Adult Survival and Breeding Dispersal of Common Terns (Sterna hirundo) in a Declining Population

Authors: Palestis, Brian G., and Hines, James E.

Source: Waterbirds, 38(3) : 221-228

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.038.0302

WATERBIRDS

JOURNAL OF THE WATERBIRD SOCIETY

VOL. 38, NO. 3 2015 PAGES 221-320

Adult Survival and Breeding Dispersal of Common Terns (*Sterna hirundo*) in a Declining Population

BRIAN G. PALESTIS[1,*] AND JAMES E. HINES[2]

[1]Department of Biological Sciences, Wagner College, 1 Campus Road, Staten Island, New York, 10301, USA

[2]U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland, 20708, USA

[*]Corresponding author; E-mail: bpalesti@wagner.edu

Abstract.—The population of Common Terns (*Sterna hirundo*) in Barnegat Bay, New Jersey, USA, has recently experienced poor productivity with complete or near-complete breeding failure at multiple colonies, and the number of breeding pairs has declined. Adult Common Terns were captured and banded at Pettit Island from 2010 through 2014 and at four additional islands from 2011 through 2014. Although the number of breeding pairs on Pettit Island decreased and reproductive success was generally poor, this colony was more productive than the other colonies. Data from the other colonies were too sparse to treat each site separately, and the analysis is instead based on two "locations": Pettit Island and all other sites. Apparent survival and movement probabilities were estimated using multistate capture-recapture modeling based on recaptures combined with resighting of color-banded Common Terns. The two best supported models included location, transience, and presence or absence of color bands as variables and produced very similar parameter estimates. Adult survival at Pettit Island was estimated at approximately 0.88, which is within the range of previous estimates for Common Terns. Survival estimates for the other sites had high uncertainty but appeared to be very low, at approximately 0.71. There was no evidence that apparent survival changed across time (2010-2012 compared to 2012-2014). Movement probabilities suggest a frequency of breeding dispersal within Barnegat Bay above 6%. Detection probabilities were much higher for color-marked birds than for those with metal bands only. Low apparent survival and decreases in the number of adults probably reflect permanent emigration out of the study area. The most likely cause of this decline in the Barnegat Bay population is frequent flooding due to sea level rise and severe storms. *Received 26 March 2015, accepted 5 May 2015.*

Key words.—adult survival, Barnegat Bay, breeding dispersal, capture-recapture models, climate change, Common Tern, population dynamics, *Sterna hirundo*.

Waterbirds 38(3): 221-228, 2015

The Common Tern (*Sterna hirundo*) is widely distributed with a large, stable global population (Nisbet 2002; Becker and Ludwigs 2004; Nisbet *et al.* 2013). However, declines have been observed in particular regions (Erwin *et al.* 2011; Morris *et al.* 2012; Szostek and Becker 2012; Nisbet *et al.* 2013). In New Jersey, USA, as barrier islands have been developed, Common Terns have been restricted to nesting mainly in saltmarsh habitat (Erwin *et al.* 1981), including small saltmarsh islands in Barnegat Bay (Burger and Gochfeld 1991). The number of Common Terns nesting in Barnegat Bay increased from the late 1970s to the early 1980s then declined and leveled off in the 1990s with peak adult counts between approximately 1,200 and 1,500 birds (Burger *et al.* 2001). Over this period, the number of colonies steadily decreased, but has been largely stable since the late 1990s. Limited data from statewide aerial surveys suggest that the number of Common Terns breeding in New Jersey as a whole may be about half the number in 2001 and earlier years, but has perhaps stabilized since around 2004 (New Jersey Department of Environmental Protection, unpubl. data). However, ground-based counts of adults, nests and fledglings within Barnegat Bay suggest poor productivity over the last few years and a sharp decline in the number of breeding pairs (J. Burger, unpubl. data). A decrease in the number of adults could result from increased mortality, increased emigration, and/or decreased recruitment (Szostek and Becker 2012; Breton *et al.* 2014).

Our main objective was to provide the first estimates of adult survival and breeding dispersal for the Barnegat Bay Common Tern population. Although this species is well-studied, few previous studies of Common Terns have simultaneously examined survival and dispersal across multiple sites using capture-mark-recapture methodology (Nisbet and Cam 2002; Breton *et al.* 2014). A secondary objective was to document the recent population decline and provide estimates of productivity. If the population is rapidly declining and breeding failure common, then we predict that emigration should be frequent, which should result in relatively low apparent survival and relatively high movement probability compared to previously published estimates from more stable locations (Nisbet and Cam 2002; Szostek and Becker 2012, 2015; Breton *et al.* 2014).

METHODS

Study Area and Data Collection

The Barnegat Bay ecosystem in New Jersey, USA, is a "shallow lagoon-type estuary" separated from the Atlantic Ocean by narrow barrier beaches (U.S. Fish and Wildlife Service 1996; Fig. 1). The ecosystem is broadly defined to include Barnegat Bay *sensu stricto*, Manahawkin Bay and Little Egg Harbor. The study area includes Common Tern colonies on three islands in Barnegat Bay proper (Little Sedge Island, 39° 59' N, 74° 04' W; Little Mike's Island, 39° 57' N, 74° 05' W; a nearby unnamed island referred to as "Ortley Cove", 39° 57' N, 74° 05' W) and two islands in Manahawkin Bay (Pettit Island, 39° 40' N, 74° 11' W, the main study site; an unnamed island referred to as "Cedar Bonnet East", 39° 39' N, 74° 11' W). The farthest distance between sites is 38 km, from Little Sedge Island to Cedar Bonnet East. Other than Little Sedge Island, the islands are tiny saltmarsh islands (< 1 ha) covered mostly with *Spartina alterniflora*, and the Common Terns nest mainly on mats of dead vegetation, especially eelgrass (*Zostera marina*; Burger and Gochfeld 1991; Palestis 2009; see Frontispiece). Little Sedge Island is the largest island (approximately 10 ha), but Common Terns nest on only a small portion of this island because of the presence of trees (hosting a mixed-species heronry) and a colony of Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls. In addition to nesting on wrack among *Spartina*, on Little Sedge many of the nests are placed on a narrow strip of sand along an edge of the island.

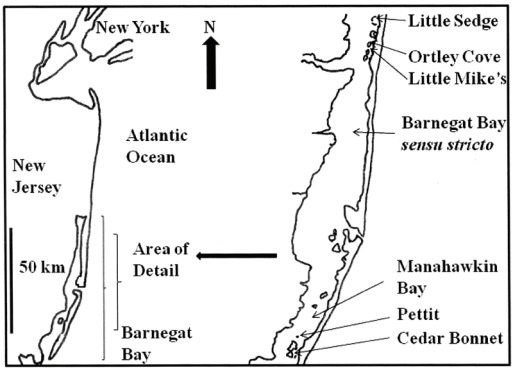

Figure 1. The location of Barnegat Bay (New Jersey, USA) and the locations of the study colonies within the area of detail.

We captured and banded Common Tern adults during incubation using walk-in traps. Traps were set at least 1 week after appearance of the first egg in a nest and were removed if an adult did not enter within approximately 20 min. Trapping of adults began in 2010 at Pettit Island and in 2011 at the other sites. Total trapping effort and captures from 2010 through 2014 are as follows: 403 captures in 976 trapping attempts (41.3% capture success). Excluding recaptures and birds captured in 2014 (which could not be recaptured within the time scale of the study), we captured 327 separate individual Common Tern adults from 2010-2013. All birds were banded with a stainless steel bird band. From 2012 through 2013, 133 previously unbanded adults were also marked with unique combinations of celluloid color bands (sealed with super glue) to allow resighting. Resighting was performed with binoculars from a boat anchored at the edge of an island, binoculars from the ground within or near a colony, and a spotting scope from the ground near a colony. Of eight color-banded birds that were recaptured, none had lost color bands. Analysis is based on both recaptures and resightings at the colonies through 2014, totaling 59 reencounters of banded birds. Birds identified more than once in the same year count as one reencounter, because the analysis is based on survival between years.

Common Tern chicks have been banded at Pettit Island since 1996, but not intensively in most years prior to 2005. Banding of chicks began in 2011 at the other sites. All captured chicks were given a stainless steel bird band. Chicks that survived more than 2 weeks and were never found dead were assumed to have fledged, thus estimates of fledging success are likely to be higher than their true values. Productivity was estimated as fledglings per breeding pair.

Analysis

We separated the analysis into two "locations": Pettit Island and other islands in Barnegat Bay. We did so for two reasons. First, Pettit Island is our main study site and the other sites do not have enough data to treat individually. At Pettit Island (including recaptures but excluding renesting in the same season), 265 adults were trapped between 2010 and 2014, compared to none at the other sites in 2010 and 134 from 2011 through

2014. Pettit Island was also visited more frequently than any other site, making resighting of color-banded adults more likely (41 observation dates from 2013-2014, compared to 52 observation dates at the other four sites combined). Second, although also declining, our data suggested that Pettit Island was more successful than the other sites, which typically experienced complete or near-complete breeding failure and thus may have differed from Pettit Island in important variables relevant to the analysis. For example, if the other colonies experienced a higher dispersal rate, then movement probability and the frequency of transience would be expected to increase and apparent survival could decrease due to permanent emigration (Lebreton *et al.* 2003; Szostek and Becker 2012).

The analysis was also separated into two time periods, reflecting apparent survival from 2010-2012 in one period and 2012-2014 in the other. This decision reflects extremely low productivity in 2012 and 2013 and declines in the number of breeding adults, which reached their lowest point in 2014. We did not test for changes in movement probability between time periods, because we could not detect movements from Pettit Island to the other sites prior to 2011 and from the other sites to Pettit Island prior to 2012.

Encounter histories of individual birds were not age-specific and began when a bird was first encountered as an adult, regardless of whether that adult was unbanded or had been banded as a chick (Spendelow *et al.* 2008). Multistate capture-recapture models (Brownie *et al.* 1993; Lebreton *et al.* 2009) were fitted to encounter histories to estimate apparent survival (S^{r}_{t}, probability that a bird at site r at time t survives and remains in the study area at time $t + 1$; note that $1 - S$ = adult mortality + permanent emigration out of the study area); recapture probability (p^{r}_{t}, probability that a live, marked bird at site r is recaptured or resighted if present at time t); and movement probability (Ψ^{rs}_{t}, among birds surviving from time t to $t + 1$, the probability that a bird at site r at time t is at site s at time $t+1$, indicating breeding dispersal).

Variables included in the various models are as follows: 1) location, a stratum term that allowed comparisons of Pettit Island with the other sites; 2) a transience term comparing those captured as adults for the first time and those with at least one prior encounter (Pradel *et al.* 1997) – this term accounts for individuals that are captured once and then have a near-zero chance of being reencountered, which may occur if first time breeders are more likely to die or permanently emigrate than experienced birds or if trap-shyness is present; 3) a variable labeled "band" to account for differences in detection probabilities of birds with metal bands only (which had to be recaptured to be identified) and those with color bands (which could be identified via resighting or recapture); 4) a direction term to test whether birds were more likely to move from other islands to Pettit Island as predicted (Lebreton *et al.* 2003; Ratcliffe *et al.* 2008) or vice-versa, or whether movement probabilities were symmetric and did not differ between locations; and 5) a time variable with two states allowed comparison of the two time intervals (2010-2012 and 2012-2014). Interactions between terms were also included in particular models, and a total of 86 models were evaluated. Reduced-parameter models were used to allow parsimonious estimation of parameters and to test the hypothesized effects of time interval and location on survival and movement probabilities (Spendelow *et al.* 2008).

Goodness-of-fit was tested with the median ĉ procedure in program MARK (Braby *et al.* 2012; Cooch and White 2014). The variance inflation factor (ĉ) was small at 1.12, suggesting a good fit of the most general model with the data (ĉ = 1.0 indicates a perfect fit), and was used in model selection and estimation of the uncertainty around parameter estimates (Spendelow *et al.* 2008; Breton *et al.* 2014). Model selection was therefore based on $QAIC_c$ (AIC corrected for overdispersion and small sample size; Burnham and Anderson 2002).

We fitted the models using RMARK (Laake and Rexstad 2014). Transition probabilities were set to zero if they were impossible, because of the lack of trapping and banding at the other sites before 2011. For example, no bird could be recorded moving from another site in 2010 to Pettit Island in 2011, because no birds were marked at the other sites in 2010. As recommended (Burnham and Anderson 2002; Arnold 2010), $QAIC_c$ scores were not used blindly but instead were balanced with plausibility and parsimony. Estimates of population parameters were based only on models in which all parameters were identifiable.

RESULTS

The number of Common Terns breeding at Pettit Island decreased steadily from about 300 breeding pairs in 2010 to approximately 80 in 2014. Fledging success was low in 2010 and 2011 (0.32 and 0.36 fledglings per pair, respectively), extremely low in 2012 and 2013 (0.08 and 0.17), and increased to 0.58 in 2014. When causes for low productivity could be identified, flooding was the most common cause. Many young chicks were lost to apparent starvation in 2012. The number of breeding pairs also decreased each year at Little Sedge Island from 2011 through 2014, from greater than 200 down to approximately 125 breeding pairs. All of the Common Terns abandoned the island in 2014 during incubation or soon after chicks hatched, and no fledglings were produced. Fledging success was also near zero in both 2012 and 2013 (0.04 and 0.03, respectively). From 2011 through 2014, the other three islands all hosted very small colonies that

typically suffered complete breeding failure due to frequent flooding. At Cedar Bonnet East, 2014 was the only year that any chicks fledged (three fledglings from 10 breeding pairs) and the largest number of breeding pairs was present in 2011 (27 pairs). Little Mike's Island and Ortley Cove produced no fledglings during the study period, and each had a maximum of about 25 breeding pairs. Little Mike's Island was almost completely abandoned in 2014.

The top five models, four of which have $\Delta QAIC_c$ values below 2.0, are shown in Table 1. The second-ranked model produced unrealistic parameter estimates for birds at sites other than Pettit Island, including an impossibly high detection probability for color-banded birds (1.00, SE = 0.00) and unusually low apparent survival (0.52 ± 0.20). It appeared that the location x band type interaction term was uninformative (Arnold 2010), and this model was not considered further. The top-ranked and third-ranked models included effects of location (Pettit Island vs. other sites) and transience on survival estimates and of presence/absence of color bands on detection probability. These two models had similar $QAIC_c$ scores and differed only in whether movement probability varied with location. Both models gave survival estimates of approximately 0.88 at Pettit Island and values of 0.70 to 0.72 at the other locations, but with relatively large standard errors (Table 2). Detection probabilities were nearly identical in the two models, and were clearly higher for color-banded birds than for birds banded only with metal bands. Model A gave a constant movement probability of 0.06, while Model C suggested more frequent movement to Pettit Island from the other sites (0.13) than the reverse (0.05). Despite the large numerical difference in these movement probabilities, they were estimated imprecisely, such that the estimates ± SE overlapped (Table 2).

Models that included the transience term performed better than those that did not account for transience: four of the top five models included transience (Table 1). The fourth-ranked model did not include a transience term and had a ΔAIC_c value below 2.0, but this model gave an unrealistically low survival estimate for the other sites (other sites: 0.45 ± 0.13; Pettit: 0.81 ± 0.13). The model ranking showed no effect of time interval on apparent survival. Only one of the five models depicted in Table 1 included variable *t*. This model had a $\Delta QAIC_c$ value > 2.0, and the time variable appeared in detection probability, not survival.

DISCUSSION

We observed a declining number of Common Tern breeding pairs on islands in Barnegat Bay, and very few fledglings were produced at most sites in most years. The decline at Little Sedge Island was more dramatic than we observed, as approximately 600 adult Common Terns were counted at Little Sedge Island in 2010 (J. Burger, unpubl. data), before our study included that site. By 2014, the numbers of breeding pairs at Little Sedge was down to approximately 125, and no fledglings were produced. The three small colonies were frequently flooded and typically experienced complete breeding failure. One of these three colonies, Little Mike's Island, hosted a productive colony of

Table 1. Selection of models for Common Tern survival and dispersal estimation based on $QAIC_c$ (AIC corrected for overdispersion and small sample size). Only the top five models are shown. Model terms are: survival (*S*), breeding dispersal (Ψ), and detection probabilities (*p*). Model variables are: location (loc), transience (trans), band type (band), time (t), direction (dir) and constant (const).

Model Name	Weight	$\Delta QAIC_c$	Parameters	Deviance
A. S(loc,trans) p(band) Ψ(const)	0.164	0.000	6	43.817
B. S(loc,trans) p(loc*band) Ψ(dir)	0.118	0.666	9	38.208
C. S(loc,trans) p(band) Ψ(dir)	0.108	0.833	7	42.570
D. S(loc) p(band) Ψ(const)	0.091	1.180	5	47.065
E. S(loc,trans) p(band,t) Ψ(const)	0.058	2.074	7	43.811

Table 2. Point estimates of Common Tern survival (S), breeding dispersal (Ψ), and detection probabilities (p) based on models A and C in Table 1. Probabilities are compared based on location (Pettit Island vs. other locations) and banding methodology (presence or absence of color bands).

Model	Parameter	Estimate	SE
A	Pettit S	0.875	0.111
	Other S	0.698	0.219
	Color banded p	0.433	0.119
	Metal only p	0.115	0.042
	Constant Ψ	0.061	0.029
C	Pettit S	0.882	0.115
	Other S	0.717	0.227
	Color banded p	0.434	0.119
	Metal only p	0.114	0.042
	Pettit to other Ψ	0.045	0.027
	Other to Pettit Ψ	0.133	0.093

approximately 250-500 breeding pairs in the 1990s (Burger 1998). In 2014, we found no evidence for breeding by Common Terns at this site, although J. Burger (unpubl. data) later counted two nests. Although the number of breeding pairs greatly decreased at Pettit Island and productivity was generally low, this site was more productive than the other colonies observed.

Apparent survival at Pettit Island was estimated at 0.88 in the two most parsimonious models. This number is within the range of previous adult survival estimates for Common Terns based on capture-recapture modeling. Most published estimates fall between approximately 0.88 and 0.92 with lower numbers for young adults or very old birds (Nisbet and Cam 2002; Szostek and Becker 2012, 2015; Zhang *et al.* 2015), and Breton *et al.* (2014) found peak survival of 0.88 in middle-aged adults. However, our estimate for the less productive sites was very low, at 0.70 to 0.72 depending on the model, but with high uncertainty around these estimates.

Immigration and emigration can be key drivers of population dynamics in terns (Tims *et al.* 2004; Ledwón *et al.* 2014; Szostek *et al.* 2014). Low apparent survival and declining numbers of breeding pairs are unlikely to actually reflect adult mortality in a long-lived species like the Common Tern, and instead probably indicate high rates of permanent emigration out of the study area. Some emigration from our sites may reflect movements to other islands within Barnegat Bay, because other colonies are present that were not included in the study. However, the declines in numbers are apparently occurring bay-wide (J. Burger, unpubl. data), suggesting high rates of emigration out of the bay. The importance of including a transience term in the models may also indicate frequent emigration. Although we predicted that apparent survival would be lower in the last two years of the study than the first two, we did not detect a difference. Studies using much larger datasets have found little evidence for temporal patterns in Common Tern adult survival rates (Szostek and Becker 2012; Breton *et al.* 2014). Spendelow *et al.* (2008) demonstrated that adult survival of Roseate Terns (*S. dougallii*) varied among years and among colonies, but found no difference in mean apparent survival between a period of population increase and a period of decrease.

Our overall estimate for movement probability was 0.061, very similar to the average value of 0.065 for Common Terns in Buzzards Bay, Massachusetts (Breton *et al.* 2014). Values reported by Breton *et al.* (2014) ranged from below 0.01 to 0.27 across years and 0.04 to 0.19 across sites, and other studies of Common Terns also show wide variation in the frequency of breeding dispersal (Nisbet 2002; Becker and Ludwigs 2004; Palestis 2014). The movement probabilities reported here for Barnegat Bay are lower than their true values. Because we had to lump the sites other than Pettit Island together, movements among these sites were treated in the models as returns. In addition, because individuals that disperse outside the study area cannot be detected, site fidelity tends to be overestimated (Coulson and Coulson 2008). Movement probability only quantifies movements between study sites, not emigration out of the study system. We predicted higher rates of movement from other sites to Pettit Island than the reverse (Lebreton *et al.* 2003; Ratcliffe *et al.* 2008), and while there was some evidence supporting this prediction, the evidence was weak.

Combining sites also means that we cannot test for differences in movement probability based on distance between colonies. Although terns can easily fly farther than the distances between colonies and characteristics of destination colonies are probably more important than distance (Spendelow *et al.* 1995; Szostek *et al.* 2014), Breton *et al.* (2014) found that dispersal among Common Tern colonies decreased as distance increased from 10 to 16 to 26 km. It does appear that if distance had any effect in our study system, it would have been very weak. The same number of movements was recorded between Pettit Island and Cedar Bonnet East (separated by 2 km, $n = 3$) as between these two sites and the farthest other site, Little Sedge Island at a distance of 36 to 38 km ($n = 3$).

Why the Common Tern population in Barnegat Bay has recently declined is not entirely clear, but the most likely key factor is sea level rise in combination with more frequent severe storms (van de Pol *et al.* 2010). These impacts of climate change reduce suitable nesting habitat and increase the frequency of flooding (van de Pol *et al.* 2010; Erwin *et al.* 2011; Nisbet *et al.* 2013). Although flooding leads to decreased productivity in Common Terns (Becker and Anlauf 1988; Palestis 2009) and not adult mortality, the number of breeding pairs can still decrease due to a combination of increased emigration and decreased recruitment (Erwin *et al.* 2011; Szostek and Becker 2012). Barnegat Bay lies within a region that has experienced elevated rates of sea level rise (Sallenger *et al.* 2012), and the Barnegat Bay saltmarsh islands appear to have lost elevation over time. For example, Little Mike's Island was previously high enough that *Phragmites* was present and provided nesting substrate (Palestis and Burger 2001), but now is covered almost entirely with *Spartina* grasses that are more resistant to saltwater inundation. Little Sedge Island was formerly a U-shaped island, but is now divided into two curved islets. Other factors have further increased the risk of flooding. Nest site competition with gulls at Little Sedge Island forces Common Terns to nest along the periphery of the island where the nests are frequently washed out. This indirect effect of gulls may have a greater impact than nest predation by the gulls (Palestis 2014). Eelgrass mats provide elevated nesting substrate that reduces losses to flooding (Palestis 2009), but coastal development has led to eutrophication of Barnegat Bay, resulting in declining eelgrass abundance (Fertig *et al.* 2013).

An increased frequency of flooding is not the only predicted impact of climate change on terns. Oceanic warming is also predicted to cause poleward shifts in the ranges of temperate seabirds, including terns, via changes in the distribution and abundance of prey (Brommer and Møller 2010; Nisbet *et al.* 2013). The geographic pattern of changing tern populations in North America is consistent with the predicted range shifts. Declining Common Tern populations have been documented in states south of New Jersey (Erwin *et al.* 2011; Nisbet *et al.* 2013), but Common Tern numbers farther north along the Atlantic coasts of the USA and Canada have been stable or increasing (Morris *et al.* 2012; Nisbet *et al.* 2013). Similarly, Roseate Terns have disappeared from the southern part of their Northwest Atlantic breeding range, but may have stabilized farther north (Nisbet *et al.* 2014). Because Common Terns breeding all along the Atlantic coast of North America mix during the nonbreeding season (Nisbet 2002; Nisbet *et al.* 2011), it is unlikely that the regional declines reflect increases in wintering mortality or carry-over effects from poor environmental conditions away from the breeding grounds (Szostek and Becker 2015).

Most of the extant Barnegat Bay colonies have been so unproductive in recent years that one may ask why Common Terns continue to nest there at all. It may be that individuals that were successful at a site in the past are slow to leave even if current reproductive success is low (Tims *et al.* 2004; Braby *et al.* 2012; Szostek *et al.* 2014). Abandonment may also be less likely in response to an unpredictable threat, such as flooding, than a predictable threat, such as predation (Burger 1982). Productivity on Barnegat Bay saltmarsh islands had long been highly vari-

able across years, such that a colony could produce no fledglings in one year and more than one fledgling per breeding pair in the next year (Burger and Gochfeld 1991). It is only recently that the Common Terns have experienced consistently poor reproductive success here.

Without management, the Barnegat Bay Common Tern population will likely continue to decline. Creation of eelgrass mats or other elevated substrate on a larger scale than currently performed should help reduce losses to flooding (Palestis 2009, 2014). Other possible management actions include placement of signs near the colonies, creation of artificial islands or restoration of unoccupied islands, and identification and removal of specialist nest predators (Nisbet 2002; Palestis 2014). However, if the current decline results from long-term changes in climate, it may be impossible to reverse.

ACKNOWLEDGMENTS

We thank Jim Nichols for invaluable advice on capture-recapture modeling, Joanna Burger and Chris Davis for providing unpublished data, and Jeff Spendelow and Ian Nisbet for discussion. Joanna Burger, Jim Nichols, Ian Nisbet, and two anonymous referees provided comments on the manuscript. Funding was provided by the John Deane Fund for Environmental Studies and Wagner College. We also thank Kaitlin Eppinger, Mark Fealey, Margaret Shaw and Alexandria Zummo for assistance in the field, and Richard Buzby and the Edwin B. Forsythe National Wildlife Refuge for allowing our fieldwork on their properties. Trapping and banding operations were conducted under BGP's Federal bird-banding permit (no. 23100) and scientific collecting permits from the New Jersey Division of Fish and Wildlife. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175-1178.

Becker, P. H. and A. Anlauf. 1988. Nest site choice and breeding success of marsh nesting Common Terns (*Sterna hirundo*). II. Flooding. Ökologie der Vögel 10: 45-58.

Becker, P. H. and J.-D. Ludwigs. 2004. *Sterna hirundo* Common Tern. Birds of the Western Palearctic Update 6: 91-137.

Braby, J., S. J. Braby, R. J. Braby and R. Altwegg. 2012. Annual survival and breeding dispersal of a seabird adapted to a stable environment: implications for conservation. Journal of Ornithology 153: 809-816.

Breton, A. R., I. C. T. Nisbet, C. S. Mostello and J. J. Hatch. 2014. Age-dependent breeding dispersal and adult survival within a metapopulation of Common Terns *Sterna hirundo*. Ibis 156: 534-547.

Brommer, J. E. and A. P. Møller. 2010. Range margins, climate change, and ecology. Pages 275-294 *in* Effects of Climate Change on Birds (A. P. Møller, W. Fiedler and P. Berthold, Eds.). Oxford University Press, New York, New York.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173-1187.

Burger, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). Auk 99: 109-115.

Burger, J. 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of Common Terns. Condor 100: 528-534.

Burger, J. and M. Gochfeld. 1991. The Common Tern: its breeding biology and social behavior. Columbia University Press, New York, New York.

Burger, J., C. D. Jenkins, Jr., F. Lesser and M. Gochfeld. 2001. Status and trends of colonially-nesting birds in Barnegat Bay. Journal of Coastal Research SI-32: 197-211.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, New York.

Cooch, E. and G. White. 2014. Goodness of fit testing. Pages 5.1-5.41 *in* Program MARK: a Gentle Introduction, 12th ed. (E. Cooch and G. C. White, Eds.). Colorado State University, Fort Collins, Colorado. http://www.phidot.org/software/mark/docs/book/, accessed 11 March 2015.

Coulson, J. C. and B. A. Coulson. 2008. Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. Ibis 150: 288-299.

Erwin, R. M., J. Galli and J. Burger. 1981. Colony site dynamics and habitat use in Atlantic coast seabirds. Auk 98: 550-561.

Erwin, R. M., D. F. Brinker, B. D. Watts, G. R. Costanzo and D. D. Morton. 2011. Islands at bay: rising seas, eroding islands, and waterbird habitat loss in Chesapeake Bay (USA). Journal of Coastal Conservation 15: 51-60.

Fertig, B., M. J. Kennish and G. P. Sakowicz. 2013. Changing eelgrass (*Zostera marina* L.) characteristics in a highly eutrophic temperate coastal lagoon. Aquatic Botany 104: 70-79.

Laake, J. and E. Rexstad. 2014. RMark – an alternative approach to building linear models in MARK. Pages C.1-C.113 *in* Program MARK: a Gentle Introduction, 12th ed. (E. Cooch and G. C. White, Eds.). Colorado State University, Fort Collins, Colorado.

http://www.phidot.org/software/mark/docs/book/, accessed 11 March 2015.

Lebreton, J. D., J. E. Hines, R. Pradel, J. D. Nichols and J. A. Spendelow. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. Oikos 101: 253-264.

Lebreton, J.-D., J. D. Nichols, R. J. Barker, R. Pradel and J. A. Spendelow. 2009. Modeling individual animal histories with multistate capture-recapture models. Advances in Ecological Research 41: 87-173.

Ledwón, M., J. Betleja, T. Stawarczyk and G. Neubauer. 2014. The Whiskered Tern *Chlidonias hybrida* expansion in Poland: the role of immigration. Journal of Ornithology 155: 459-470.

Morris, R. D., C. Pekarik and D. J. Moore. 2012. Current status and abundance trends of Common Terns breeding at known coastal and inland nesting regions in Canada. Waterbirds 35: 194-207.

Nisbet, I. C. T. 2002. Common Tern (*Sterna hirundo*). No. 618 *in* The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.

Nisbet, I. C. T. and E. Cam. 2002. Test for age-specificity in survival of the Common Tern. Journal of Applied Statistics 29: 65-83.

Nisbet, I. C. T., M. Gochfeld and J. Burger. 2014. Roseate Tern (*Sterna dougallii*). No. 370 *in* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. http://bna.birds.cornell.edu/bna/species/370, accessed 20 February 2015.

Nisbet I. C. T., R. R. Veit, S. A. Auer and T. P. White. 2013. Marine birds of the eastern United States and the Bay of Fundy: distribution, numbers, trends, threats, and management. Nuttall Ornithological Monographs No. 29, Nuttall Ornithological Club, Cambridge, Massachusetts.

Nisbet, I. C. T., C. S. Mostello, R. R. Veit, J. W. Fox and V. Afanasyev. 2011. Migrations and winter quarters of five Common Terns tracked using geolocators. Waterbirds 34: 32-39.

Palestis, B. G. 2009. Use of artificial eelgrass mats by saltmarsh-nesting Common Terns (*Sterna hirundo*). In Vivo 30(3): 11-16.

Palestis, B. G. 2014. The role of behavior in tern conservation. Current Zoology 60: 500-514.

Palestis, B. G. and J. Burger. 2001. Development of Common Tern (*Sterna hirundo*) sibling recognition in the field. Bird Behavior 14: 75-80.

Pradel, R., J. E. Hines, J.-D. Lebreton and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics 53: 60-72.

Ratcliffe N., S. Newton, P. Morrison, O. Merne, T. Cadwallender and M. Frederiksen. 2008. Adult survival and breeding dispersal of Roseate Terns within the northwest European metapopulation. Waterbirds 31: 320-329.

Sallenger, A. H., Jr., K. S. Doran and P. A. Howd. 2012. Hotspot of accelerated sea-level rise on the Atlantic coast of North America. Nature Climate Change 2: 884-888.

Spendelow, J. A., J. E. Hines, J. D. Nichols, I. C. T. Nisbet, G. Cormons, H. Hays, J. J. Hatch and C. S. Mostello. 2008. Temporal variation in adult survival rates of Roseate Terns during periods of increasing and declining populations. Waterbirds 31: 309-319.

Spendelow, J. A., J. D. Nichols, I. C. T. Nisbet, H. Hays, G. D. Cormons, J. Burger, C. Safina, J. E. Hines and M. Gochfeld. 1995. Estimating annual survival and movement rates of adults within a metapopulation of Roseate Terns. Ecology 76: 2415-2428.

Szostek, K. L. and P. H. Becker. 2012. Terns in trouble: demographic consequences of low breeding success and recruitment on a Common Tern population in the German Wadden Sea. Journal of Ornithology 153: 313-326.

Szostek, K. L. and P. H. Becker. 2015. Survival and local recruitment are driven by environmental carry-over effects from the wintering area in a migratory seabird. Oecologia 178: 643-657.

Szostek, K. L., M. Schaub and P. H. Becker. 2014. Immigrants are attracted by local pre-breeders and recruits in a seabird colony. Journal of Animal Ecology 83: 1015-1024.

Tims, J., I. C. T. Nisbet, M. S. Friar, C. Mostello and J. J. Hatch. 2004. Characteristics and performance of Common Terns in old and newly-established colonies. Waterbirds 27: 321-332.

U.S. Fish and Wildlife Service. 1996. Significant habitats and habitat complexes of the New York Bight watershed. U.S. Department of the Interior, Fish and Wildlife Service, Southern New England – New York Bight Coastal Ecosystems Program, Charlestown, Rhode Island. http://nctc.fws.gov/resources/knowledge-resources/pubs5/begin.htm, accessed 15 January 2015.

van de Pol, M., B. J. Ens, D. Heg, L. Brouwer, J. Krol, M. Maier, K.-M. Exo, K. Oosterbeek, T. Lok, C. M. Eising and K. Koffijberg. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds?. Journal of Applied Ecology 47: 720-730.

Zhang, H., M. Rebke, P. H. Becker and S. Bouwhuis. 2015. Fitness prospects: effects of age, sex and recruitment age on reproductive value in a long-lived seabird. Journal of Animal Ecology 84: 199-207.