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Spatial and Temporal Changes in Nesting Behavior by Black Skimmers (*Rynchops niger*) in New Jersey, USA, from 1976-2019

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Abstract.—Sea level rise from anthropogenic climate change threatens waterbird species worldwide. In New Jersey, USA, one such waterbird, the Black Skimmer (*Rynchops niger*), uses both salt marsh islands and beaches for nesting colony sites. Both habitats vary in flood risk, with salt marsh islands typically being more vulnerable especially in the face of sea level rise. Given that sea level has increased in the mid-Atlantic region over the past four decades, we hypothesized that Black Skimmers have shifted their colonies from salt marshes to beaches, and that this change has led to an increase in coexistence with Least Terns (*Sternula antillarum*). We analyzed 44 years of seabird population census data from New Jersey and found that the probability that a Black Skimmer colony was located on a salt marsh island, as opposed to a beach, significantly declined over the survey period. Additionally, the probability of coexistence with Least Terns significantly increased. Such climate change driven population shifts of endangered species may have significant consequences for their conservation in human modified systems where habitat is already limiting. *Received 18 December 2020, accepted 15 January 2021.*

Key words.—Beach nesting birds, climate change, coexistence, endangered species, habitat loss, Least Tern, interspecific interactions, sea level rise, *Sternula antillarum*

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The effects of anthropogenic climate change have been documented at all levels of biological organization, from genetics (Kovach *et al.* 2012) to ecosystem structure (Saatchi *et al.* 2013). Among ecosystems, coastal habitats are particularly vulnerable to climate change because their formation, structure, and persistence depends on interactions between sea level, land elevation, primary production, and sedimentation (Morris *et al.* 2002). Species that utilize habitats in coastal areas will need to adapt, migrate to track their current climate, or both, in order to persist into the future (Parmesan 2006; Loarie *et al.* 2009).

Mean global sea level has increased by 0.19 m from 1901 - 2010 and is predicted to increase as much as an additional 0.82 m by the end of this century (Pachauri *et al.* 2015). These changes have been documented more locally, with tidal gauge data across the mid-Atlantic and Northeast regions showing trends towards higher relative sea level (Erwin *et al.* 2006). Salt marsh ecosystems will be threatened if the rate of sea level encroachment exceeds that of buffering processes such as sedimentation (Reed 1990; Morris *et al.* 2002). During previous periods of sea level rise, many salt marshes retreated inland (Adam 2002); however, static human coastal development may act as a barrier and squeeze ecosystems, resulting in less favorable habitat available for marsh-dependent wildlife (Doody 2013; Pontee 2013).

Sea level rise will negatively impact many coastal waterbird species through direct mortality of nests and young (Pol *et al.* 2010), as well as indirectly through habitat loss (Hunter *et al.* 2015). Two such waterbirds, Black Skimmer (*Rynchops niger*) and Least Tern (*Sternula antillarum*), nest colonially in coastal habitats across eastern North America. Like many waterbirds, both species were negatively impacted by egg hunting and the millinery trade in the 19^{th} century and were nearly extirpated from New Jersey, USA, (Boyle 2011; Gochfeld *et al.* 2020; Thompson *et al.* 2020). Population recovery (USFWS 1996) was short lived, as intensified coastal development and recreation of the mid-20^{th} century caused further declines (Gochfeld et al. 2020; Thompson et al. 2020). Both spe-

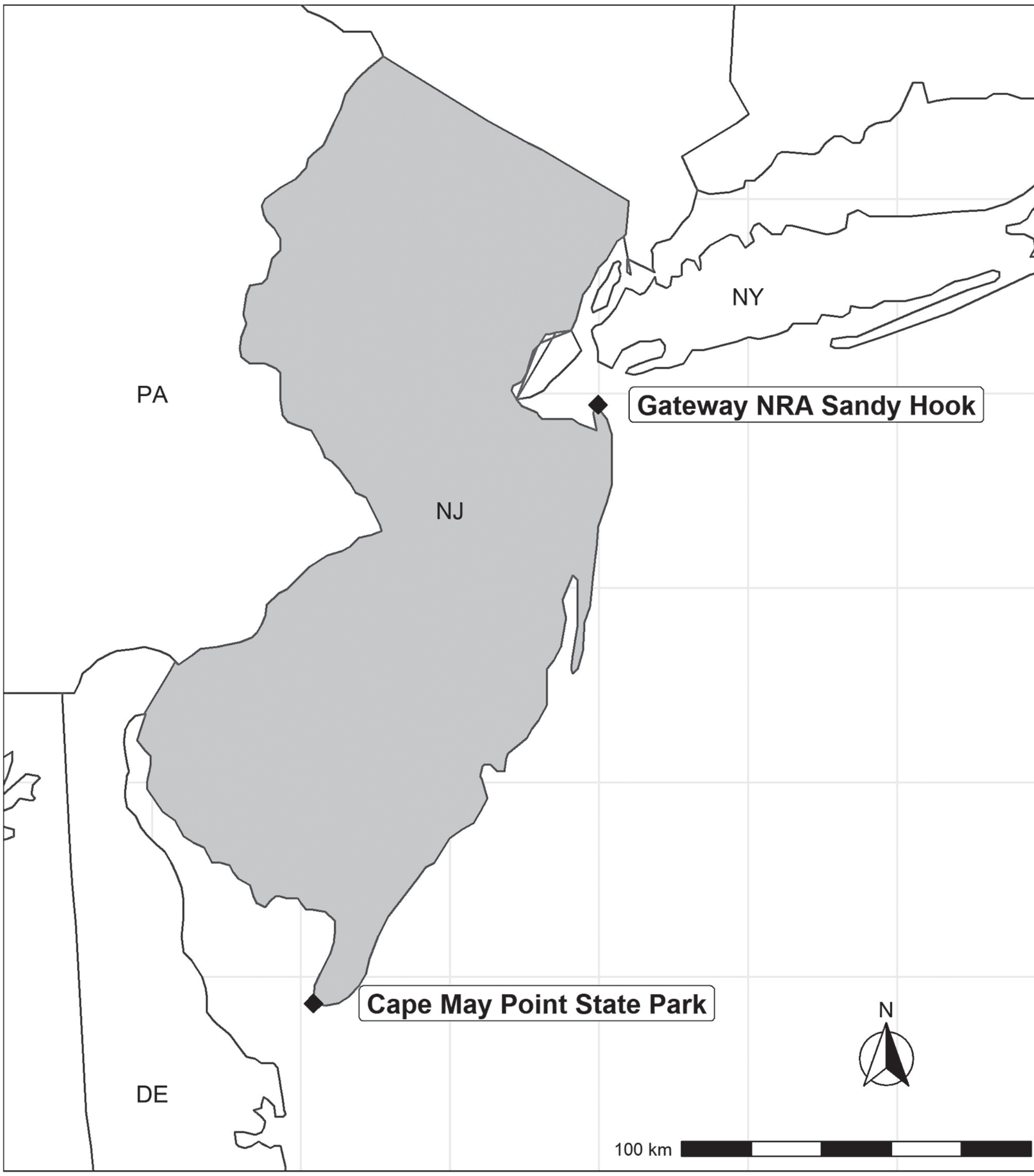

Figure 1. Study area for Black Skimmer (*Rynchops niger*) and Least Tern (*Sternula antillarum*) monitoring from 1976-2019, New Jersey, USA. Monitoring occurred along the entire Atlantic coast from the Sandy Hook Unit of Gateway National Recreation Area to Cape May Point State Park.

cies are listed as state endangered in New Jersey (Davis and Heiser 2020).

At the time of state listing, New Jersey's breeding population of Black Skimmers formed colonies in salt marsh habitat with greater frequency than populations in nearby geographic regions (Erwin 1980). Researchers suggested that the greater development and disturbance of beaches in New Jersey, as compared to other regions at the time, had pushed Black Skimmers out of their preferred beach habitat (Erwin 1980; Erwin *et al.* 1981; Burger 1984; Burger and Gochfeld 1990). In recent years it has appeared, however; that Black Skimmers have been shifting their spatial distribution to include more beach nesting colonies. Our objective was to determine whether there was a significant change in the distribution of

Table 1. Summary of Black Skimmer (*Rynchops niger*) and Least Tern (*Sternula antillarum*) monitoring efforts in New Jersey, USA, 1976-2019. Annual counts represent maximums summed across each nesting colony. In New Jersey, Black Skimmers form nesting colonies in both salt marsh island and beach habitat, whereas Least Terns form nesting colonies almost exclusively in beach habitat. Therefore, only the Black Skimmer data is separated by habitat.

Year	Number of Black Skimmer Colonies		Annual Max. Count of Adult Black Skimmers		Number of Least Tern Colonies	Annual Max. Count of Adult Least Terns
	Beach	Marsh	Beach	Marsh		
1976	3	11	1,190	1,032	22	1,368
1977	2	11	725	1,312	18	938
1978	2	11	390	1,561	25	1,879
1979	2	18	87	1,889	23	1,806
1980	2	12	744	951	19	2,095
1981	2	11	930	616	18	2,049
1982	3	8	1,156	436	16	2,459
1983	4	6	1,506	175	17	2,132
1984	3	8	1,103	607	19	2,495
1985	6	14	1,015	653	16	2,277
1986	5	11	901	1,095	16	2,179
1987	3	9	886	856	20	2,931
1988	1	16	730	1,090	15	1,862
1989	2	7	1,152	1,276	15	2,630
1990	2	7	808	1,145	20	2,220
1991	3	11	540	1,002	14	2,104
1992	3	9	825	831	17	1,627
1993	3	5	1,940	857	15	1,785
1994	2	7	878	1,656	17	1,806
1995	3	11	1,293	1,431	16	2,177
1996	4	10	1,404	1,535	19	1,310
1997	1	7	1,391	1,239	14	2,032
1998	2	8	1,880	837	14	1,870
1999	2	6	2,181	440	16	1,966
2000	4	6	2,368	360	21	1,667
2001	2	5	2,082	673	21	1,510
2002	5	7	1,596	590	26	1,936
2003	4	6	2,314	578	27	2,610
2004	3	4	1,323	388	26	2,024
2005	2	5	1,904	1,094	24	1,569
2006	1	5	704	2,593	25	1,943
2007	0	6	0	2,165	25	2,332
2008	2	8	1,968	2,738	15	1,177
2009	2	3	2,543	584	18	1,601
2010	4	4	2,314	404	21	1,812
2011	4	4	1,937	197	21	1,784
2012	5	5	2,887	198	23	1,834
2013	6	5	2,620	584	20	1,901
2014	3	6	2,069	222	21	1,602
2015	5	5	3,187	70	20	1,264
2016	4	6	2,019	144	26	1,713
2017	4	5	2,518	293	25	1,659
2018	4	1	2,422	83	17	1,912
2019	4	0	2,114	0	20	1,825

Black Skimmer nesting colonies between salt marshes and beaches in New Jersey since 1976. We hypothesized that the frequency of beach nesting behavior has increased over time. Further, given the limited beach habitat availability, we expected a concurrent increase in the frequency of coexistence between Black Skimmers and Least Terns.

METHODS

Study Area

Our study area included all salt marshes, barrier islands, and mainland beaches in New Jersey , USA, from a northern extent of the Sandy Hook Unit of the Gateway National Recreation Area (40° 28′ N, 74° 00′ W) to a southern extent of the Cape May Point State Park (38° 55′ N, 74° 57′ W; Fig. 1). Much of this coastal region is highly developed and urbanized. Beach habitat is generally made of sandy substrates and vegetation at a low density. Common beach plants include American beachgrass (*Ammophila breviligulata*) and American sea rocket (*Cakile edentula*). In contrast, salt marshes in New Jersey have high vegetation density. Common salt marsh plants include saltgrass (*Distichlis spicata*), saltmeadow cordgrass (*Spartina patens*), and smooth cordgrass (*Spartina alternaflora*).

Data Collection.

We acquired Black Skimmer and Least Tern monitoring data from the New Jersey Department of Environmental Protection, Division of Fish and Wildlife, Endangered and Nongame Species Program (NJENSP, unpubl. data). Yearly population censuses of Least Tern and Black Skimmer colonies have been conducted each breeding season since 1976 by NJENSP staff and contractors (C. Davis, pers. commun.). Census data from 1976-2002 reliably includes the locations of active nesting sites and maximum number of adults counted during the breeding season; however, individual survey records were not always retained (C. Davis, pers. commun.). In contrast, individual survey records exist starting in 2003 (NJENSP, unpubl. data). At the beginning of the breeding season most possible nesting areas were visited to determine where Black Skimmers and Least Terns were establishing colonies. These locations were visited on a bi-weekly schedule from approximately 10 May-15 September. Colony surveys involved trained staff and contractors of NJENSP counting the number of adults present while walking the perimeter of each colony (C. Davis, pers. commun.). Years when Black Skimmer nesting was prolonged past 15 September additional survey periods were added (NJENSP, unpubl. data). Beach colonies were typically surveyed more frequently than salt marsh colonies due to the greater threat of human disturbance, limited staff and resources, and the difficulty of accessing salt marsh islands (C. Davis, pers. commun.).

Perimeter surveys were supplemented with annual helicopter surveys of almost all Atlantic coast waterbird habitat in New Jersey (C. Davis, pers. commun.). Additionally, during the earlier years of this monitoring effort (particularly 1976-1982), more invasive ground surveys were conducted where researchers entered the nesting colonies to count active nests and follow nest success (Erwin 1980; Erwin et al. 1981; Burger 1984). It is unclear if the annual counts from this period were drawn from multiple survey types. Therefore, we restricted our data analyses to the colony, as opposed to individual, level. While surveys were not designed to estimate colony detection probabilities, we are confident that due to the geographic conditions of this region (highly developed beaches with few available nesting areas), as well as the survey extent (full coverage of coastal habitats with helicopter surveys), that very few, if any, entire colonies went undetected.

Other species of terns, including Common (*Sterna hirundo*), Royal (*Thalasseus maximus*), and Gull-billed (*Gelochelidon nilotica*) terns, occasionally nested in multispecies colonies with Black Skimmers and Least Terns. However, regular counts were not always conducted of these species and therefore they could not be included in analyses. In most instances where this occurred, the numbers of these species were much smaller than those of both Black Skimmers and Least Terns.

Statistical Analyses

We used logistic regression models to estimate both the probability that a Black Skimmer colony was on a salt marsh island and the probability of coexistence between Black Skimmers and Least Terns. We considered both naturally occurring islands as well as those modified by dredge materials to be "salt marsh islands" due to the difficulty of determining which islands had been modified across the 44 yrs. We classified colonies as beach or salt marsh island based on our experience conducting field work in this region as well as through consultation with biologists from NJENSP. We define coexistence as the co-occurrence of at least one pair of each species in the same colony. We observed instances in which Black Skimmers and Least Terns were nesting in the same area but partitioned their nesting sites such that one part of a colony may have more of one species than would be expected with random mixing. Such instances were still considered coexistence due to the regular interspecific interactions that characterized these colonies. For the first model, we treated habitat as a binary variable for whether a Black Skimmer colony was on a salt marsh island (1) or on a beach (0). For the second model, we treated coexistence as a binary variable for whether a colony included Least Terns (1) or

Table 2. Summary of posterior distributions for the model of the probability of salt marsh island nesting in the New Jersey, USA, population of Black Skimmers (*Rynchops niger*) 1976-2019.

			Quantile	
Parameter	Mean	SD	2.5%	97.5%
Intercept	1.67	0.21	1.26	2.09
Year coefficient	-0.039	0.0082	-0.055	-0.023

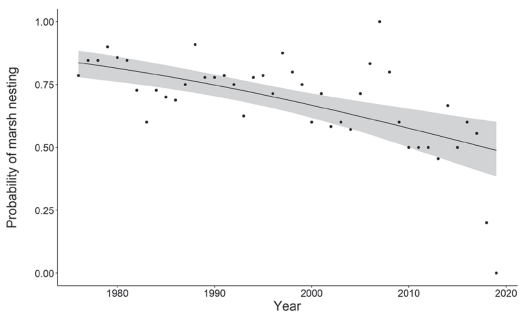

Figure 2. Predictions for the probability of marsh nesting for Black Skimmer (*Rynchops niger*) colonies in New Jersey, USA, 1976-2019, from a Bayesian logistic regression model based on nesting survey data. Dots represent raw data, the thick black line represents mean estimates, and the shaded gray area represents 95% Bayesian credible intervals.

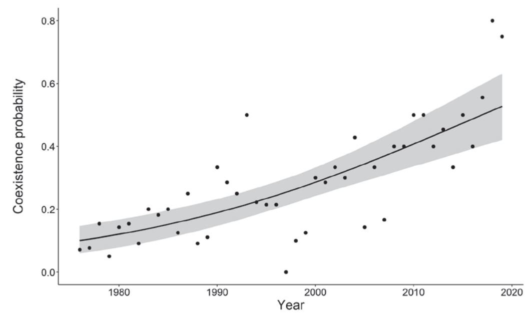

Figure 3. Predictions for the probability of coexistence between Black Skimmers (*Rynchops niger*) and Least Terns (*Sternula antillarum*) in seabird colonies in New Jersey, USA, 1976-2019, from a Bayesian logistic regression model based on nesting survey data. Dots represent raw data, the thick black line represents mean estimates, and the shaded gray area represents 95% Bayesian credible intervals.

only Black Skimmers (0). We included year as a covariate in both models, and we generated predicted values for the probability of coexistence between Black Skimmers and Least Terns from 1976 to 2019.

All analyses were conducted in R 3.4.2 (R Core Team 2017). We analyzed logistic regression models in a Bayesian framework by specifying models in the BUGS language, with posterior distributions of parameters of interest estimated using Markov Chain Monte Carlo (MCMC) simulation with Gibbs sampling as implemented in JAGS v. 4.3.0 (Plummer 2017) called from program R via the package 'jagsUI' (Kellner 2019). We checked for convergence of 3 parallel MCMC chains per model by visually inspecting the trace plots and by using the Brooks–Gelman–Rubin diagnostic ($\hat{R}$; Gelman *et al.* 2004); we considered convergence to be achieved at $\hat{R} < 1.1$ for all parameters. We deemed covariates to be important predictors if the 95% Bayesian credible intervals (BCI) on the regression coefficient did not overlap zero (Kuo and Mallick 1998; Link and Barker 2006).

Results

We acquired data from NJENSP that included approximately 3,000 surveys at over 74 nesting sites for Least Terns and Black Skimmers from 1976-2019 for all coastal marshes and beaches in New Jersey (NJENSP, unpubl. data). From 2003-2019 (the years where individual survey records were available), beach nesting sites were surveyed an average of 6.6 times (SD = 2.1) each season, whereas salt marsh nesting sites were surveyed an average of 4.9 times (SD = 2.1) each season. Across all years and sites, we found that the number of adult Black Skimmers counted was highest in 2008 with 4,670 individuals and lowest in 1991 with 1,620 individuals and the number of adult Least Terns counted was highest in 1987 with 2,931 individuals and lowest in 1977 with 938 individuals (Table 1). Based on the 95% BCI on the regression coefficient, the probability of a Black Skimmer colony being in marsh habitat decreased with time (Table 2). The probability of a colony being in marsh habitat was 1.71 times more likely in 1976 (mean = 0.837, 95% BCI = 0.778-0.884) than 2019 (mean = 0.487, 95% BCI = 0.379-0.596; Fig. 2). Similarly, the probability of coexistence between Black Skimmers and Least Terns increased with time, based on the 95% BCI on the regression coefficient (Table 3). The probability of coexistence was 5.46 times

Table 3. Summary of posterior distributions for the model of the probability of coexistence with Least Terns (*Sternula antillarum*) in Black Skimmer (*Rynchops niger*) colonies in New Jersey, USA, 1976-2019.

			Quantile	
Parameter	Mean	SD	2.5%	97.5%
Intercept	-2.25	0.24	-2.73	-1.78
Year coefficient	0.055	0.0091	0.037	0.074

higher in 2019 (mean = 0.530, 95% BCI = 0.425-0.633) than 1976 (mean = 0.097, 95% BCI = 0.061-0.144; Fig. 3).

DISCUSSION

Surveys over 44 years show dramatic changes in the distribution of Black Skimmer colonies in New Jersey which has important consequences for the management and recovery of this endangered species. Historic data suggests that Black Skimmers in New Jersey were originally beach nesters and pushed into salt marshes due to human domination of beaches in the mid-20th century (Erwin 1980; Erwin *et al.* 1981). While conservation efforts over the past four decades have protected key beach nesting areas, beach use for recreational purposes has increased dramatically (USFWS 1996). It is notable that in recent years, Black Skimmers have established nesting colonies on multiple unprotected public beaches with high human use. Consequently, the shift of the Black Skimmer population back to beaches likely signals major changes in the marshes that have deleterious effects greater than that of the direct human disturbance on beaches.

There is already evidence that large scale climate change impacts—such as the increased storm severity related to Hurricane Sandy (Lackmann 2015)—has reduced the amount of suitable salt marsh nesting habitat for Black Skimmers in New Jersey (Maslo *et al.* 2019). However, the smaller changes of natural tide cycles may be no less important. For example, among Saltmarsh Sparrows (*Ammodramus caudacutus*) in the northeastern United States, nest success was significantly linked to tide height relative to nest elevation and the frequency of regular flood events (Bayard and Elphick 2011). Unlike Saltmarsh Sparrows, the recent invasion of Black Skimmers to salt marsh habitat means they lack a long-term evolutionary relationship with the dynamic patterns of salt marshes and may be poorly suited to adapt to rising sea levels. Our analyses suggest that rather than adapt to changing conditions in the salt marshes, Black Skimmers in New Jersey are returning to beaches.

The resulting increase in coexistence with Least Terns hints at the most significant consequence of our findings: the concentration of Black Skimmers into habitats used by other state and federally listed beach nesting birds. Habitat suitability modeling based on the use of salt marsh islands by Black Skimmers showed that much of the adequate nesting area would be available to them without current conservation efforts (Maslo *et al.* 2018). In sharp contrast, current conservation efforts increase the available nesting habitat for Least Terns by over 211 times (Maslo *et al.* 2018). This suggests that as Black Skimmers become more reliant on beaches for nesting, they will also become more reliant on conservation work. Further, as Black Skimmers and Least Terns overlap in space more frequently, any single disturbance now has the potential to negatively impact more individuals of more listed species.

Understanding the mechanisms that drive local changes in the distribution of endangered species is critical for informing population recovery efforts in a rapidly changing world. The movement of Black Skimmers from marsh islands to beach habitat, which is more developed and has greater human disturbance, presents novel management challenges. While much of the conservation management infrastructure is already in place on beaches, owing to other listed species, it is unclear how coexistence influences the population dynamics of these two species and what the long-term impacts will be. Future work should compare the population dynamics between single species and multi-species colonies of both Black Skimmers and Least Terns to better understand the implications that the changes documented in this paper present to recovery.

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