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RESEARCH ARTICLE

How will sea-level rise affect threats to nesting success for Seaside Sparrows?

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ABSTRACT

Sea-level rise (SLR) threatens the nesting success of salt marsh breeding birds, including Seaside Sparrows (*Ammodramus maritimus*), by increasing the magnitude and frequency of extreme high tides that flood nests. However, the threat to nesting success from tidal flooding is intertwined with that of predation because the threats are connected through a trade-off along a nest height gradient. Therefore, to understand the risk to nesting success from SLR, it is necessary to consider predation threats simultaneously. I used an individual-based model of Seaside Sparrow nesting behavior, calibrated using empirical data on nest success rates and nest-site selection behaviors, to project the effects of SLR conditions on the relative importance of predation and flooding threats in affecting nesting success, and to investigate whether nest-site selection along a gradient of nest height can modulate the risk of SLR. Outputs from the model revealed that present-day levels of predation risk pose as great a risk to nesting success as tidal flooding under simulated SLR conditions with extreme flooding risks. Nest success rates could become very low under extreme SLR scenarios, especially when predation risk is very high. The risks of failure from either threat are linked through nest-site selection behaviors: In high-predation-risk seasons, failure probability from flooding is greater than it would be under lower predation risk, due to the predation avoidance behavior of nesting closer to the ground. Therefore, management actions to reduce the risk of excessive failures from predation could reduce the risk of failures from both threats—a potentially useful management strategy, given that controlling predation is more tractable than controlling increased flooding from SLR at a local level.

Keywords: Ammodramus maritimus, individual based model, nest success, predation, sea-level rise, Seaside Sparrow

¿Cómo afectará el aumento del nivel del mar las amenazas al éxito de anidación de *Ammodramus maritimus*?

RESUMEN

El aumento del nivel del mar (ANM) amenaza el éxito de anidación de las aves que anidan en marismas, incluyendo a *Ammodramus maritimus*, mediante el incremento de la magnitud y la frecuencia de las mareas altas extremas que inundan los nidos. Sin embargo, la amenaza al éxito de anidación por las inundaciones mareales está entrelazada con la de depredación, debido a que las dos amenazas están conectadas a través de una solución de compromiso a lo largo de un gradiente de altura del nido. Por ende, para entender el riesgo del éxito de anidación por el ANM, es necesario considerar simultáneamente los riesgos de depredación. Utilicé un modelo de base individual del comportamiento de anidación de *A. maritimus*, calibrado con datos empíricos de tasas de éxito de anidación y de comportamiento de selección del sitio de anidación, para proyectar las consecuencias de las condiciones del ANM sobre la importancia relativa de las amenazas de depredación e inundación en el éxito de anidación, y para investigar si la selección del sitio de anidación a lo largo de un gradiente de altura del nido puede modular el riesgo del ANM. Los resultados del modelo revelaron que los niveles actuales del riesgo de depredación representan un riesgo tan grande al éxito de anidación como la inundación mareal bajo condiciones simuladas de ANM con riesgos extremos de inundación. Las tasas de éxito de anidación podrían volverse muy bajas ante escenarios extremos de ANM, especialmente cuando el riesgo de depredación es muy alto. Los riesgos de fracaso derivados de cada amenaza están vinculados a través de los comportamientos de selección del sitio de anidación: en las estaciones de alto riesgo de depredación, la probabilidad de fracaso por inundación es mayor de lo que sería frente a un bajo riesgo de depredación debido al comportamiento de evasión de la depredación anidando más cerca del suelo. Por ende, las acciones de manejo para reducir el riesgo de fracasos excesivos causados por la depredación podrían reducir el riesgo de fracasos derivados de ambas amenazas– una estrategia de manejo potencialmente útil, ya que el

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control de la depredación es más manejable que el control del aumento de la inundación debido al ANM a nivel local.

Palabras clave: Ammodramus maritimus, aumento del nivel del mar, depredación, éxito de anidación, modelo de base individual

INTRODUCTION

Sea-level rise (SLR) poses a conservation problem for many salt marsh bird species, through both direct habitat loss (Kern and Shriver 2014, Hunter et al. 2016a) and decreasing population productivity rates caused by more frequent and severe tidal flooding of nesting sites (van de Pol et al. 2010, Bayard and Elphick 2011, Field et al. 2016). Most salt marsh breeding birds have adaptations to avoid tidal flooding, including nesting at higher elevations and within tall vegetation (Gjerdrum et al. 2005, Valdes et al. 2016) and synchronizing their nesting cycle to the tidal cycle (Marshall and Reinert 1990, Reinert 2006, Shriver et al. 2007). However, such adaptations may not be sufficient to maintain nest success rates in the face of rapid changes to the tidal regime caused by SLR, leading to widespread concern regarding population viability over the coming decades (Erwin et al. 2006, Bayard and Elphick 2011, Kern and Shriver 2014, Field et al. 2016).

In addition to tidal flooding, salt marsh breeding birds contend with a large diversity of nest predators, including other birds such as Fish Crows (*Corvus ossifragus*), Boat-tailed Grackles (*Quiscalus major*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Marsh Wrens (*Cistothorus palustris*) (Post 1981, E. A. Hunter personal observation) and mammals such as northern raccoons (*Procyon lotor*), American mink (*Neovison vison*), and marsh rice rats (*Oryzomys palustris*) (Post 1981, Kern 2015, E. A. Hunter personal observation). Salt marsh breeding sparrows—Seaside Sparrows (*Ammodramus maritimus*), Saltmarsh Sparrows (*A. caudacutus*), and Nelson's Sparrows (*A. nelsoni*)—may be particularly vulnerable to nest predation, given their small size (compared to rails and shorebirds) and open-cup nests (compared, e.g., to dome nests of Marsh Wrens). Because salt marsh breeding sparrows' nests are vulnerable to both predation and tidal flooding, we might expect nest success rates to be very low, but rates are similar to those of inland-breeding relatives that only contend with predation, possibly due to a trade-off between nest sites that reduce predation risk and those that reduce flooding (Greenberg et al. 2006, Hunter et al. 2016b).

Seaside Sparrows (which occur in salt marshes along the Gulf and Atlantic coasts of North America from southern Texas to southern Maine) experience this trade-off in risks to nest success and have behavioral adaptations to address it (Figure 1). Seaside Sparrows can reduce chances of nest loss to either threat by shifting their nest-site placement along a gradient of nest height: lower nests are more likely to be flooded but less likely to be depredated, and vice versa (Greenberg et al. 2006, Hunter et al. 2016b). Some Seaside Sparrow populations have apparently adopted 2 different strategies to avoid these threats. In seasons with high predation risk (seasons with higher predator abundances or activity in nesting habitat), Seaside Sparrows place nests at lower heights for the duration of the season and do not respond to individual nest losses from predation (Hunter et al. 2016b). Conversely, following an experienced loss from tidal inundation, Seaside Sparrows place subsequent nests higher in vegetation (Hunter et al. 2016b). Seaside Sparrows have presumably adopted these behaviors to cope with threat levels that the species has experienced in the recent past. However, when climate change causes more losses from tidal flooding as sea levels rise and extreme high tides become more frequent (van de Pol et al. 2010, Bayard and Elphick 2011), will these behaviors still be adaptive? Will flooding become a greater threat to nesting success than predation? And what will the additional threat of SLR mean for populations that are already experiencing high predation rates?

I explore these questions using a simulation model calibrated with data from a population of Seaside Sparrows in coastal Georgia, USA. Salt marshes in Georgia experience the largest tidal range and highest spring tides (period of extreme tides occurring every ~28 days) of any salt marshes in the southern United States (Howard and Frey 1985). Being in the southern portion of the species' range may also expose the population to higher rates of nest predation than populations farther north (due, e.g., to the longer nesting season and more diverse predator community; Martin 2004, McKinnon et al. 2010). Thus, Georgia's population is likely already under high stress from threats to nesting success, as suggested by low daily nest success rates (0.84–0.93; Hunter et al. 2016b) compared to more northern populations in Maryland (0.88–0.97; Kern et al. 2012), New Jersey (0.95–0.97; Kern 2015), and Connecticut (0.95; Gjerdrum et al. 2005). I hypothesized that the increase in flooding risk caused by SLR would affect not only rates of failure from flooding but also those from predation.

METHODS

Individual-Based Model Description

I created an individual-based model of Seaside Sparrow nesting behaviors and outcomes using NetLogo 5.1

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FIGURE 1. Seaside Sparrow nests (**A**) can fail to produce fledglings (**B**) as a consequence of 2 primary threats: predation by various avian and mammalian predators, such as northern raccoons (**C**), and flooding from high spring tides (**D**). Flooding risk will likely increase with sea-level rise.

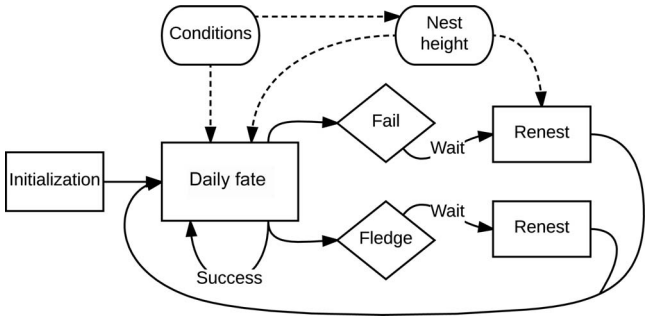


FIGURE 2. Schematic of an individual-based model of Seaside Sparrow nesting success. Boxes are model processes, diamonds are nest fates, and ovals and inline words are parameters or input data. Solid arrows indicate model flow path, and dashed arrows indicate variable effects. The model is initialized at random nest heights for all nesting females. Nests' daily fates are affected by conditions (tidal height and predation risk) and nest height. Each day, nests may fail or succeed, and nests that succeed over the requisite number of days fledge. Females then wait to renest, and previous nest height affects renesting height for females that had nest failure from flooding. Average nest height for a season is also affected by conditions of predation risk.

(Wilensky 1999). Here I provide a narrative model description (Figure 2); a full description of the model using the ODD protocol for describing individual-based models (Grimm et al. 2006, 2010) is presented in Supplemental Material Appendix A. Model parameters are named using NetLogo hyphenation conventions (Wilensky 1999), and model code is available in Supplemental Material Appendix B. I calibrated this model using data collected from a Seaside Sparrow population in coastal Georgia, USA, from 2013 to 2015 (Hunter et al. 2016b), including estimates of daily nest survival and failure rates (Table 1) and their relationships to nest heights and tidal heights, as well as structural information such as the number of renesting attempts and breeding-season length. Simulated nesting success emerges as a function of environmental conditions (predation and flooding risks) and nest-site selection behaviors along a nest height gradient (Seaside Sparrows' nesting success in Georgia is primarily affected by nest height and tidal height and not by other variables, such as distance to uplands, distance to channel, and territory density; Hunter et al. 2016b).

The only model entities are nesting female Seaside Sparrows. In each model run, 25 females are simulated. Females have state variables that pertain to the nests they produce during the breeding season, which are nest height (height above ground at which females place their nests in marsh grasses), number of days that nests have survived, nest fates, and the number of days since last nest if the female has no active nest. Females are modeled exclusively because they are most active in nest-site selection, nest construction, and incubation.

The time scale of the model is a breeding season (April 15–July 31; Hunter 2016) with a daily time step. Each female's first nest of the breeding season is assigned a nest height randomly at initialization. The variability of nest heights does not change among simulations, but the range of nest heights changes depending on seasonal predation risk (Hunter et al. 2016b). Nest-height range is based on data of observed nest heights (Hunter et al. 2016b; Table 1). Here, I model the behavior of nesting at lower nest heights in high-predation-risk seasons by restricting the available nest heights—in high-risk seasons (pred-risk = 1), the range of available nest heights is lower than in low-risk seasons (pred-risk = 0) (Hunter et al. 2016b; Table 2).

Every day, each female's nest is assigned a fate of surviving, flooding, or being depredated. Both predation

TABLE 1. Empirical estimates of daily nest survival rates and average nest heights from Hunter et al. (2016b) used to calibrate an individual-based model of Seaside Sparrow nesting success (values are means, with 95% confidence intervals in parentheses).

Year	Survival rate	Predation rate	Flooding rate	Nest height (m)
2013	0.85 (0.80–0.89)	0.05 (0.04–0.07)	0.06 (0.04–0.09)	0.68 (0.65–0.71)
2014	0.93 (0.90–0.95)	0.09 (0.06–0.12)	0.02 (0.01–0.03)	0.76 (0.73–0.79)
2015	0.84 (0.81–0.87)	0.15 (0.13–0.18)	0.01 (0.003–0.02)	0.64 (0.61–0.67)

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TABLE 2. Parameters and values used in an individual-based model of Seaside Sparrow nesting success.

Parameters	Stochastic process	Value/equation	Rationale
Initialization			
Pred-risk	Constant	0 (low), 1 (high)	Pred-risk controls both pred-response and pred-intercept
Pred-response	Constant	Pred-risk(0): 1.1 Pred-risk(1): 1.6	Calibrated to fit empirical nest-height ranges
Min-nest	Constant	0.5 * (1 / pred-response)	Produces relationship between pred-risk and nest-height range
Max-nest	Constant	Min-nest + 0.7	Empirical range of nest heights
Elevation	Normal	1.15 – (nest-height * $N[\mu = 0.6, \sigma = 0.07]$) [a]	Empirical, statistical relationship between nest height and elevation
Daily-fate			
Days to fledging	Uniform	22–26 days (median 24)	Empirical days to fledging
Pred-intercept	Constant	Pred-risk(0): −3.4 Pred-risk(1): −2.25	Calibrated [b]
Pred-prob	Bernoulli	*Logistic*(0.5 * nest-height + pred-intercept)	Coefficient (0.5) based on empirical relationship between nest height and predation probability
Flood-intercept	Normal	$N[\mu = -13.4, \sigma = 1.25]$ [a]	Calibrated [b]
Flood-prob	Bernoulli	e((10 * tide-height / total-height) + flood-intercept)	Calibrated to produce pattern of flooding failures primarily occurring during monthly lunar tides
Renest			
Nest-attempts	Constant	5 nests	Maximum number of observed nesting attempts
Wait-time	Uniform	Fledge: 7–21 days (median 14) Fail: 3–7 days (median 5)	Empirical waiting times

[a] Normal distribution (*N*) parameters: μ (mean), σ (standard deviation).
[b] Parameter values were calibrated to empirical data on Seaside Sparrow nesting success in Brunswick, Georgia, USA, in 2013–2015.

probability and flooding probability are functions of nest height and a baseline rate of predation or flooding failure. The effect of nest height on predation is based on general empirical evidence that nests closer to the ground are less vulnerable to predators (Martin 1993, Pietz and Granfors 2000), as well as evidence specific to the Georgia population of Seaside Sparrows, which indicated that higher nests were more likely to be depredated (Hunter et al. 2016b), and the coefficient of the predation probability function in Table 2 is drawn directly from that finding. However, this result was not found in every year of Hunter et al.'s (2016b) study, likely because in some years females nested at lower nest heights, on average, and therefore a relationship between nest height and predation rate could not be detected because of high overall predation rates. I assumed that the positive relationship between nest height and predation probability was constant across all years.

The likelihood that a nest will be flooded is affected not only by the height of the nest above the ground, but also by the elevation of the ground above sea level. However, Seaside Sparrows likely cannot sense small differences in elevation (Gjerdrum et al. 2005, Nordby et al. 2009); therefore, I added an elevation height to each nest height, based on the observed statistical relationship between nest height and elevation (Table 2). Flooding probability is a function of total height (nest height plus elevation) and daily tidal height (Table 2). I used daily maximum tidal height from the Fort Pulaski NOAA tidal gauge station (http://tidesandcurrents.noaa.gov/; height in meters above mean sea level) to create a realistic daily flooding risk. Data were downloaded for the period of the breeding season in years 1979–2015 (determination of the year used for each simulation is described below). I calibrated the flooding probability function (Table 2) to match a pattern in which nest flooding occurred almost exclusively during high spring tides that exceeded 1.5 m above sea level (Hunter et al. 2016b).

If a nest survives, its survival time increases by 1 day. Once a nest survives 22–26 days (2–3 days for laying, 11–12 days for incubation, 9–11 days as a nestling; Marshall and Reinert 1990), it fledges. The female then must wait 7–21 days (the number of days before renesting after a fledged nest is highly variable) before nesting again. If a nest fails, females must wait only 3–7 days before renesting (Marshall and Reinert 1990, Hunter 2016). Once the appropriate number of days has passed since a successful or failed nest, females select a new nest height and begin the nesting period over again. If a female's previous nest

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fledged or was depredated, she selects new habitat randomly (there is no evidence of selection along the nest height gradient following either of those fates). However, if her previous nest flooded, she selects a patch with a higher nest height; there is evidence of this behavior. There is no evidence that females can sense elevation or select for greater total heights following failure from flooding (Hunter et al. 2016b). Each female is allowed only 5 nesting attempts during a breeding season, which is the maximum observed number of attempts in Georgia (Hunter 2016). At the end of each model run (breeding season), average daily nest survival, predation, and flooding rates and average nest heights across all nests are calculated.

Model Calibration

I calibrated 2 parameters in the model to fit empirical data from Georgia: the baseline probabilities of predation (pred-intercept) and flooding (flood-intercept), which allow the predation and flooding probability equations to produce realistic outputs (Table 2). As a starting point for these parameters, I used logit equation parameters estimated using empirical data (Hunter et al. 2016b). However, because of potential unknown differences between the individual-based model and the conditions under which the empirical data were collected, these parameters needed to be calibrated to the mechanics of the model to produce observed daily nest survival rates (Table 1). For each year in 2013–2015, I ran the simulation for 30,000 breeding seasons, using a range of potential flood-intercept and pred-intercept values (centered around estimated logit parameters), and selected model runs that produced daily rates and average nest heights within 10% of their observed values (Table 1). For each year, 30–50 runs satisfied the criteria, and I averaged the parameter values across those runs. I then ran the model 10,000 times with those averaged, calibrated parameter values to ensure that daily rates and nest heights were close to the desired levels.

Scenarios

I used calibrated parameters to assess the effects of 2 types of scenarios on nest survival rates: (1) historical flooding risks vs. higher flooding risk under SLR conditions, and (2) low vs. high predation risks. To create higher-flooding-risk scenarios under SLR conditions, I first assessed changes in flooding risk over the recent past. I downloaded tidal gauge data (Fort Pulaski NOAA tidal gauge station; http://tidesandcurrents.noaa.gov/) for the breeding seasons from 1979 to 2015 (1979 was the first year that a complete dataset for the breeding season was available). For each year, I counted the number of days with "very high tides" (>1.5 m above mean sea level, which is a tidal height at which many Seaside Sparrow nests will flood; Hunter et al. 2016b) as a measure of each year's flooding risk (hereafter the parameter "flood-risk"). Regressing flood-risk against time (years) showed that flooding risk has been significantly increasing over the past 37 yr at a rate of 0.13 days yr^{-1} ($t = 2.6$, df = 35, $P = 0.01$). This increase is likely a function of sea-level rise, given that similar increases in maximum tidal height have been reported in other areas of the world (van de Pol et al. 2010, Field et al. 2016). I extrapolated this relationship forward in time to create 2 SLR scenarios of increased flooding risk, using 2013 as a baseline year because it was one of 2 yr that had the highest flood-risk value (12 days with very high tides). For a moderate SLR scenario, I increased all 2013 tidal heights that were greater than the mean tidal height by 10%, and for a severe SLR scenario, I increased those tidal heights by 20%. The moderate scenario's highest tide was 1.8 m above mean sea level, which is a value observed in the 2012 dataset and, thus, was within the realm of potential current conditions. The severe scenario's highest tide was 1.97 m, which is a value well above those observed in the past 37 yr. The moderate scenario had a flood-risk of 27 days, and the severe scenario had 39 days, which are approximately the flood-risk values that might be observed if the trend of the past 37 yr were extrapolated linearly to 100 and 200 yr into the future.

I ran each flooding- and predation-risk scenario combination 100 times and monitored outputs of daily nest survival, flooding, and predation rates. To investigate the effect that flooding risk (both observed, historical flood-risk and the simulated SLR flood-risk) has on nest success rates, I used tidal data that represented the full range of observed flood-risk by randomly selecting a year in the 1979–2015 tidal gauge dataset to represent each observed flood-risk value (0–12 days of very high tides) in addition to the simulated tidal data for the 2 SLR "years," for a total of 13 flood-risk scenarios. Each scenario was run with the selected year's data, using a normal distribution for the flood-intercept parameter with the mean and standard deviation calculated from the calibrations described above. Doing this meant that any differences in flooding probability among the scenarios would come from the tide data, and not from the calibrated flood-intercept parameter. For predation-risk scenarios, I used a different approach to see the effects of high and low predation risk on nest survival under each flood-risk value. For the low-predation-risk scenario, I used 2014 values for the pred-response and pred-intercept parameters (this year had the lowest average daily predation rate [0.05] from 2013 to 2015). Years 2013 and 2015 both had high average predation rates (0.09 and 0.15, respectively), so I used average values from these 2 yr for the pred-response and pred-intercept parameters for the high-predation-risk scenario.

The nest-height selection behaviors included in the model may be plastic, depending on future conditions. To determine what effect these behaviors have on the

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outcomes of the scenario testing, I reran all scenarios using a model without behaviors. I removed the "nest-height selection following flooding" behavior by making nest-site selection random following a failure from flooding; and I removed the "nest-height selection in response to predation risk" behavior by removing the pred-response effect on the min-nest parameter (thus, females could choose from among the full range of nest heights).

Analysis

I assessed the relative contribution of predation risk (high or low) and flooding risk (measured as number of days with extreme high tides) to nest survival rates with random forests (Liaw and Wiener 2002). I generated 10,000 regression trees and calculated the percent increase in mean squared error (MSE) when each variable was removed from the model, with greater increases in MSE indicating more important variables. The random forest process was completed separately for observed flood-risk scenarios from SLR flood-risk scenarios in order to assess any changes in variable importance as a result of increased tidal magnitude. I also measured changes in nest survival, flooding, and predation probabilities as a function of predation and flooding risk, and compared probabilities when models did not include habitat selection behaviors. All statistical analyses were conducted in R 3.2.1 (R Development Core Team 2016). Results are reported as means ± SD.

RESULTS

Testing the calibrated model revealed that it could produce average daily rates and nest heights that were close to the observed values in 2013–2015 (Table 1). For 2013, the model produced a daily predation rate of 0.09 ± 0.01, daily flooding rate of 0.06 ± 0.008, and average nest height of 0.70 ± 0.02 m. For 2014, the model produced a daily predation rate of 0.05 ± 0.006, daily flooding rate of 0.02 ± 0.003, and average nest height of 0.82 ± 0.02 m. For 2015, the model produced a daily predation rate of 0.15 ± 0.02, daily flooding rate of 0.006 ± 0.003, and average nest height of 0.71 ± 0.02 m. All model-produced values were within 10% of observed values, except for average nest height in 2015, which was higher than the observed value.

In the 37 yr period from 1979 to 2015, flood-risk (number of days with "very high tides") ranged from none (8 yr) to 12 (1999 and 2013). Running the model with selected years to represent the range of flood-risk observed in this 37 yr period indicated that pred-risk had a much greater influence than flood-risk on daily nest survival rates (17× greater influence of pred-risk than of flood-risk, according to relative percent increases in MSE). Flood-risk had essentially no effect on predation probability, which was determined almost completely by pred-risk, except at the highest flood-risk values in the SLR scenarios (Figure 3A). Conversely, pred-risk had nearly as much of an effect on flooding probability as did flood-risk (Figure 3A and Supplemental Material Appendix C). The removal of nest-height selection behaviors had a greater effect on flooding probability than on predation probability (Figure 3A, 3B). Flooding probability in low-predation-risk scenarios was most affected, with an average 26.1% increase in flooding probability when nest-height selection behaviors were removed. Flooding probability also increased by 23.5% in high-flood-risk scenarios and by 21.4% in low-flood-risk scenarios when behaviors were removed (Figure 3A and Supplemental Material Appendix C). Predation probability increased by 1.9–2.8% when nest-height selection behaviors were removed in both high- and low-flood-risk scenarios and the high-predation-risk scenario. Removing behaviors actually decreased predation probability by 1.8% in the low-predation-risk scenario and decreased flooding probability by 5.9% in the high-predation-risk scenario (Figure 3B and Supplemental Material Appendix C). In general, the behaviors had small positive effects on the overall daily nest survival rates across scenarios, with the exception of flood-risk = 11 (represented by the year 2007), where the behaviors caused substantially lower nest survival probabilities in the high-predation-risk scenario (Figure 3C). This flood-risk scenario (flood-risk = 11; year 2007) also showed much higher flooding probabilities than would be expected from the trend of other flood-risk scenarios (Figure 3A); year 2007 was a year not only with high spring tides but with 2 high tides that occurred between spring tides (at 1.43 and 1.52 m).

In the SLR scenario runs, the relative importance of flood-risk in determining daily nest survival increased, but pred-risk was still 6.8× more important than flood-risk. Daily flooding probability increased from 0.03 ± 0.01 for the observed flood-risk years to 0.08 ± 0.02 for the moderate SLR scenario and 0.13 ± 0.03 for the extreme SLR scenario, which caused declines in daily nest survival probability (Figure 3C). The difference in flooding probability between high- and low-predation-risk scenarios increased under SLR conditions (Figure 3A). The effects of the habitat selection behaviors became even clearer in the SLR scenarios, with the greatest effects of the behaviors being a reduction of flooding probability in low-predation-risk and high-flood-risk scenarios; however, the behaviors also increased flooding probability in high-predation-risk scenarios (Figure 3A). The effects of the behaviors on survival probability were small, although the effects were larger for the SLR scenarios (Figure 3C). Compared to a baseline daily nest survival rate (0.93 ± 0.01) where both flooding and predation risk were very low, the reduction in nest survival caused by increasing predation risk (daily survival rate = 0.83 ± 0.03) was almost exactly equal to that caused by the severe SLR scenario (daily survival rate = 0.84 ± 0.02; Figure 3C).

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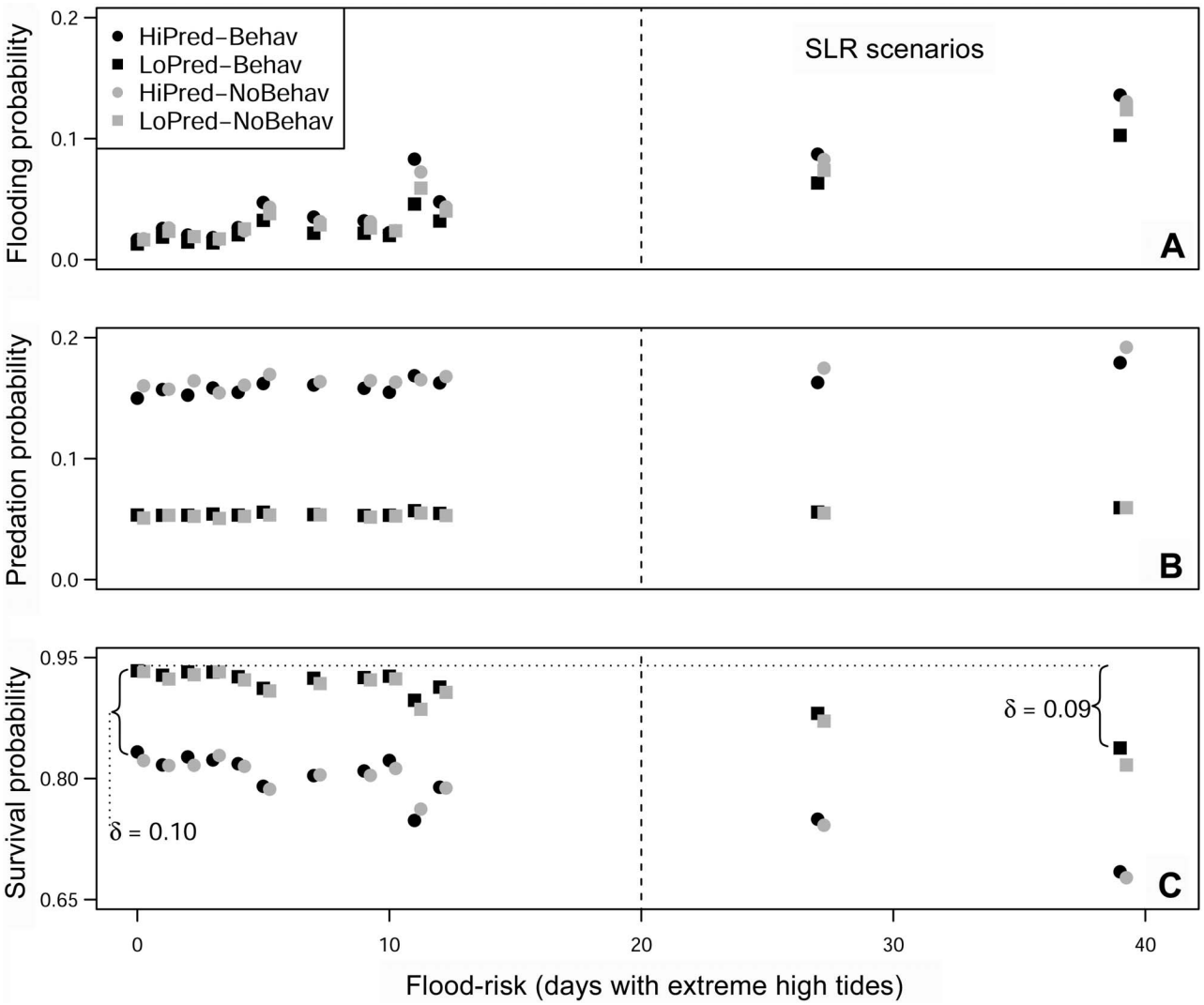


FIGURE 3. Flooding (**A**), predation (**B**), and survival (**C**) probabilities (averaged across 100 simulations for each point) as a function of flooding risk (*x*-axis) and high (circles) and low (squares) predation risk for an individual-based model of Seaside Sparrow nesting success. Left of the dotted line are observed flooding risks from tidal gauge data from 1979–2015, and right of the dotted line are simulated flooding risks under sea-level-rise (SLR) conditions. Black points are mean probabilities from models including nest-height selection behaviors, and gray points are mean probabilities from models without those behaviors. Brackets in C indicate the difference in nest survival rate between scenarios of lowest and highest predation (left bracket) and flooding (right bracket) risks at the lowest risk for the other threat.

DISCUSSION

Using an individual-based model of Seaside Sparrow nesting behaviors and risks to nesting success, I found that predation risk has a greater effect on daily nest survival than flooding risk, even if flooding risk increases substantially with SLR. At low flooding risk, the difference in nest survival probability between high and low predation risks is the same as the difference in nest survival probability that would be achieved between a very low-flooding-risk year and the severe SLR scenario (Figure 3C). The severe SLR scenario is actually very unlikely to be realized, because suitable nesting habitat would be lost before such high levels of flooding could occur (Erwin et al. 2006, van de Pol et al. 2010). Therefore, currently observed levels of predation cause a greater threat to nesting success than SLR is likely to cause. The primacy of predation is due to the fact that a nest can be destroyed by a predator on any day during a nest's lifetime, but flooding caused by extreme high tides can only occur during a few days of the nesting period (Greenberg et al. 2006, Shriver et al. 2007), a situation that is likely to continue with SLR (van de Pol et al. 2010).

The probability of a nest being depredated was almost entirely determined by the risk of predation, but flooding

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probability was almost equally determined by predation risk and flooding risk. This discrepancy was caused, at least in part, by 2 habitat selection behaviors: placing nests higher in vegetation following a failure from flooding and placing nests lower in vegetation in a breeding season with high predation risk (Hunter et al. 2016b). The largest effect of these behaviors was in reducing flooding probability in high-flooding-risk and low-predation-risk scenarios (Figure 3A). Under such conditions, choosing a higher nesting site following failure from flooding was advantageous: higher nests are more vulnerable to predators (Martin 1993, Pietz and Granfors 2000); therefore, this behavior did not result in lower nest survival in low-predation-risk scenarios. Conversely, in high-predation-risk years, the behaviors increased flooding probability because nests were placed lower in vegetation throughout a high-predation-risk season and also because the response to flooding made nests more vulnerable to predation. In terms of overall nest survival, the positive effects of the behaviors outweigh the negative effects, which only increase the probability of flooding when predation risk is very high (Figure 3A and Supplemental Material Appendix C).

Under SLR conditions, the relative importance of flooding risk in determining nest survival increases (as expected with higher values of flood-risk), but predation risk is still more important. That predation risk should be more important than flooding risk even under extremely high flooding risk is likely due to interactions between these parameters caused by the nest-height selection behaviors. Effects of the behaviors on nest survival rates are even more pronounced under SLR scenarios, again producing a greater increase in nest survival under low-predation-risk scenarios than the reduction in nest survival under high-predation-risk scenarios. Given this mostly positive effect on nest survival, Seaside Sparrows' nest-height selection behaviors will likely contribute to the population's resiliency to SLR. However, this will depend on the frequency of high- and low-predation-risk breeding seasons, about which very little is known. Predation rates for Seaside Sparrow nests reported in the literature vary widely, including 0.06–0.12 (Post 1981), 0.03–0.13 (Lockwood et al. 1997), 0.03 (Gjerdrum et al. 2005), 0.02–0.05 (Kern et al. 2012), 0.06 (Lehmicke 2014), and 0.01–0.03 (Kern 2015) (daily nest predation rates in some of these cases were calculated from nest survival rates and proportion of failures reported from predators). Few studies are conducted for more than 1 or 2 field seasons, however, so little can be inferred about the frequency of high-predation-risk seasons. The variability in predation rates may reflect not only year-to-year variability in predation pressure, but also differences in predator communities among sites. Little is known about which specific predators cause the majority of nest failures in Seaside Sparrows, or whether nesting Seaside Sparrows change their behaviors to changing predator composition, which could influence the results of this model. Whether habitat selection behaviors contribute to Seaside Sparrow population resiliency will also depend on behavioral plasticity (Williams et al. 2008, Reed et al. 2010, Beever et al. 2016). If behaviors shift in response to changing conditions, such as a reduction in the nest-height response to high-predation-risk years, resiliency could be further improved. However, given the very small effect that the behaviors had on predation probability (Figure 3B), it is unlikely that small shifts in behaviors would make much difference in overall nest survival rates in the short term. Another missing piece of the puzzle is the effect of SLR on the predator community, with the possibility that SLR could reduce predator population resiliency and nest predation rates. Little is understood about how tidal and marsh conditions may affect predator populations in coastal habitats; however, given that generalist predators that use aquatic, terrestrial, and urban habitats make up a substantial portion of potential nest predators (e.g., raccoons, grackles), it is unlikely that overall predation risk for Seaside Sparrows will decrease as a result of SLR.

Effects of nest-height selection behaviors do not entirely explain the difference in flooding probability between high- and low-predation-risk scenarios (Figure 3A). The remaining difference is likely explained by the relationship between the timing of flooding events and the timing of failures from predation. Salt marsh breeding sparrows typically display nesting synchronization with high spring tide events (Marshall and Reinert 1990, Shriver et al. 2007). Thus, the 24–26 days required to complete all the nesting stages (building, laying, incubation, hatching, and nestling) fit within the 26–28 days between 2 spring tides. In order for this synchronization to occur, sparrows renest immediately following a nest failure (Reinert 2006, Shriver et al. 2007). However, if nest failure is caused by a predator in the middle of a tidal cycle, this immediate renesting behavior will make it more likely that the subsequent nest will be flooded during a spring tide. When predation risk is high, any nest that can avoid predation is likely to be vulnerable to flooding, simply due to the timing of nest initiation. Thus, even without nest-height selection behaviors, predation risk can have an effect on flooding probability, but this effect is readily apparent only in higher-flooding-risk years.

I modeled SLR as an increase in the magnitude of high tides during monthly spring tide events, which resulted in an increase in the number of days with extreme high tides, but the exact effect of SLR on the tidal regime needs to be better understood to accurately predict effects on nesting success (Field et al. 2016). In a study of tidal dynamics in the Wadden Sea estuary in northwestern Europe, researchers found that over a 38 yr period, maximum tidal heights

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increased twice as fast as mean tidal heights as sea levels rose, which provides support for the kind of change I have modeled here (van de Pol et al. 2010). However, SLR combined with climate change may affect not only regular tidal cycles, but also the frequency and severity of storms (Bender et al. 2010). Storms have been shown to affect not only nesting success, but also nest-site selection behaviors (Bonter et al. 2014). Because storms may come at any point during a tidal cycle, they may affect Seaside Sparrow nesting success similarly to predation by disrupting the synchronization between nest initiation and cycles of lunar tides. This effect can be readily seen in the flood-risk = 11 scenario (represented by year 2007) that had extremely high flooding probabilities, comparable to those of the moderate SLR scenario (Figure 3A), due to flooding events that occurred between high spring tides in that year.

Interactions among predation and flooding risk, individuals' behavioral responses to the trade-off between those threats, and present-day high rates of nest predation all indicate that predation risk poses as great a threat to Seaside Sparrow fecundity as SLR. The conservation implications of this finding are stark: nest survival rates could become very low, perhaps so low as to preclude the production of any young within a subpopulation's breeding season, especially during years with both high flooding and predation risk. To better estimate this possibility, more investigation into the links and feedbacks among Seaside Sparrow population size, individuals' behaviors, predator populations, and tidal conditions is warranted, with a potential first step being the establishment of long-term monitoring sites similar to those in the northeastern United States (Wiest et al. 2016). However, given the results of the present study and of others showing high vulnerability of Seaside Sparrows to SLR (Kern and Shriver 2014, Hunter et al. 2016a), it is likely that in the coming decades, management actions (in conjunction with continued research on the population) will be necessary to maintain population viability. Flooding risk will be difficult to mitigate, but predator control options could be available on a small scale at sites with known predator community composition. Fences to exclude mammalian predators at high-nest-density sites or individual nest cages (excluding both mammalian and avian predators) could improve nest success rates (Post and Greenlaw 1989, Smith et al. 2011). To best take advantage of Seaside Sparrows' habitat selection behaviors, predator exclusion measures should be implemented early in the breeding season (under the assumption that nest-height selection is in response to early encounters with predators; Ibáñez-Álamo et al. 2015), so that Seaside Sparrows' early interactions with predators are minimized and they do not place their nests lower in vegetation. Therefore, a management action to mitigate predation risk could simultaneously reduce flooding risk. Although the risks of both SLR and predation are severe, by taking advantage of Seaside Sparrows' behavioral adaptations, managers could improve populations' resiliency.

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