focused on the estimate of survival from our top model. The top-supported model for Sandwich Terns also held apparent survival constant, with detection probability varying among years (Φ(.) $p(t)$). Apparent survival for Sandwich Terns was similar to that for Royal Terns (0.68, 95% CI 0.39–0.87), and annual detection probabilities ranged from 0.06 to 0.37. The remaining Sandwich Tern survival models all had minimal support (ΔQAICc > 2).

One Royal Tern captured at IDBIR in May of 2012 was previously banded at a different location. According to the North American Bird Banding Laboratory (www.pwrc.usgs.gov/BBL), the tern was originally banded as a chick on 24 June 1986 in North Carolina. At the time of recapture at IDBIR in 2012, this Royal Tern was 26 years old. Additionally, one Royal Tern adult banded in 2013 was found dead at a fishing camp in a salt marsh 23 km north of IDBIR on 5 May 2014 and reported to us through the North American Bird Banding Laboratory. The finder could not determine any cause of death. This is the sole report of mortality that we have received concerning terns banded in this study.

TABLE 1
Encounter histories for banded adult Royal Terns and Sandwich Terns at Isles Dernieres Barrier Island Refuge, Louisiana, 2012–2016

Species	Year banded	No. banded	Year of next re-encounter			
			2013	2014	2015	2016
Royal Tern	2012	97	15	17	0	2
	2013	100		38	8	2
	2014	61			17	1
	2015	25				1
Sandwich Tern	2012	80	10	11	1	0
	2013	100		25	6	0
	2014	78			7	6
	2015	27				0

TABLE 2
Model[a] rankings for Royal Tern and Sandwich Tern adult survival and detection probability at Isles Dernieres Barrier Island Refuge, Louisiana, 2012–2016

Species	Model	ΔQAICc	AICc weights	K[b]	QDeviance
Royal Tern	Φ(.) $p(t)$	0[c]	0.516	5	21.126
	$\Phi(t)$ $p(.)$	0.985	0.316	5	22.111
	$\Phi(t)$ $p(t)$ (global)	2.246	0.168	7	19.237
	Φ(.) $p(.)$	18.713	0.000	2	45.962
Sandwich Tern	Φ(.) $p(t)$	0[d]	0.721	5	12.636
	$\Phi(t)$ $p(t)$ (global)	3.303	0.138	7	11.786
	$\Phi(t)$ $p(.)$	3.342	0.136	5	15.978
	Φ(.) $p(.)$	10.753	0.005	2	28.848

[a] Model parameters are survival (Φ) and detection probability (p) that are either variable among years (t) or held constant (.).
[b] Number of model parameters.
[c] QAICc score 421.802.
[d] QAICc score 246.681.

DISCUSSION

Although only 36% of Royal Terns and 23% of Sandwich Terns were re-encountered as returning to breeding colonies at IDBIR, CJS modeling, which accounted for imperfect detection probability, estimated annual apparent survival at 0.68 for both species. Detection probabilities were higher for Royal Terns than Sandwich Terns, with the highest detection probabilities for both species recorded in 2014, when we could spend more time looking for banded terns than in any other year. As we found no biological rationale for a difference in survival among study years, but did have differing levels of resighting experience and effort among years, the models with constant survival and time-dependent detection probability appeared appropriate.

The 68% apparent survival rate of Royal Tern adults at IDBIR is notably lower than the 95% rate found by Collins & Doherty (2006) in California, the only published estimate for Royal Terns. Possible reasons for the difference in estimates include the much larger size of breeding colonies in our study as well as the unsurveyed colonies nearby. Additionally, there may be differences in site fidelity, survival rates, or both, between the two populations, due to differences in habitat stability or breeding success. Maness & Emslie (2001) suggest that Royal Tern site fidelity could be 80% to 94% regionally, but do not describe how site fidelity was estimated. The Royal Tern captured in 2012 that was originally banded in 1986 represents one of the oldest known Royal Terns, at 26 years of age (Lutmerding & Love 2016). This individual also demonstrates that Royal Terns do not necessarily breed in their natal colonies and that there is some degree of dispersal between the Gulf of Mexico and Atlantic Ocean populations (see Coulson 2016).

Sandwich Terns are thought to show low rates of site fidelity (Veen 1977), but no data are available for North American populations. The 68% annual survival rate of Sandwich Tern adults in Louisiana is on the low end of European estimates, which range from 70% to 90% (Møller 1983, Green *et al.* 1990, Robinson 2010). Annual survival rates of Sandwich Terns during their first three years are thought to range from 36% to 74 % (Robinson 2010), but estimates specific to North American populations are needed, as European Sandwich Terns may represent a distinct species (Efe *et al.* 2009).

Estimates of apparent survival confound permanent emigration and mortality; thus, we cannot ascertain true survival rates for these species. In both species, our estimates of apparent survival are lower than expected survival rates for Sternidae, which are typically estimated at 0.80–0.95 (Ledwoń *et al.* 2013). We suspect that emigration from IDBIR to alternative breeding sites is responsible for the lower survival estimates.

Apparent survival is a function of study site size (Marshall *et al.* 2004), meaning that apparent (or local) survival might increase if additional colonies near IDBIR were included. Although breeding sites in Louisiana are limited (Visser & Peterson 1994), there are colonies in southeastern Louisiana other than those we investigated (Fontenot *et al.* 2012, Shealer *et al.* 2016). The closest Royal and Sandwich tern colony to the IDBIR is on Timbalier Island, approximately 38 km from IDBIR. We surveyed the approximately 150 breeding terns on Timbalier Island in 2016, but no banded Royal or Sandwich terns were detected. The other main breeding colonies of Royal and Sandwich terns in Louisiana are on the Chandeleur Islands (Fontenot *et al.* 2012, Shealer *et al.* 2016), approximately 200 km from IDBIR. Logistic constraints prevented us from surveying these sites, but emigration of our banded terns to these breeding colonies is possible.

Royal and Sandwich tern colonies in Louisiana commonly show annual variability in number of breeding pairs. For example, the breeding population on IDBIR varied from a low of 9 273 pairs to a high of 22 070 pairs during the 2008–2011 period (Raynor *et al.* 2013, Pierce, unpubl. data). Given the low reproductive potential and high mobility of these species, we attribute this variability to individuals shifting between breeding colonies rather than to drastic changes in survival or recruitment in the breeding population. Terns may demonstrate weaker site fidelity to specific breeding colonies, but demonstrate a stronger level of fidelity to the region, as seen with interior Least Terns *Sterna antillarum* (Renken & Smith 1995). Although Royal and Sandwich terns demonstrate some site fidelity in the Gulf of Mexico, factors influencing dispersal (e.g., breeding success, habitat instability, food resource availability) remain unknown and need to be studied. Strong levels of site fidelity can be maladaptive if populations remain unwilling to move sites as habitat quality deteriorates (e.g., Southern & Southern 1982, Cooch *et al.* 1993, Ganter & Cooke 1998).

TABLE 3
Parameter estimates from top Cormack–Jolly–Seber models for Royal and Sandwich tern annual adult survival and detection probability at Isles Dernieres Barrier Island Refuge, Louisiana, 2012–2016

Species	Parameter	Estimate	SE	95% CI
Royal Tern	Apparent survival	0.682	0.067	0.539–0.797
	2013 detection probability	0.235	0.070	0.125–0.397
	2014 detection probability	0.545	0.087	0.376–0.704
	2015 detection probability	0.301	0.074	0.178–0.462
	2016 detection probability	0.132	0.053	0.058–0.274
Sandwich Tern	Apparent survival	0.676	0.134	0.386–0.874
	2013 detection probability	0.187	0.080	0.075–0.392
	2014 detection probability	0.367	0.115	0.180–0.604
	2015 detection probability	0.130	0.060	0.049–0.297
	2016 detection probability	0.059	0.042	0.014–0.217

CONCLUSION

This study provides the first information on site fidelity and apparent survivorship of Royal Terns in the southeastern United States, where the vast majority of US Royal Terns breed (Buckley & Buckley 2002). Additionally, this study provides the first survival estimates for Sandwich Terns outside of Europe. Although Royal and Sandwich terns returned to breed on IDBIR, we also speculate that there is some breeding dispersal, which supports McNicholl's (1975) hypothesis that site fidelity is weaker in unstable habitats. True (rather than apparent) survival rates remain difficult to ascertain but have important consequences for lifetime reproduction in species with low annual fecundity. Understanding true survival rates and movement between breeding colonies is critical to assess population status and viability. Continued monitoring of adult survival and breeding productivity, as well as estimates of juvenile survival rates and natal site fidelity, are needed for a better understanding of population dynamics of these two species. In Louisiana, long-lived species such as terns are likely to experience drastic changes to breeding sites throughout their lives, and conservation efforts should include the protection and restoration of multiple islands, not just current colony sites.

REFERENCES

BUCKLEY, P.A. & BUCKLEY, F.G. 2002. Royal Tern (*Thalasseus maximus*). In: RODEWALD, P.G. (Ed.) *The Birds of North America*. Ithaca, NY: Cornell Lab of Ornithology. [Available online at: https://birdsna.org/Species-Account/bna/species/royter1. Accessed 22 February 2017]. doi:10.2173/bna.700.

BURNHAM, K.P. & ANDERSON, D.R. 2002. *Model selection and multimodel inference: a practical information theoretic approach*, 2nd ed. New York, NY: Springer-Verlag.

COLLINS, C.T. & DOHERTY, P.F. 2006. Survival estimates for Royal Terns in southern California. *Journal of Field Ornithology* 77: 310-314.

COOCH, E.G., JEFFERIES, R.L., ROCKWELL, R.F. & COOKE, F. 1993. Environmental change and the cost of philopatry: an example in the Lesser Snow Goose. *Oecologia* 93: 128-138.

COULSON, J.C. 2016. A review of philopatry in seabirds and comparisons with other waterbird species. *Waterbirds* 39: 229-326.

EFE, M.A., TAVARES, E.S., BAKER, A.J. & BONATTO, S.L. 2009. Multigene phylogeny and DNA barcoding indicate that the Sandwich tern complex (*Thalasseus sandvicensis*, Laridae, Sternini) comprises two species. *Molecular Phylogenetics and Evolution* 52: 263-267.

FONTENOT, W.R., CARDIFF, S.W., DEMAY, R.A., ET AL. 2012. *A Catalog of Louisiana's Nesting Seabird Colonies*. Report Number 34. Thibodaux, LA: Barataria-Terrebonne National Estuary Program.

GANTER, B. & COOKE, F. 1998. Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of Lesser Snow Geese. *Auk* 115: 642-652.

GREEN, R.D., BAILLIE, S.R. & AVERY, M.I. 1990. Can ringing recoveries help to explain the population dynamics of British terns? *The Ring* 13: 133-137.

GREENWOOD, P.J. & HARVEY, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1-21.

KHALIL, S.M. & LEE, D.M. 2006. Restoration of Isles Dernieres, Louisiana: some reflections on morphodynamic approaches in the Northern Gulf of Mexico to conserve coastal/marine systems. In: KLEIN, A.H.F., FINKL, C.W., SPERB, R.M., ET AL. (Eds.) Proceedings of the 8th International Coastal Symposium, *Journal of Coastal Research*, Special Issue No. 39: 65-71.

KHALIL, S.M., FINKL, C.W. & RAYNIE, R.C. 2013. Development of new restoration strategies for Louisiana barrier island systems, northern Gulf of Mexico, USA. In: CONLEY, D.C., MASSELINK, G., RUSSELL, P.E. & O'HARE, T.J. (Eds.) Proceedings of the 12th International Coastal Symposium (Plymouth, England), *Journal of Coastal Research*, Special Issue No. 65: 1467-1472.

LEBERG, P.L., DESHOTELS, S., PIUS, S. & CARLOSS, M. 1995. Nest sites of seabirds on dredge islands in coastal Louisiana. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 49: 356-366.

LEBRETON, J., BURNHAM, K.P., CLOBERT, J. & ANDERSON, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.

LEDWOŃ, M., NEUBAUER, G. & BETLEJA, J. 2013. Adult and pre-breeding survival estimates of the Whiskered Tern *Chlidonias hybrida* breeding in southern Poland. *Journal of Ornithology* 154: 633-643.

LESTER, G.D., SORENSEN, S.G., FAULKNER, P.L., REID, C.S. & MAXIT, I.E. 2005. *Louisiana Comprehensive Wildlife Conservation Strategy*. Baton Rouge, LA: Louisiana Department of Wildlife and Fisheries.

LUTMERDING, J.A. & LOVE, A.S. 2016. Longevity Records of North American Birds. Version 2016.1. Laurel, MD: Patuxent Wildlife Research Center, Bird Banding Laboratory. [Available online at: http://www.pwrc.usgs.gov/bbl/longevity/longevity_main.cfm. Accessed 22 February 2017].

MANESS, T. & EMSLIE, S. 2001. An analysis of possible genotoxic exposure in adult and juvenile Royal Terns in North Carolina, USA. *Waterbirds* 24: 352-360.

MARSHALL, M.R., DIEFENBACH, D.R., WOOD, L.A. & COOPER, R.J. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. *Animal Biodiversity and Conservation* 27: 59-72.

McBRIDE, R.A. & BYRNES, M.R. 1997. Regional variations in shore response along barrier island systems of the Mississippi River Delta Plain: historical change and future prediction. *Journal of Coastal Research* 13: 628-655.

McNICHOLL, M.K. 1975. Larid site tenacity and group adherence in relation to habitat. *Auk* 92: 89-104.

MØLLER, A.P. 1983. Time of breeding, causes of recovery and survival of European Sandwich Terns (*Sterna sandvicensis*). *Vogelwarte* 32: 123-141.

PENLAND, S., CONNOR, P.F. JR., BEAL, A., FEARNLEY, S. & WILLIAMS, S.J. 2005. Changes in Louisiana's shoreline: 1855–2002. In: FINKL, C.W. & KHALIL, S.M. (Eds.) Saving America's Wetland: Strategies for Restoration of Louisiana's Coastal Wetlands and Barrier Islands Symposium, *Journal of Coastal Research,* Special Issue No. 44: 7-39.

RAYNOR, E.J., PIERCE, A.R., OWEN, T.M., LEUMAS, C.M. & ROHWER, F.C. 2013. Short-term demographic responses of a coastal waterbird community after two major hurricanes. *Waterbirds* 36: 88-93.

RENKEN, R.B. & SMITH, J.W. 1995. Interior Least Tern site fidelity and dispersal. *Colonial Waterbirds* 18: 193-198.

ROBINSON, R.A. 2010. Estimating age-specific survival rates from historical ringing data. *Ibis* 152: 651-653.

SHEALER, D., LIECHTY, J.S., PIERCE, A.R., PYLE, P., PATTEN, M.A. 2016. Sandwich Tern (*Thalasseus sandvicensis*). In: RODEWALD, P.G. (Ed.) *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology. [Available online at: https://birdsna.org/Species-Account/bna/species/santer1. Accessed 22 February 2017].

SOUTHERN, L.K. & SOUTHERN, W.E. 1982. Effect of habitat decimation on Ring-billed Gull colony- and nest-site tenacity. *Auk* 99: 328-331.

SPENDELOW, J.A. & PATTON, S.R. 1988. *National Atlas of Coastal Waterbird Colonies in the Contiguous United States, 1976–82.* Biological Report 88 (5). Washington, DC: US Fish and Wildlife Service.

SWITZER, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7: 533-555.

VEEN, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.) *Behaviour* Supplement 20: 1-193.

VISSER, J.M. & PETERSON, G.W. 1994. Breeding populations and colony site dynamics of seabirds nesting in Louisiana. *Colonial Waterbirds* 17: 146-152.

WALTER, S.T., CARLOSS, M.R., HESS, T.J. & LEBERG, P.L. 2013. Hurricane, habitat degradation, and land loss effects on Brown Pelican Nesting Colonies. *Journal of Coastal Research* 29: 187-195.

WEIMERSKIRCH, H. 2002. Seabird demography and its relationship with the marine environment. In: SCHREIBER, E.A. & BURGER, J. (Eds.) *Biology of Marine Birds*. Boca Raton, FL: CRC Press.

WHITE, G.C. & BURNHAM, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120-138.