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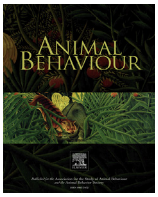

Threat predictability influences seaside sparrow nest site selection when facing trade-offs from predation and flooding

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Habitat selection trade-offs between avoiding predation and gaining energy are well studied, but similar trade-offs resulting from multiple threats to survival remain poorly understood. We studied how seaside sparrows, *Ammodramus maritimus*, approach nest site selection decisions to avoid threats to nesting success from predation and tidal flooding. Along a nest height gradient, nest site selection to avoid tidal flooding (i.e. placing nests higher) may make seaside sparrow nests more vulnerable to predation, and selection to avoid predation may make nests susceptible to flooding. We monitored nesting success rates and nest site selection decisions of breeding seaside sparrow pairs at five sites near Brunswick, Georgia in April–July of 2013–2015. We found that seaside sparrows encountered a nest site selection trade-off along a gradient of nest height. Nest height had an effect on survival probability during each of our study years, with positive effects of nest height on predation probability and negative effects of nest height on flooding probability observed in some years. Sparrows dealt with this trade-off by altering their nest site selection in relation to a threat's predictability; low within-season variability in predation risk and high information about predator presence in open marshes make predation risk more predictable than the magnitude of tidal flooding, which is governed by unpredictable and variable winds. Sparrows responded to predictable predation threats by nesting at lower nest heights in years with higher predation risk, but sparrows responded to unpredictable flooding threats by placing nests higher off the ground but only following nest failure from flooding. Understanding decision making through a lens of threat predictability could provide a useful approach for studies of other animals' habitat selection trade-offs.

The threat of predation drives many habitat selection trade-offs (Houston, McNamara, & Hutchinson, 1993), particularly during an animal's nesting stage when movement to avoid predators is not possible (Clark & Shutler, 1999; Martin, 1995). Avian responses to predation have evolved to produce life history trade-offs among clutch sizes, number of renesting attempts and nest site selection (Martin, 1995), and these traits are also affected by predation on an ecological timescale (e.g. within a breeding season; Lima, 2009). Many bird species change the location of their nests following predation (Chalfoun & Martin, 2010; Clark & Shutler, 1999; Lima, 2009), which may improve their chances of finding an area with lower predator densities. Birds also shift their nest site placement after predation along habitat gradients to improve nest concealment or avoid predators (Chalfoun & Martin, 2010; Forstmeier & Weiss, 2004; Marzluff, 1988). In addition to making renesting decisions after a nest failure, birds can assess predation risk at the beginning of a breeding season and alter their nest site selection and other behaviours accordingly (Fontaine & Martin, 2006; Kearns & Rodewald, 2012).

Habitat selection to avoid predation often comes at a cost of reduced foraging opportunities (Forstmeier & Weiss, 2004; Werner & Hall, 1988), but less well understood is whether nest site selection to avoid predators might make nests more vulnerable to other threats (as opposed to simply increasing foraging effort for parents). For example, ectothermic animals (such as reptiles, fish and insects) that are unable to incubate their eggs must select nest or oviposition sites that protect nests from both the threat of overheating or underheating and the threat of predation, which can cause a trade-off in habitat selection (Stahlschmidt & Adamo, 2013; Warner & Shine, 2008). However, it is not necessarily the case that the proper thermal habitat overlaps with high predator abundances or low concealment opportunities, and so solutions that

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simultaneously minimize both threats may exist (Kolbe & Janzen, 2002). A similar possible trade-off is faced by marsh-nesting birds that encounter threats from nest predation and from nest flooding (Greenberg et al., 2006). It is unknown whether these threats trade off to prohibit parents from avoiding both predation and flooding, or whether parents can obtain sufficient information about temporally varying threats to optimize this trade-off in ecological time. Can adults assess the relative strength and predictability of multiple, opposing threats and respond by selecting favourable nesting sites?

We addressed this question in seaside sparrows, *Ammodramus maritimus*, a bird species that breeds in coastal areas where many nesting species face dual threats of predation and tidal flooding. Salt marsh breeding birds, such as seaside sparrows, have adapted to tidal flooding by rapid renesting to ensure that nesting cycles fit between high lunar tides that occur approximately every 28 days during the breeding season (Reinert, 2006; Shriver, Vickery, Hodgman, & Gibbs, 2007). The frequency of lunar tide events is predictable, but the magnitude varies widely with wind speed and direction, which makes the minimum nest height for flood avoidance unpredictable. Salt marsh breeding birds avoid tidal flood waters by building nests higher above the ground compared to nests of inland breeding relatives (Greenberg et al., 2006), but this response may put nests at a higher risk of predation because nests closer to the ground often have a lower predation risk, likely due to greater concealment from predators (Martin, 1993; Pietz & Granfors, 2000). Thus, nest site selection solutions to avoid tidal flooding may make seaside sparrow nests more vulnerable to predation, and vice versa.

We studied how seaside sparrows approach this trade-off in coastal Georgia, U.S.A., where tidal amplitudes are the highest along the southeastern Atlantic coast of the United States. Seaside sparrows at our study area near Brunswick, Georgia, are also exposed to a variety of nest predators including raccoons, *Procyon lotor*, mink, *Neovison vison*, rice rats, *Oryzomys palustris*, fish crows, *Corvus ossifragus*, boat-tailed grackles, *Quiscalus major*, red-winged blackbirds, *Agelaius phoeniceus*, and marsh wrens, *Cistothorus palustris* (E. A. Hunter, personal observation). Seaside sparrows renest multiple times, often four or more times, throughout the breeding season following unsuccessful nesting attempts, which is predicted for species exposed to a variety of predators (Filliater, Breitwisch, & Nealen, 1994; Kearns & Rodewald, 2012). We predicted that seaside sparrows would (1) be able to affect their nest success rate through nest site selection and (2) respond to threats of predation and tidal flooding by shifting their nest site selection for renesting attempts along habitat gradients that affect nesting success.

METHODS

Location Description

This study took place in April–July 2013–2015 in five 10–15 ha salt marsh sites near the city of Brunswick, Georgia. Sites were chosen based on observed moderate to high densities of breeding seaside sparrows (~2 pairs/ha), which are typical of occupied seaside sparrow breeding sites elsewhere in the species' range (Lehmicke, 2014; Post & Greenlaw, 2009). Two sites were monitored for 3 years, one site was monitored for 2 years, and two sites were monitored for 1 year. Because no site differences were detected in daily survival or failure rates (indicating a lack of difference in predation or flooding risks among sites), sites were grouped for analysis (see Analysis). All sites were relatively mature high-elevation salt marshes, dominated by smooth cordgrass (*Spartina alterniflora*), with salt marsh pickleweed (*Salicornia virginica*) present at the highest marsh elevations (Fig. 1). Small, well-defined channels (1–3 m wide) with tall *S. alterniflora* grasses (1–2 m tall) intersect higher-elevation marsh with shorter *S. alterniflora* (~0.5 m). Seaside sparrows tended to nest in higher grasses near channels, but a few nests were found in shorter grasses as well (Fig. 1). All nests at our sites were woven out of and placed in *S. alterniflora* grasses.

Nest Searching and Monitoring

We searched for and monitored nests from mid-May to late July in 2013 and for the entire breeding season in 2014–2015 (early April – late July). Searches took approximately 4–5 person-hours per site to search for nests at all known seaside sparrow territories, identified by the activities of singing males. In 2013, we conducted nest searches and nest checks every 2–4 days, but in subsequent years this interval was extended to once per week to reduce trampling and disturbance of sites and nests. Searches were conducted using a combination of systematic searching in known nesting territories and locating nests from behavioural cues of breeding pairs (Martin & Geupel, 1993).

Upon finding a nest, we collected information on nest height above ground (measured from the top of the nest cup, Fig. 1), the number of eggs or nestlings, and parental identity, if banded (see Pair Identification). We also placed an iButton temperature data logger (Thermochron iButton DS1921G, Maxim Integrated Products, San Diego, CA, U.S.A.) in each nest to aid in the determination of the timing and cause of nest fates (Bayard & Elphick, 2011). To determine nest fates (depredated, flooded or fledged), we used a combination of field information and iButton temperature data. Field information for depredated nests included eggshells or eggshell fragments in the nest, mammal tracks near the nest, tilted or pulled apart nests and adult bird faecal matter (single, discrete dropping from a presumed predator) in the nest. Field information for flooded nests included mud inside the nest, and wet and cold eggs. Field information for fledged nests included adult nest-guarding behaviour when no chicks were in the nest, sightings of fledglings, and young bird faecal matter (messy accumulation of droppings throughout the nest deposited by fledglings immediately before nest departure) in the nest. Nest abandonment was documented only four times as determined by the presence of eggs with no initiation of incubation or incubation termination. Nests' fates were corroborated with iButton temperature data, as well as nest fate time and date, by comparing nest temperatures to ambient temperatures collected from iButtons placed in inactive nests (Bayard & Elphick, 2011).

In addition to nest height, we measured other nest habitat variables that could affect nest fate, including stem density around the nest (a measure of nest concealment from predators), total height (nest height plus elevation, which likely affects flooding probability; Fig. 1) and distance to forested areas (which can be predator sources, Picman, Milks, & Leptich, 1993). These data were collected after nests fledged or failed. Stem density was measured by centering a 1 m^2 quadrat on a nest, placing a dowel marked in 20 cm increments in each corner and counting stems touching the dowel within each increment (Lehmicke, 2014). In 2014–2015, we collected elevation data with a real-time kinematic global position system (RTK GPS) with a Trimble R6 RTK Glonass-enabled antenna (Trimble Navigation Limited, Sunnyvale, CA) with corrections through eGPS Virtual Reference System and elevations derived using Geoid12a. We did not collect RTK GPS elevations in 2013, but instead used elevation data from a Digital Elevation Model (DEM, 1.2 m cell size) derived from Light Detection and Ranging (LiDAR) data collected in 2008–2010 for Glynn and Camden counties. We corrected nest elevations from LiDAR data using vegetation species and height at each nest as outlined in Hladik and Alber (2012), thus

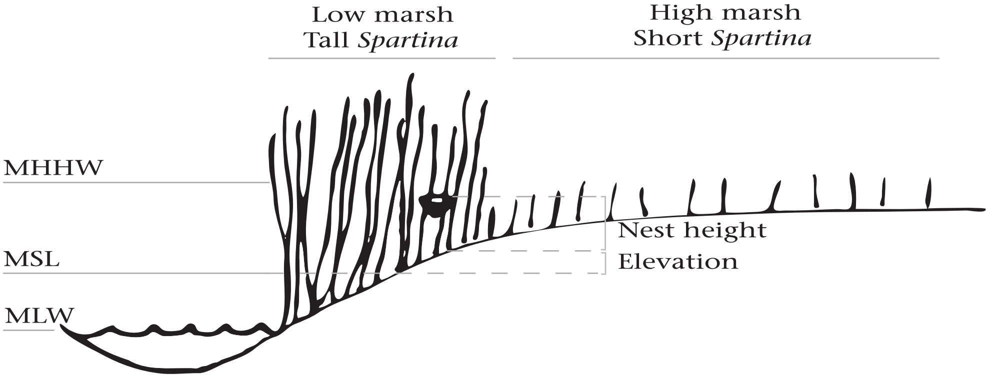

Figure 1. Schematic of the salt marsh platform in seaside sparrow nesting sites in coastal Georgia, U.S.A. Three tidal datums are depicted: mean lower water (MLW), mean sea level (MSL) and mean higher high water (MHHW). Seaside sparrows typically placed their nests in tall *Spartina* grasses in low marshes. Nest height was measured from the top of a nest cup to the ground, and elevation was measured from the ground to the MSL datum. Total height is the sum of these two measures. The nest depicted would likely be flooded by a high lunar tide as it is below MHHW.

accounting for poor laser penetration in dense vegetation. Marshes in the area accrete and erode sediment slowly, with average yearly elevation change rates of less than 0.7 cm (Morris, Sundareshwar, Nietch, Kjerfve, & Cahoon, 2002), which is well below our elevation measurement error rate (approximately ± 2 cm for RTK GPS, and ±5 cm for LiDAR).

We measured distance to forested areas using National Land Cover Database (NLCD) data from 2011 and a Euclidian distance tool in the 'raster' package in program R (Hijmans, 2015). Finally, nest flooding probabilities are affected not only by total nest height, but also by the maximum tidal height that a nest experiences. We used tidal gauge data from the Fort Pulaski NOAA station (http://tidesandcurrents.noaa.gov/), approximately 100 km from our sites, to assign the maximum tidal height in metres above mean sea level (MSL) to each nest during that nest's period of observation (from date found to date of fledging or failure).

Pair Identification

We marked adult breeding seaside sparrows using unique colour band combinations in 2014 ($N = 28$, from 16 pairs) and 2015 ($N = 46$, from 23 pairs) using mist nets placed around active nest sites. Seaside sparrows are socially monogamous within a breeding season (Post & Greenlaw, 2009), so marked females or males could be used to monitor a pair's nesting activities; however, only females construct nests and make nest site choices. From these marked pairs, we observed strict adherence to nesting territories that were almost always exclusive to a well-defined channel. Pairs did not move to a new territory following nest failure (although renesting attempts were typically several metres away from failed nests), and other pairs did not invade nesting territories during the course of the breeding season. Based on this information, we assigned unbanded pairs to nests that were unambiguously geographically separated from other territories and had no concurrent nest activity. To do this, we drew polygons around groups of geographically isolated nests and assigned each group to a pair, but we did not assign nests to pairs for groups that had multiple nests active at the same time (potentially indicating multiple pairs nesting in the same area).

Capture and handling time of adults was very brief (usually less than 5 min, no more than 15 min), and no adult or nestling birds were injured in the course of banding or placing iButtons inside of nests. All fieldwork was permitted by the Georgia Department of Natural Resources (29-WJH-15-5) and approved by University of Georgia's Institutional Animal Care and Use Committee (A2013 03-002-Y3-A0).

Analysis

To determine whether nest site selection affects nest fate, we tested for effects of habitat variables on daily flooding and predation rates. We used the program MCestimate that simultaneously estimates daily survival and failure probabilities from multiple causes using a multinomial logit Markov chain exposure model (Environmental Protection Agency Mid-continent Ecology Division, Duluth, MN, U.S.A.; Etterson, Nagy, Robinson, & Johnson, 2007). Because each year had widely varying daily rates (see Results), we modelled each year's data separately. We constructed models of effects of habitat variables on predation and flooding rates, and selected the most informative models using Akaike's Information Criterion corrected for small sample size (AIC_c). Each model had predation and flooding submodels that could be expressed as a function of habitat covariates or as a null submodel with no habitat effects (each component required a specified submodel). We first ran predation and flooding components with a null submodel for the other component (predation or flooding), which allowed us to estimate effects of habitat covariates for each fate. If both components had submodels that were better (lower AIC_c score) than the 'global null' (null submodels for both predation and flooding), then we would have combined the top submodels for both components to create a model with covariates for both components (however, this was never the case, see Results). Predation submodels were constructed from all linear combinations of nest height, stem density and distance to forested areas. Flooding submodels included a total height and maximum tide interaction submodel (i.e. total height only affects flooding probability during high tides), a nest height and maximum tide interaction submodel, submodels excluding those interactions and a maximum tide submodel. All covariates were centred and standardized. We assessed models' goodness of fit using a bootstrapped Pearson's test with 100 iterations (Yin & Ma, 2013).

Next, we determined whether seaside sparrows altered their nest site selection in response to predation and flooding threats. We first examined changes in selection on a nest-by-nest basis, comparing the habitat variables of each pair's nests to their immediately previous nests using paired *t* tests, with a separate test for each fate type and each year. To test the possibility that seaside sparrows can assess predation risk at the beginning of a breeding season and respond accordingly with nest site selection to avoid predation, we also assessed nest height as a function of predation rate (as a proxy for predation risk). We regressed all nest heights against the estimated mean predation rate (for the year in which each nest was built) while controlling for date (number of days past initiation of the breeding season, 1 April), to account for vegetation growth and a shorter monitoring period in 2013. All analyses were conducted in program R (v.3.2, R Core Team, 2015), and estimates are reported as means and 95% confidence intervals (95% CI).

RESULTS

We found 354 nests and assigned fates to 323 nests (2013: 91 found, 78 for which fates could be determined ('fated'); 2014: 101 found, 87 fated; 2015: 162 found, 158 fated). Of those nests, we were able to assign 81 to banded pairs and 147 to unbanded pairs; the remaining nests could not be assigned to pairs with certainty (because of concurrently active nests within territories) or were 'singleton' nests not associated with a renesting attempt. Daily rates of survival, predation and flooding varied substantially among all three years, with 2013 and 2015 having significantly lower survival rates (2013 mean: 0.85, 95% CI: 0.80–0.89; 2015 mean: 0.84, 95% CI: 0.81–0.87) than 2014 (mean: 0.93, 95% CI: 0.90–0.95). Predation rates were highest in 2015 (mean: 0.15, 95% CI: 0.13–0.18), with lower rates in 2013 (mean: 0.09, 95% CI: 0.06–0.12) and 2014 (mean: 0.05, 95% CI: 0.04–0.07), whereas flooding rates were highest in 2013 (mean: 0.06, 95% CI: 0.04–0.09), with lower flooding rates in 2014 (mean: 0.02, 95% CI: 0.01–0.03) and 2015 (mean: 0.01, 95% CI: 0.003–0.02). Flooding risk varied within a year more than did predation risk when examining risk variation among lunar months (defined here as 28-day periods between first quarter moons) within a year (Fig. 2). Tidal amplitude was most severe in 2013, with 10 days during the study period having tides greater than 1.5 m above mean sea level, whereas 2014 had 5 days and 2015 had 3 days (Fig. 3). Nest height above ground also varied among years (2013: 0.68 ± 0.03 m (95% CI); 2014: 0.76 ± 0.03 m (95% CI); 2015: 0.64 ± 0.03 m (95% CI)).

None of the years had models better than the 'global null' for both components; either the predation component or the flooding component had models better than the null, but not models for both components (Table 1). In 2013, flooding models performed better than the null model, with the model including effects of maximum tide and nest height performing best. Maximum tidal amplitude increased the probability of flooding ($\beta = 0.78 \pm 0.25$ (95% CI)), and increasing nest height decreased flooding probability ($\beta = -0.41 \pm 0.17$ (95% CI)). In 2014, predation models performed better than the null, with the top model being a combination of nest height and stem density. Nests higher off the ground ($\beta = 0.52 \pm 0.33$ (95% CI)) and nests surrounded by fewer stems ($\beta = -0.45 \pm 0.35$ (95% CI)) were more likely to be depredated. In 2015, flooding models again performed better than the null; the model of maximum tide and nest height again performed best. As in 2013, maximum tidal amplitude increased the probability of flooding ($\beta = 1.17 \pm 1.9$ (95% CI)), and increasing nest height decreased flooding probability ($\beta = -0.88 \pm 0.74$ (95% CI)). However, this model had a poor fit. The model including an interaction between maximum tide and nest height shared substantial weight (0.32), and was a better fitting model (Pearson's goodness of fit = 0.23), indicating that tides were only high enough to cause flooding for very low nests in this year. Thus, nest height only affected either predation (2014) or flooding probability (2013, 2015), but not both in the same year (Fig. 4).

For tests of changes in seaside sparrow nest site selection following nest failure, there was a significant increase in nest height following failure from flooding in both 2013 ($t_{22} = 2.7$, $P = 0.01$) and 2015 ($t_5 = 4.5$, $P = 0.01$; Table 2). All other responses, including changes in total height following flooding, nest height and stem density following predation and nest height following fledging, were not significant (Table 2). However, we did find an effect of yearly predation rate on nest height: higher predation rates led to lower average nest heights, and this effect was significant ($t_{336} = -5.4$, $P < 0.001$; Fig. 5), but the effect of days past initiation of the breeding season was not ($t_{336} = 0.2$, $P = 0.84$). Conversely, yearly flooding rate had no effect on nest heights ($t_{336} = 0.4$, $P = 0.67$).

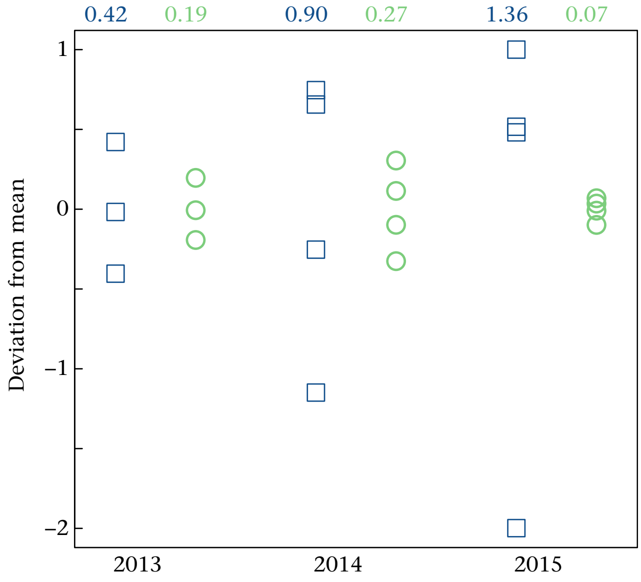

Figure 2. Variation in flooding and predation risk for seaside sparrow nests during 2013–2015. Each point represents the flooding risk (squares) or predation risk (circles) within a lunar month (defined here as the 28-day period between first quarter moons) and its deviation from the yearly mean. Risks were calculated as the number of nests flooded or depredated divided by the total number of active nest days per lunar month and standardized by the mean yearly predation or flooding risk. Top margin values indicate each category's and year's coefficient of variation.

DISCUSSION

Our results reveal that seaside sparrows do encounter a trade-off between nest predation and tidal flooding. As suggested in the literature, this trade-off plays out through nest site selection along a gradient of nest height: higher nests may be more vulnerable to predation (Martin, 1993; Pietz & Granfors, 2000), and lower nests may be more vulnerable to flooding (Greenberg et al., 2006). Nest height had an effect on survival probability during each of our study years, with positive effects of nest height on predation probability and negative effects of nest height on flooding probability observed in some years. Nests with lower nest heights and greater cover (higher stem density) had a lower probability of being depredated only in 2014, which was the year with the lowest predation rate. Conversely, sparrows could influence the probability of flooding by nesting higher in both low (2015) and high (2013) flooding risk years, so it is not clear why nest height had no effect on flooding probability in 2014. Nests were higher on average in 2014, so it is possible that there was not a large enough advantage for the highest nests (compared to the lowest) to produce a signal of a benefit from habitat selection. Lack of a consistent effect of nest height on nest success has been reported in the literature for other tidal marsh sparrows, often despite a strong effect of tidal height on flooding probability (Bayard & Elphick, 2011; Gjerdrum, Elphick, & Rubega, 2005; Shriver et al., 2007). Our findings demonstrate that whether nest site selection along a nest height gradient will affect predation or flooding probability is variable from year to year.

Variability in threat strength and the effectiveness of nest site selection produces an unpredictable environment for seaside

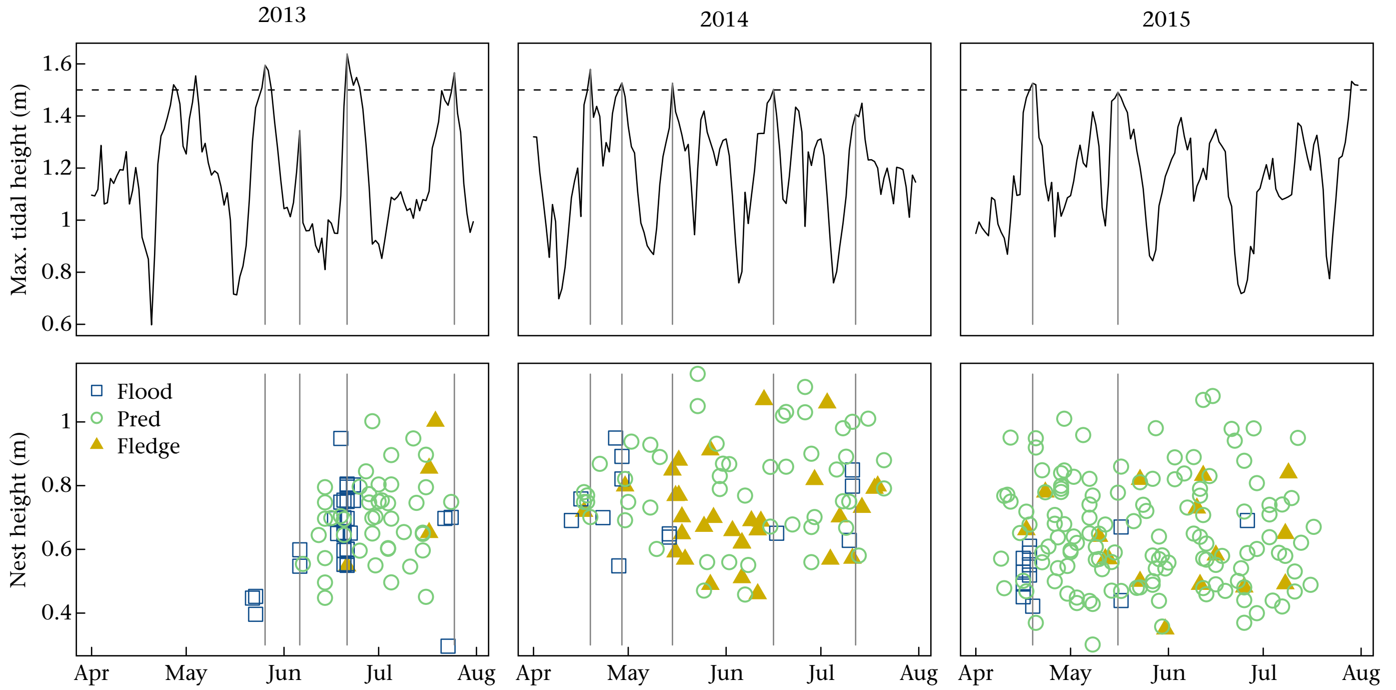

Figure 3. Top row: daily maximum tidal heights during the seaside sparrow breeding season taken from the Fort Pulaski, Georgia, NOAA tidal gauge station. Dotted horizontal lines indicate tides greater than 1.5 m above mean sea level. Grey vertical lines indicate maximum high tide during a lunar tide event that resulted in flooded seaside sparrow nests. Bottom row: seaside sparrow nest heights as a function of date of nest fate and fate type (flooding, predation, fledging). Grey vertical lines correspond to those in the top panels showing maximum high tides during a lunar tide event.

Table 1

Models of nest site selection effects on predation and flooding probability for seaside sparrow nests near Brunswick, Georgia, U.S.A.

Year	Model		K	dAIC$_c$	Weight	P[a]
2013	Flood(MT+NH)	Pred(.)	4	0.00	0.60	0.32
	MT(0.29–1.27)					
	NH(−0.74 to −0.08)					
	Flood(MT∗NH)	Pred(.)	5	2.04	0.22	0.20
	Flood(MT)	Pred(.)	3	3.63	0.10	0.50
	Flood(MT+TH)	Pred(.)	4	5.01	0.05	0.74
	Flood(MT∗TH)	Pred(.)	5	5.63	0.04	0.34
	Flood(.)	Pred(.)	2	13.13	0.00	0.55
2014	Flood(.)	Pred(NH+ST)	4	0.00	0.65	0.70
		NH(0.19–0.85)				
		ST(−0.80 to −0.10)				
	Flood(.)	Pred(NH+ST+DF)	5	1.81	0.26	0.72
	Flood(.)	Pred(NH)	3	5.91	0.03	0.71
	Flood(.)	Pred(NH+DF)	4	7.00	0.02	0.70
	Flood(.)	Pred(ST)	3	8.36	0.01	0.72
	Flood(.)	Pred(.)	2	10.04	0.00	0.22
2015	Flood(MT+NH)	Pred(.)	4	0.00	0.38	0.02
	MT(−0.73–3.07)					
	NH(−1.62 to −0.14)					
	Flood(MT∗NH)	Pred(.)	5	0.31	0.32	0.23
	Flood(MT∗TH)	Pred(.)	5	2.16	0.13	0.72
	Flood(MT+TH)	Pred(.)	4	2.33	0.12	0.01
	Flood(MT)	Pred(.)	3	4.27	0.04	0.03
	Flood(.)	Pred(.)	2	9.32	0.00	0.26

Underneath the top model for each year are parameter estimates (95% confidence intervals) of habitat variable effects. Models shown are only those with dAICc values less than or equal to the global null. Variables: maximum tide (MT), total height (TH), nest height (NH), stem density (ST), distance to forest (DF).

[a] Goodness of fit as measured by a bootstrapped Pearson's test. Significance ($P < 0.05$) indicates a poorly fitting model.

sparrows, but the degree of predictability differs between threats. Whether a threat is predictable is composed of two elements: variability in threat severity (low variability makes a threat more predictable, Colwell, 1974), and information about the threat available to sparrows (high information makes a threat more predictable, Schmidt, Dall, & van Gils, 2010). In terms of variability, we found that (lunar) month-to-month variation in flooding risk was higher than variation in predation risk within each year (Fig. 2). And although we did not collect data on the amount of information available to sparrows, it is apparent that there is more information about predation than tidal flooding. There is essentially no information available to a sparrow about the magnitude of high lunar tides ahead of the tidal event, due to the strong and variable influence of wind speed and direction on tidal magnitude (Bayard & Elphick, 2011; van de Pol et al., 2010). However, there is at least some information about predation threats because sparrows can observe predator presence and activity throughout a breeding season; and, given the wide-open nature of the salt marsh, these observations are easy to make when compared to more closed habitats, such as forests (Devereux, Whittingham, Fernández-Juricic, Vickery, & Krebs,, 2005). Thus, given that predation has lower variability and more information, it is relatively more predictable than flooding.

Differences in predictability between the two threats affect sparrows' nest site selection decisions: we found that seaside sparrows respond seasonally to predictable predation risk, but on a nest-by-nest basis to unpredictable flooding risk. In years with higher estimated predation rates, seaside sparrows nest closer to the ground on average throughout the entire breeding season. We used predation rate as an estimate of predation risk, but observed predation rates include not only predation risk but the effects of antipredator behaviours (Creel & Christianson, 2008). However, given the large range of our observed predation rates (the 2015 predation rate was three times higher than the 2014 rate), predation risk very likely played a large role in the resultant predation rate, not just seaside sparrow behaviours. Experimental verification (e.g. predator removals, Fontaine & Martin, 2006) of the negative effect of predation risk on nest height would bolster our findings; however, our observational results are highly suggestive that

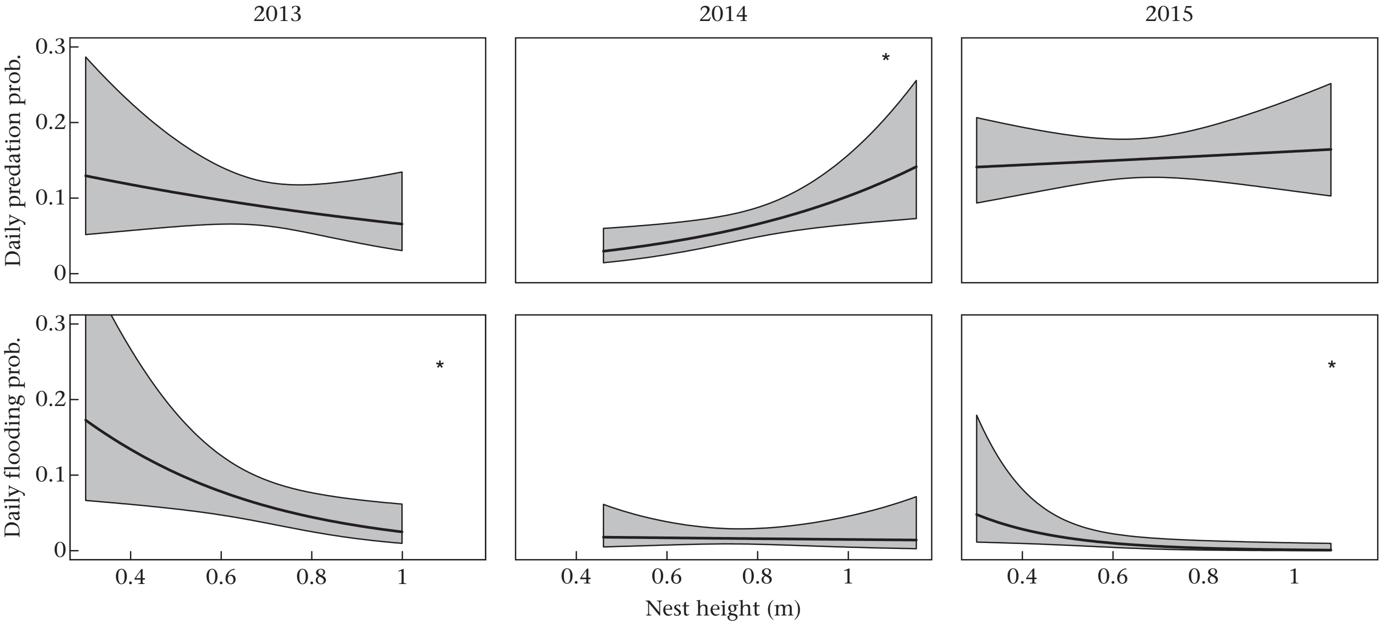

Figure 4. Effect of nest height on predation (top panels) and flooding (bottom panels) probabilities for seaside sparrow nests near Brunswick, Georgia, U.S.A. Effects are only plotted for the range of nest heights observed in each year. Lines are mean effects and shaded areas are 95% confidence intervals. Asterisks indicate that nest height was included in the top model for that year. All other effects had essentially zero slope.

Table 2
Changes in nest habitat variables in response to a previous nest's fate for seaside sparrow pairs nesting near Brunswick, Georgia, U.S.A.

Year	Previous fate	Variable	Effect	*df*	*P*
2013	Flooded	NH	0.07 m	22	0.01*
	Flooded	TH	0.12 m	22	0.26
	Predated	NH	−0.04 m	16	0.36
	Predated	ST	1.20 stems	14	0.49
2014	Flooded	NH	0.07 m	7	0.38
	Flooded	TH	0.03 m	7	0.78
	Predated	NH	−0.004 m	18	0.95
	Predated	ST	2.47 stems	16	0.26
	Fledged[a]	NH	0.09 m	5	0.24
2015	Flooded	NH	0.13 m	5	0.01*
	Flooded	TH	0.08 m	5	0.15
	Predated	NH	−0.02 m	57	0.37
	Predated	ST	−0.29 stems	57	0.63

Variables: nest height (NH), total height (TH), stem density (ST).
*Significant change in the habitat variable compared to a pair's previous nest.
[a] 2014 was the only year in which pairs made renesting attempts after successfully fledging nests.

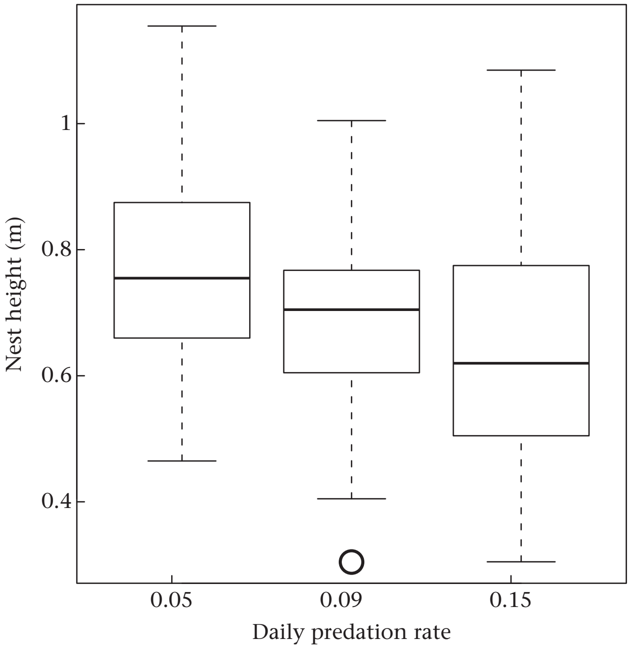

Figure 5. Nest height as a function of daily predation rate, estimated from data on seaside sparrow nesting success (mean predation rate: 2013 = 0.09; 2014 = 0.05; 2015 = 0.15). Dark central lines are medians; boxes are first and third quartiles.

seaside sparrows alter their nest site selection behaviours in response to predators.

How seaside sparrows assess predation risk is unclear, but a variety of bird species do shift their reproductive strategies immediately following experimental changes in predation risk, both actual and perceived (Fontaine & Martin, 2006; Peluc, Sillett, Rotenberry, & Ghalambor, 2008). That we did not see a shift in nest height over the course of a breeding season indicates that sparrows assessed predation risk at the beginning of the breeding season (possibly through encounters with predators while establishing territories, Ibáñez-Álamo et al., 2015), as opposed to using ‘public information’, such as other sparrows' nest failures from predation throughout the breeding season (Kearns & Rodewald, 2012; Valone & Templeton, 2002). High threat predictability should favour using such public information (Doligez, Cadet, Danchin, & Boulinier, 2003), but information about predator presence and activity in the open habitat of salt marshes may actually be easier to acquire than conspecific nesting success. We found no evidence of sparrows using personal experiences of predation (past nest failures) to inform nest site selection (Table 2), so seaside sparrows respond to the predictable threat of predation by choosing a lower nest height in high predation years and sticking with it. However, it is precisely those high predation years in which selecting a lower nest site makes no difference for a nests' probability of being depredated: in high predation risk years, all nests have a high chance of being depredated, regardless of nest height (years 2013 and 2015; Fig. 4). Other recent studies have similarly found a lack of adaptive advantage resulting from habitat selection in response to predation (Clark & Shutler, 1999; Ruskin, Hodgman, Etterson, & Olsen, 2015), so why is there evidence of habitat selection if there is no conferred benefit of increased nest survival? In our study, it is possible that if any higher nests had existed in high predation years, they would have suffered an even greater predation risk; thus an effect of nest height on predation probability would have been observable, and the behaviour viewed as adaptive. Another possible explanation is a rise in mesopredator populations (Prugh et al., 2009), which may make nest predation rates higher than the conditions under which birds' habitat selection behaviours evolved (Schlaepfer, Runge, & Sherman, 2002). Thus, habitat selection strategies based on the predictability of predation may no longer be adaptive.

Unpredictability of wind effects on tidal flooding has led some researchers to conclude that tidal flooding is not a selective force on coastal breeding birds' renesting decisions (Burger, 1982; Pakanen, Rönkä, Thomson, & Koivula, 2013), especially when compared to the strong selective force of predation (Martin, 1995). However, we found that sparrows did respond to unpredictable tidal flooding by shifting nest site selection following failures from flooding. Seaside sparrows nested at a higher nest height following flooding failures in both 2013 and 2015, which are years that we found had lower flooding probabilities for higher nests. Thus, it seems that sparrows' behavioural responses to flooding are adaptive, in that they shift their nest site selection when doing so will improve their nests' survival chances.

That sparrows select nest sites along a gradient of nest height and not total height (sum of nest height and elevation) is somewhat perplexing, as total height should be the true determinant of whether a nest will be flooded. However, other studies provide evidence that tidal marsh nesting sparrows select nest sites based on grass heights and not elevation (Gjerdrum et al., 2005; Nordby, Cohen, & Beissinger, 2008), perhaps because grass height is much easier to perceive than elevation. In 2015, when we had high-quality nest elevation data, total height performed almost as well as nest height in predicting flooding probability. Therefore, the two measures are nearly equivalent in this regard, likely because sparrows never nest at very low nest heights at low elevations, and nests at higher elevations have a limited gradient of nest heights (because shorter grasses grow at higher elevations). Additionally, *S. alterniflora* height is a function of both local elevation and tidal amplitude (McKee & Patrick, 1988), so nest height may be more comparable across sites with different elevations and tidal regimes. The relative ease of precisely measuring nest height instead of elevation makes this equivalency between the measures good news for field researchers, although other tidal marsh species do select nest sites based on elevation (Valdes, Hunter, & Nibbelink, 2016; van de Pol et al., 2010), and so whether nest height or total height will be a better predictor of flooding probability may be species and habitat specific.

Our results indicate that seaside sparrows do encounter a nest site selection trade-off between avoiding threats of predation and tidal flooding, and that sparrows navigate this trade-off with different strategies for each threat. We do not know of any other studies that have examined behavioural responses to trade-offs among opposing threats to nest survival, but such studies may become more prevalent, especially as technology provides for easier identification of nest predators (Pietz & Granfors, 2000; Rodewald & Kearns, 2011). The monolithic threat of ‘predation’ could be viewed as multiple opposing threats if nest predators could be identified (Benson, Brown, & Bednarz, 2010), which would be particularly useful when strategies to avoid mammalian or avian predation oppose each other (Fisher & Wiebe, 2005). Understanding how species approach multiple-threat trade-offs using a lens of threat predictability could help shed light on some species' conservation problems. For instance, federally (U.S.) threatened piping plovers, *Charadrius melodus*, that nest on reservoir shorelines have presumably evolved to manage both predation and seasonal flooding threats in riverine systems, but flooding predictability has been drastically altered by water containment and releases from dams, creating an ecological trap where plovers' habitat selection strategies are no longer adaptive and nest success has plummeted (Anteau et al., 2012). Seaside sparrows are also a species of conservation concern (Hunter et al., 2015), and will likely suffer substantial habitat loss and degradation from sea level rise (Hunter, Nibbelink, & Cooper, 2016; Kern & Shriver, 2014). Sea level rise will not only reduce habitat availability but increase the frequency of very high tides (Bayard & Elphick, 2011; van de Pol et al., 2010). Seaside sparrows' responses to trade-offs between predation and flooding may make them even more vulnerable to sea level rise if predation rates also remain high because sparrows nest lower during high predation years. Thus, understanding the behaviour of this species in response to multiple opposing threats may provide an important key to its management and protection.

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