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Research Paper

Suboptimal conditions lead to differences in habitat use and nest survival of imperiled tidal marsh sparrows between an urban marsh and nearby non-urban island

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ABSTRACT. Sea level rise and human development are threatening the extinction of some saltmarsh birds. Nests risk failure because of flooding when built low to the ground, but taller nests face increased predation risk. To better understand how habitat characteristics and urbanization influence reproductive success in saltmarsh ecosystems, we modeled factors discriminating nest sites from unused available sites and nest survival of a high-marsh specialist, Saltmarsh Sparrow (*Ammospiza caudacuta*), and a low-marsh specialist, Seaside Sparrow (*A. maritima*), at three sites representing different degrees of surrounding urbanization and degradation in New York, 2018–2019. The two most urban sites contained mammalian predators, and the non-urbanized island contained a colony of gulls that are potential predators. Sparrow nest site use depended positively on cover by the tall grass *Spartina alterniflora*. At the most degraded urban site, this relationship was strongest at high elevation, and at the island site it was strongest near the gull colony. Nest survival of both species was positively related to average vegetation height around nests, and negatively related to daily tide height. At the island site, nest survival was unrelated to proximity to the gull colony. Nests were highest off the ground at the most urbanized site, which experienced the highest tides, but nest survival was still low in one year. The effect of nest height on survival was not always positive and depended on tide height, nest stage, and sparrow species. Predation risk may explain why at higher elevations, sparrows placed nests in taller vegetation. At the island site, nest survival was high even within an active predator colony, but at the most urbanized site Saltmarsh Sparrows appeared unable to mitigate factors threatening nest survival. Restoration designs that include tall vegetation at high elevation may help tidal marsh sparrows to find a tradeoff between flooding and predation risk.

Des conditions sous-optimales entraînent des différences dans l'utilisation des habitats et le taux de survie des nids des espèces menacées de bruants des zones intertidales dans le cas d'un marais urbanisé et d'une île voisine non urbanisée

RÉSUMÉ. L'élévation du niveau de la mer et l'expansion humaine menacent d'extinction certains oiseaux des marais salés. Alors que les nids construits à faible hauteur risquent l'échec par submersion, ceux localisés à des hauteurs plus élevées sont plus exposés au risque de prédation. Pour mieux comprendre comment les caractéristiques de l'habitat et le degré d'urbanisation influencent le succès reproducteur dans les écosystèmes des marais salés, nous avons modélisé les facteurs qui permettent de distinguer les sites de reproduction par rapport aux sites disponibles mais non utilisés, ainsi que le taux de survie des nids pour une espèce spécialiste du haut marais, le Bruant à queue aiguë (*Ammospiza caudacuta*), et une espèce spécialiste du bas marais, le Bruant maritime (*A. maritima*), dans trois sites représentant différents degrés d'urbanisation environnante et de dégradation à New York, en 2018 et 2019. Les deux sites les plus urbanisés étaient fréquentés par des mammifères prédateurs, et l'île non urbanisée abritait une colonie de laridés qui sont des prédateurs potentiels. Il existe une corrélation positive entre l'utilisation des sites de reproduction par les bruants et l'augmentation du recouvrement par la grande graminée *Spartina alterniflora*. Sur le site urbanisé le plus dégradé, cette relation était plus forte à une altitude supérieure, et sur l'île, la relation était la plus forte à proximité de la colonie de laridés. La survie des nids des deux espèces était positivement corrélée à la hauteur de la végétation moyenne à proximité des nids, et négativement corrélée avec la hauteur de la marée quotidienne. Sur l'île, la survie des nids ne dépendait pas de la proximité de la colonie de laridés. Les nids étaient plus élevés par rapport au sol sur les sites les plus urbanisés, qui étaient exposés aux marées les plus importantes, toutefois la survie des nids restait faible sur une année. L'effet de la hauteur des nids sur la survie n'était pas toujours positif et dépendait de la hauteur de la marée, du stade du nid, et de l'espèce concernée. La pression de prédation pourrait expliquer pourquoi, à des altitudes plus élevées, les bruants plaçaient leurs nids dans de la végétation plus haute. Sur l'île, la survie des nids était élevée, même au sein d'une colonie de prédateurs actifs, mais sur le site le plus urbanisé, les Bruants à queue aiguë ne semblaient pas en mesure d'atténuer l'effet des facteurs menaçant la survie des nids. Des plans de restauration incluant des végétations hautes sur les secteurs les plus hauts pourraient contribuer à aider les bruants des zones intertidales à concilier les risques de submersion et la pression de prédation.

Key Words: *gulls; New York; Saltmarsh Sparrow; Seaside Sparrow; specialist; trade-offs; urban*

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INTRODUCTION

Saltmarshes in North America have been in steep decline for years because of land conversion, hydrological alteration, and disturbance caused by human activity (Tiner 1984, Watson et al. 2016, Campbell et al. 2022), with more than half of all saltmarshes lost in the United States over the past century (Kennish 2001). As rising sea levels continue to increase tidal inundation frequency and intensity in coastal areas, tidal marsh specialist birds may not be able to adapt to changes fast enough to persist (Hunter 2016, Correll et al. 2017). One such species, the Saltmarsh Sparrow (*Ammospiza caudacuta*), a North American saltmarsh obligate, has been a species of high conservation concern for the last decade (Correll et al. 2016, Wiest et al. 2016) and current models project the functional extinction of the species as soon as 2035 (Field et al. 2017). This dim forecast represents range-wide population declines constructed from a long-term data set (Field et al. 2017). At the same time, populations of Seaside Sparrows (*Ammospiza maritima*), which are also saltmarsh obligates and nest sympatrically with Saltmarsh Sparrows in part of their range, are not projected to go rapidly extinct. Both species spend the entirety of their life cycles in tidal saltmarshes (Greenberg et al. 2006a, Greenlaw et al. 2020, Post and Greenlaw 2020); therefore, understanding the factors that are leading to rapid decline in one species but relative security in the other will be important for planning strategies to prevent Saltmarsh Sparrow extinction.

The breeding strategies of these species have been shaped by the inherent trade-off in tidal marshes between the pressures of inundation and predation (Greenberg et al. 2006b). Both species weave small nest cups attached to marsh grass just above the marsh floor, and although saltmarshes provide ample food resources (Post and Greenlaw 2006), survival of nests requires precise timing of construction relative to tidal cycles to avoid flooding. Predation and flooding caused by the lunar tide cycle have been identified as the primary causes of nest failure for these species, with nest survival almost always negatively related to tide height (DiQuinzio et al. 2002, Greenberg et al. 2006b, Shriver et al. 2007, Ruskin 2015). These competing risks drive habitat selection and nest construction (Götmark et al. 1995, Gjerdrum et al. 2005). Placing a nest high off the marsh floor can decrease flooding risk but increase predation risk, as the nest is more visible (Greenberg et al. 2006b, Hunter et al. 2016). Conversely, placing a nest too low to the marsh surface to conceal it from predators may result in flooding; nest success can be impacted by as little as a 6 cm variation in nest height (Gjerdrum et al. 2008). Nest survival is highest for both species when eggs are laid immediately following a monthly peak high tide, allowing time for chicks to grow and develop before the following month's highest water levels (Deragon 1988, Gjerdrum et al. 2005).

In tidal saltmarshes, vegetation composition is highly correlated with marsh elevation and inundation frequency (Pennings et al. 2005, Moffett et al. 2010), and the two sparrow species partition the marsh on the basis of elevation/vegetation zones. Seaside Sparrows tend to nest in low-elevation areas of marsh dominated by the rigid tall-form of saltmarsh cordgrass (*Spartina alterniflora*; Post and Greenlaw 2020). Conversely, Saltmarsh Sparrows are considered to be high-elevation marsh specialists, relying on habitat dominated by saltmarsh hay (*Spartina patens*), which is thin and tends to lay horizontal across the marsh surface (Greenlaw et al. 2020). Because of these differences, Saltmarsh Sparrow nests are often located closer to the marsh floor than those of Seaside Sparrows, but at higher elevations.

Marsh landscape characteristics may also determine nest site placement by Saltmarsh Sparrows. Benoit and Askins (2002) found a positive relationship between patch size and tidal marsh sparrow abundance; however, Marshall et al. (2020) found that maximum angle to horizon line was a better predictor of Saltmarsh Sparrow abundance than marsh patch area, highlighting the importance of habitat openness over an area. The potential effect of habitat openness on nest survival and predation has not yet been examined. In cases where saltmarshes border uplands, these edges may be higher in elevation than the marsh core, as well as drier and more accessible to terrestrial animals (Suvorov et al. [2014] documented higher rates of predation in wetland edges). Jobin and Picman (1997) found increased predation rates on artificial nests in marshes as water depth decreased, concluding that lower water levels increased accessibility of nests to terrestrial predators such as raccoons (*Procyon lotor*).

Both sparrow species have demonstrated a propensity to change their habitat selection both within and between breeding seasons, based on perceived threats to nest survival (Hunter et al. 2016, Kocek 2016, Benvenuti et al. 2018, Newsome and Hunter 2022). Hunter et al. (2016) found Seaside Sparrows in Georgia had lower mean nest heights in years with higher predation rates. In remnant patches of urban saltmarsh in New York City (NYC), Kocek et al. (2022) documented Saltmarsh and Seaside Sparrows nesting successfully at nest heights significantly higher than those seen in other parts of the range, as well as selecting for greater proportions of tall form *S. alterniflora*, despite potential increases in visibility to predators. NYC is considered a sea level rise hot spot (Sallenger et al. 2012). Many marshes in NYC are lacking in sediment input, leading to marsh compaction and fragmentation, which prevents them from keeping up with sea level rise (Peteet et al. 2018). Only small patches of suitable tidal Marsh Sparrow habitat are left; however, Kocek et al. (2022) recorded above range-wide average nest survival in some years. These results may indicate that NYC populations can successfully adjust their nesting strategies by building nests higher off the ground in response to increased flooding pressures and shifts in site level vegetation composition (Kocek et al. 2022). Continued research in marginal habitat patches, or in areas with high levels of threats by both predation and flooding, will be necessary to improve future conservation strategies for tidal marsh species as human development expands and tidal flooding severity increases along coastlines. Residual patches of salt marsh will become increasingly valuable to humans and wildlife (Costanza et al. 2008). As previously intact high-quality habitat becomes fragmented and suboptimal, species may be forced to occupy smaller habitat patches, thus intensifying competition and predation. Restoration plans will need to incorporate the best available knowledge on the interactions among inundation, competition, and predation, as land managers look to conserve sustainable wildlife populations in the face of climate change. However, the effects of these competing risks on habitat use and nest survival of tidal marsh sparrows in marginal or degrading habitat are not well studied.

Our goal for this study was to compare Saltmarsh Sparrow and Seaside Sparrow habitat selection and nest survival in degraded habitat and relatively intact habitat within a single region. Herein we compare characteristics of nest sites samples to those of a concurrent random sample of available points from the same patch, as an indicator of habitat selection (Jones 2001). All points in our sampled patches were equally accessible for nesting by sparrows, but differed on the basis of vegetative, hydrologic, and landscape characteristics. Therefore, using Jones (2001) terminology, we use the term nest site selection to refer to the comparison of used versus available landscape features. We chose an urban marsh in NYC and a suburban marsh in nearby Long Island, New York, as degraded sites, because we had several years of prior data from those locations and because NYC is a good model for sites that are caught between high levels of human development on one side and rapid sea level rise on the other. For comparison, we used an island nesting site with no human development at its borders and little prior history of human use. Our objectives were to (1) identify important biotic and abiotic covariates for nest site selection and nest construction at each site; and (2) determine the relationship between nest survival and tide height, elevation, habitat openness, and nest and vegetation characteristics.

METHODS

Study site

We studied tidal marsh birds nesting at three sites in NYC and Long Island, New York, with different types of land cover adjacent to their boundaries (urban, suburban, open water). Saltmarsh Sparrows were known to nest at all three sites and Seaside Sparrows were known to nest at the urban and island site. Idlewild Marsh (urban, 40°39′9.140″ N, 73°45′7.729″ W) is located in Queens County, adjacent to a major international airport on the northeast side. This 65 ha site, managed by the NYC Department of Parks and Recreation, is a highly disturbed urban marsh. Patches at this site were restored in 1993 with fill excavation and vegetation planting. However, all tidal marshes in the urbanized Jamacia Bay system are currently suffering from "sediment starvation," due to decreased input from mineral sediments and increased tidal flow, leading to structural weakness and edge failure (Hartig et al. 2002, Peteet et al. 2018). These effects were observed at Idlewild Marsh, with many areas transitioning to low-elevation marsh dominated by *S. alterniflora*, and remaining patches of high-elevation marsh dominated by *S. patens* and saltgrass (*Distichlis spicata*) had become unstable and were structurally uneven. The site is surrounded by highly developed human infrastructure, and we observed sign of human commensal mammalian predators, especially raccoons.

Marine Nature Study Area (suburban, 40°37′14.595″ N, 73°37′17.572″ W) and North Cinder Island (island, 40°36′34.545″ N, 73°36′35.0676″ W) in Oceanside, New York (Nassau County), are both managed by the Town of Hempstead. Marine Nature Study Area is a 21 ha town conservation area surrounded by a densely settled residential area and has no history of marsh restoration. Raccoons, Norway rats (*Rattus norvegicus*), and feral cats (*Felis catus*) were known to inhabit the site, their presence being facilitated by the ease of access to the marsh provided by a pedestrian trail and corridor to nearby residential areas. The vegetation at this suburban marsh is primarily composed of short form *S. alterniflora*, patches of *S. patens*, *D. spicata*, and marsh elder (*Iva frutescens*), an upland shrub.

North Cinder Island (hereafter "island") is a 21 ha tidal marsh island located 1.5 km south of Marine Nature Study Area in Middle Bay. Similar to most Long Island marshes, this site contains a network of parallel ditches created for mosquito abatement purposes in the 1930s (Riepe 2010). However, since these historical alterations, it has been left relatively undisturbed. This marsh island exhibits typical North Atlantic saltmarsh composition, with tall form *S. alterniflora* growing around frequently inundated marsh edges, channels, and interior salt pans. In patches of higher elevation, *S. patens* and *D. spicata* dominated. Upon initiation of the study, we learned the site had hosted a colony of Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) since 2010, with approximately 50 pairs laying 69 nests (65 Herring Gull and 4 Black Back-backed Gull nests) in 2019. Sparrows and other tidal marsh birds were observed nesting within the boundaries of this colony. No evidence of mammalian predators was documented at this site.

Field methods

From mid-May to mid-August 2018 and 2019, we performed weekly systematic nest searching for all avian species in six study plots (two per site, 1 ha to 2.5 ha each) using a protocol outlined in Ruskin et al. (2017). At all sites, study plots represented potentially suitable tidal marsh bird habitat and were close enough together that birds could readily move between them, and each was of a size that we could fully survey one per day. GPS locations of nests were recorded to the nearest 5 m, and nests were monitored every three to four days until their final fate (fledged or failed), classified on the basis of Ruskin et al. (2017). Eggs were considered active if they were warm and inside nest bowls. Sparrow nests were designated successful if at least one chick from the nest was observed alive in the nest bowl at or after nine days of age and without any subsequent evidence of predation or extreme flooding at the nest bowl. Nest fledging for both species typically occurs between days 8 and 11 (Greenlaw et al. 2020, Post and Greenlaw 2020). To better characterize predation risk to sparrow nests on the island, gull nest locations were recorded both years, but their fates were not monitored.

Nest construction and nest site vegetation characteristic measurements were recorded by using protocols outlined in Roberts et al. (2017). Nest height (distance of nest bowl lip to the marsh floor) to the nearest 0.5 cm was collected by using a ruler, and proportion canopy cover (live and dead grasses woven by the bird) was evaluated by placing a white paper disk horizontally in the nest bowl and visually estimating the proportion of the disk that was concealed by vegetation from a vantage point directly above the center of the nest. We visually estimated proportion foliar cover (the proportion of the ground that would be covered by a plant's shadow at noon) by each plant species within a 1-m^2 quadrat centered on the nest within one wk after the final nest fate was determined. We measured thatch (a layer of dead, matted vegetation, or semi-vertical dead stems) height at the center point of the quadrat using a meter stick, to the nearest 0.1 cm. We recorded the average height (nearest cm) of herbaceous vegetation at the quadrat center point and the midpoint of each side, using

visual approximation aided by a meter stick. We averaged the five measurements to obtain a single value for average vegetation height for each quadrat.

To characterize the habitat available for nesting, we collected vegetation data at random points within our subplots. We used the "Create Random Point" tool in ArcMap 10.5.1 (ESRI, Redlands, California, USA) to generate up to 100 random points with a minimum allowed distance of 8 m between points in each study plot. The 8 m distance was chosen to be greater than the 5 m accuracy of our GPS measurements so we could avoid measuring the same point more than once. Every time we collected vegetation data at a nest site, we also collected vegetation data from at least one of our previously generated random point locations in the order of their assigned random number. The random point was not spatially paired with the nest, but this design ensured that we were measuring marsh characteristics contemporaneously with every nest. Data were collected at a minimum of 20 random vegetation points in each study plot per month to ensure study plots with low numbers of nests were still adequately sampled. In 2019, high resolution surface elevation measurements (< 2 cm) were collected at each nest and random point by using a Trimble TSC3 data logger with a real-time kinematic (RTK) R10 Glonass-enabled antenna (Trimble Navigation Limited, Sunnyvale, California, USA). Additionally, in 2019, at each nest site and random point, habitat openness was measured by using methods from Marshall et al. (2020). The maximum horizon angle was measured by using clinometers (Suunto, Vantaa, Finland) and we recorded whether the tallest horizon object was within 50 m of the point. In 2019, water loggers (model HOBO U20L-04, Onset Computer Corp, Bourne, Massachusetts, USA) were placed at all three sites to monitor tide heights. At the island and urban sites, one logger was placed in the main channel between study plots. At the suburban site, where subplots were separated by an elevated trail, a logger was placed in each subplot. This design ensured that we captured the water flow directly impacting each of our monitored study plots. Each site also had a logger placed above the high-water level to record site-specific barometric air pressure, as required for data processing. All loggers were programmed to record temperature and air pressure every 10 min.

Data processing methods

Elevation data points were interpolated to create a continuous elevation surface by using the "Kriging Interpolation" tool in ArcMap 10.5.1. Clinometer data values were interpolated to a 0.5 m resolution raster grid by using natural neighbor interpolation methods in ArcMap 10.5.1. We used the "Extract Values to Points" tool in ArcMap 10.5.1 to assign elevation values and clinometer values to nests and random points from 2018 based on the interpolated 2019 raster. Although marsh elevation can change from year to year, without an extreme weather event annual elevation variation within salt marshes is found to be on a scale of millimeters (Peteet et al. 2018, Staver et al. 2020, Blum et al. 2021). Therefore, we have no reason to believe site elevation or horizon line at our sites experienced any change between years at a scale that would impact our interpolation. Because lidar data available at the time were collected pre–hurricane Sandy, we believe the high precision and resolution (< 2 cm) of the elevation data we collected with the Trimble RTK unit were a better representation of our sites and of sparrow nest locations during our study period. In order to understand the effects of the presence of a colony of potential predators within our island site, we chose to include a parameter for the distance of each sparrow nest on the island to the center of the gull colony. The location of the gull colony center was determined on the basis of all gull nest locations pooled across the two years by using the "Central Feature" tool in ArcMap 10.5.1.

Water level data from loggers were downloaded and water depth values were processed by using HOBOWare Pro software 3.7.16 (Onset Computer Corp, Bourne, Massachusetts, USA) with methods outlined in Haaf (2016). Using NOAA (2020)–measured water levels in the mean sea level datum from tide stations located close to our study sites (Jones Inlet station at 40°35′2.000″ N, 73° 34′6.9996″ W for the island and suburban sites, Norton Point station at 40°38′6″ N, 73°44′48.0012″ W for the urban site), we used linear regression to model the relationship between 2019 NOAA–measured water level data and our logged 2019 local water level data. The results of this model were then used to project 2018 site-specific water level from 2018 NOAA–measured water levels. Site-specific daily maximum tide heights based on 24-h periods from 0600 hours one day to 0600 hours the next day were then assigned to every date of the field season. This interval aligned with the timing of our nest checks and ensured that tide levels occurring before morning nest checks were accounted for in our nest survival models.

Analytical methods

Nest characteristics

We separately modeled sparrow nest height and proportion canopy cover as a function of interactions between sparrow species (coded as one indicator variable), site (coded as two indicator variables), and distance to the gull colony center nested within the "island" level of the site variable, using least squares regression with the glm function in Program R (10.4.1; R Core Development Team 2020). Model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AICc), ΔAICc (the difference between the top-supported model and a given model), Akaike model weights (w_i, the weight of evidence in favor of model i), and model relative likelihood ($e^{-0.5\times wi}$). If there were no unambiguous best model (model relative likelihood > 0.125), we made inferences based on model-averaged predictions of the full model set (Burnham and Anderson 2002). Model selection and model-averaging were performed by using the "AICcmodavg" (Mazerolle 2020) and "MuMIn" (Bartoń 2020) packages in program R. Comparisons of model averaged predictions were considered significant if predicted values' upper and lower 95% confidence intervals did not overlap by more than 25% (Cumming and Fidler 2005).

Nest site selection

We modeled probability of nest site selection using conditional logistic regression in Program R with package "Survival" (Therneau et al. 2020). Conditional logistic models are used when covariates are associated with groups of data, which in our case consisted of one nest and a temporally clustered group of random points. In our models, habitat characteristics at each sparrow nest were compared to characteristics of all random points that were sampled at the same site during a period three wk prior to the nest reaching its final fate. This approach ensured temporal correspondence between vegetation data collected at nests and

random points (Kocek et al. 2022). The distance to the center point of the gull colony was used to quantify the intensity of exposure of each sparrow nest to the gull colony, a potential predator source. We created separate global models for Saltmarsh and Seaside Sparrow nest site selection. Conditional logistic models do not originate at an intercept; therefore, site was included in the global model as a categorical variable within which each of the other variables was nested, rather than as a main effect. Other variables in the model included elevation, maximum horizon angle (nested within each of two binary indicators: one for the urban site, one for the suburban site because the horizon line was 0° for all nests on the island), an indicator variable for whether the horizon object was located within 50 m, thatch height, distance to gull colony center (nested only within the "island" level of the site variable) and one live vegetation variable (average vegetation height, proportion cover of *S. patens*, or *S. alterniflora*, or *D. spicata*). These four live vegetation variables were not included in models together as they were closely correlated, but identical global models and their subsets were created and run for each vegetation variable. The interaction among site, elevation, and thatch height as well as the interaction among site, elevation, and the live vegetation variable were included. Additionally, for the island only, the interaction among elevation, distance to the gull colony, and thatch height as well as the interaction among elevation, distance to the gull colony, and the live vegetation variable were included. We also included the interaction between maximum horizon angle and the binary indicator for whether the horizon object was located within 50 m of the point, nested within the urban and suburban levels of the site variable. We assessed correlations among predictors and did not include variables in the same model if their Pearson's correlation was > 0.7 (Dorman et al. 2013). In all, we tested four sets of 15 models each for both sparrow species. Conditional logistic models do not allow for the testing of the intercept-only null model. We considered a model containing just elevation nested within site to be our null model, as it did not include any vegetation characteristics. All continuous variables were standardized with a z-transformation. Model selection was carried out following the same procedures as for the nest characteristics analysis. Standard errors on model-averaged predictions were calculated by using the delta method (Powell 2007) in the "msm R" package (Jackson 2019). Model averaged predictions were considered significantly different among levels of categorical predictors if predicted values' upper and lower 95% confidence intervals did not overlap by more than 25% (Cumming and Fidler 2005). Additionally, the delta method was used to derive the main effects and their standard errors of variables of interest that were part of interaction terms, with all other variables set to site- and species-specific mean values.

Nest survival

Daily nest survival was modeled by using the logistic exposure framework (Shaffer 2004). Logistic exposure models allow for variation in the intervals between nest visits, and do not require knowledge of the exact date of nest initiation or nest failure. Analysis was performed by using Program R. We modeled nest survival of Saltmarsh and Seaside Sparrows as a function of species (indicator variable), site (as two binary indicator variables: one for the island site [island = 1, not island = 0] and one for the suburban site [suburban = 1, not suburban = 0] with the urban site as the reference level), stage (1 = eggs, 0 = chicks), nest height, proportion canopy cover, elevation, daily maximum tide height, thatch height, distance to gull colony center (nested within the "island" level of the site variable), and one of the following live vegetation variables: average vegetation height, proportion cover of *S. patens*, *S. alterniflora,* or *D. spicata.* As in our nest site selection models, the latter four variables were not included in models together as they were closely correlated. Identical global models and their subsets were run for each of the four vegetation variables, including biologically relevant interactions among variables. Maximum tide height values represented the greatest tide height that occurred between each nest check interval. The global model included the interaction of site with each of the following variables: thatch height, one live vegetation variable, elevation, maximum tide, and year. It also included two-way interactions of canopy cover × nest stage, species × year, distance to gull (nested in the island site) × thatch height, and one live vegetation variable × elevation. Additionally, it included an interaction among elevation, maximum tide height, nest height, sparrow species, and nest stage. All continuous variables were standardized with a z-transformation. In all, we tested 4 sets of 14 models each. Model selection was performed as described above for our nest site selection models. We calculated standard errors on the predictions using the delta method (Powell 2007) in the "msm" package (Jackson 2019) in Program R. We also used the delta method to derive the main effects of vegetation variables that were part of interactions, with all other variables set to site- and species-specific means. Daily nest survival for sparrows was converted to interval survival by raising daily survival estimates to the 12th power for the egg stage, and 9th power for the chick stage to represent the interval number of days for each stage, then multiplying those two products (Mayfield 1961, 1975). When stage was not included in predictions, daily survival was raised to the 21st power to calculate the survival of the entire sparrow nesting period.

RESULTS

Our study included 263 Saltmarsh Sparrow nests and 130 Seaside Sparrow nests and had known fates for 97% of them. Of all nests monitored, 29% fledged, 56% were known to have flooded, 12% were known to have been predated, and 3% had unknown fates. Nest flooding occurred at all sites in both years. Predation was observed at all sites in 2018 but was primarily observed at the urban site in 2019 (Table 1).

Nest characteristics

The top ranked nest height model contained only species and site (Table 2). Based on the degree of confidence interval overlap between model-averaged estimates, Saltmarsh and Seaside Sparrow mean nest heights at the urban site were significantly higher than at the suburban and island site (Table 3). Saltmarsh Sparrow nest heights at the urban site were 32% higher than nests at the suburban site and 57% higher than the island site. Seaside Sparrow nest heights at the urban site were 42% higher than Seaside Sparrow nests at the island site. At all sites, Seaside Sparrow mean nest heights were significantly higher (19% higher at the urban site, 33% higher at the island site) than Saltmarsh Sparrow nest heights (Table 3). At the island site, distance to gull colony did not influence nest height (Table 3).

Proportion canopy cover of sparrow nests was best explained by the species-only model; however, there was support for models containing distance to gull colony (Table 2). Mean proportion

Table 1. Known nest fates recorded for Saltmarsh Sparrow and Seaside Sparrow nests monitored at an urban, suburban, and island site in New York, 2018–2019.

	Saltmarsh Sparrow						Seaside Sparrow					
	Urban		Suburban		Island		Urban		Suburban		Island	
Nest Fate	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Fledged	4	4	2	5	18	25	12	11	0	0	13	20
Flooded	12	44	11	6	38	56	6	14	0	1	12	20
Predated	5	10	4	1	8	0	4	14	0	0	1	0
Unknown fail	1	0	0	0	1	2	0	0	0	0	0	0
Unknown fate	1	0	0	0	3	2	0	0	0	0	0	2
All	23	58	17	12	68	85	22	39	0	1	26	42

Table 2. Model structure and information-theoretic model selection criteria for Saltmarsh Sparrow (n = 252) and Seaside Sparrow (n = 127) nest height and canopy cover models in New York, 2018–2019. Models with a ΔAICc less than 2 are shown. *k* is the number of parameters in a model, ΔAICc is the difference between the top-supported model and a given model in AICc units, and *wi* is the model weight, relative likelihood is the likelihood ratio between a given model and the top model, and deviance is a measure of error between observations and predictions.

Nest characteristic	Model	*k*	ΔAICc	*wi*	Relative likelihood	Deviance
Nest height	Species + Site	5	0	0.47	1.00	1117.15
	Species × Site	7	1.16	0.26	0.56	1115.65
	Species + Site + Distance to Gull (Island)	6	1.89	0.18	0.39	1117.06
Canopy cover	Species	3	0	0.31	1.00	59.60
	Species × Distance to Gull (Island)	5	0.07	0.29	0.97	57.58
	Species + Distance to Gull (Island)	4	1.81	0.12	0.40	59.48
	Species + Site	5	1.86	0.12	0.39	58.48

canopy cover estimates were 13% greater for Saltmarsh Sparrows than Seaside Sparrows at the urban site and the island site near gulls (Table 3). At the island far from gulls, Saltmarsh Sparrow mean proportion canopy cover was 18% greater than Seaside Sparrows (Table 3). Distance to gull colony had a weak negative effect on proportion canopy cover for Seaside Sparrows at the island site but had no relationship for Saltmarsh Sparrows (Table 3).

Nest site selection

Models containing proportion cover by *S. alterniflora* had lower AICc values than models containing average vegetation height or proportion cover by the other two grass species, indicating that of the live vegetation variables, proportion cover by *S. alterniflora* best explained variation in nest site selection for both sparrow species (Table 4). There was strong support for the interactions among site, proportion cover of *S. alterniflora*, and elevation, which appeared in all of the top models (Table 4). The interaction among site, thatch height, and elevation was also strongly supported in our results and appeared in all top models (Table 4), and had regression coefficient confidence intervals that do not overlap 0 (Appendix Tables A1 and A2). The interaction between proportion cover of *S. alterniflora* and distance to the gull colony on our island site was also in the top model (Table 4) but the regression parameter confidence limits contained 0 (Appendix Tables A1 and A2). The top model contained fewer parameters than the subsequent two models that had some support, indicating the additional parameters, including openness parameters, were non-informative (Arnold 2010). Therefore, only the top model was used for further inference.

At the urban site, both sparrows strongly selected for greater proportion of *S. alterniflora* at nest sites at high elevations. In areas of low elevation, Seaside Sparrows showed no selection for the covariates in our models, and Saltmarsh Sparrows selected against proportion of *S. alterniflora* (Fig. 1). On the island site, both sparrow species also selected for greater proportion of *S. alterniflora* at high elevations and close to the gull colony. In contrast, far from the gull colony, Saltmarsh Sparrows showed no selection for *S. alterniflora* and Seaside Sparrows selected against it (Fig. 1). Nest site selection by sparrows at all sites was positively related to thatch height when all other covariates were at their site- and species-specific means (Appendix Table A3).

Nest survival

Nest survival models containing average vegetation height had a lower AICc than models containing proportion foliar cover by any of the three grass species. The top model contained 76% of the weight. The four-way interaction among tide height, species, nest height, and nest stage was significant with regression coefficient confidence intervals that did not overlap 0 (Appendix Table A4). The top model also contained elevation and the two-way interactions between tide and site, canopy cover and nest stage, year and site, year and species, and vegetation height and site. The top model did not contain distance to the gull colony or thatch height parameters (Appendix Table A4).

Mean daily and interval nest survival were greatest at the island site (Table 5) and were overall lower in 2019 than 2018 for both species, except for Saltmarsh Sparrows at the suburban site (Table 5). Nest survival was negatively associated with maximum tide height and was greater during the chick stage than egg stage for both sparrow species at all sites (Fig. 2). Nest survival of both Saltmarsh and Seaside Sparrows at the suburban and island site during both the chick and egg stage were strongly negatively associated with tide height (Fig. 2). However, at the urban site, particularly for Saltmarsh Sparrow nests at the chick stage and

Table 3. Model-averaged mean nest height and mean proportion woven canopy cover estimates, standard errors (SE), and lower 2.5% (LCL) and upper 97.5% confidence limits (UCL) of Saltmarsh Sparrow and Seaside Sparrow nests at an urban, suburban, and island site, New York, 2018–2019. Island site predictions made with distance to gull parameters set to close (30 m from colony center) and far (200 m from colony center) values.

			Nest height (cm)				Proportion woven canopy cover			
Site	Species	*n*	Mean	SE	LCL	UCL	Mean	SE	LCL	UCL
Urban	Saltmarsh Sparrow	77	21.2	0.51	20.20	22.20	0.78	0.02	0.73	0.82
	Seaside Sparrow	61	25.26	0.57	24.15	26.37	0.69	0.03	0.63	0.75
Suburban	Saltmarsh Sparrow	25	15.95	0.92	14.15	17.75	0.76	0.04	0.69	0.84
	Seaside Sparrow	1	NA[†]	NA	NA	NA	NA	NA	NA	NA
Island (near to gulls)	Saltmarsh Sparrow	150[‡]	13.55	0.38	12.80	14.29	0.78	0.02	0.74	0.82
	Seaside Sparrow	66[§]	18.02	0.55	16.94	19.10	0.69	0.03	0.63	0.74
Island (far from gulls)	Saltmarsh Sparrow	150[‡]	13.59	0.4	12.81	14.37	0.78	0.03	0.73	0.84
	Seaside Sparrow	66[§]	18.06	0.55	16.99	19.13	0.66	0.05	0.56	0.75

[†] Not enough Seaside Sparrows nests at our suburban site to include in analysis.
[‡] Distance to gull was a continuous variable; this was the total sample size of Saltmarsh Sparrow nests on the island.
[§] This was the total sample size of Seaside Sparrow nests on the island.

Seaside Sparrow nests at the egg stage, the relationship was not as pronounced, even though the greatest tide heights in our study areas occurred at the urban site (Fig. 2). Despite elevation appearing in top models, the relationship between nest survival and elevation appeared to be a poor predictor of nest survival for tidal marsh sparrows in this study, as the slopes were shallow and the confidence limits very wide.

We observed a strong positive effect of nest height on survival of Saltmarsh Sparrow nests at the egg stage at low and mean maximum tide heights, but not at high tide heights (Table 6). This relationship was reversed for Saltmarsh Sparrow chicks, with a negative effect of nest height at low maximum tide heights, but positive at high maximum tide heights (Table 6). For Seaside Sparrows, a positive relationship between nest height and nest survival at both the egg and chick stage was evident at high tide heights, but no relationship was observed at low and mean tides (Table 6). Vegetation height surrounding the nest had a strong positive effect on nest survival at the urban and island sites with sparrow species pooled, but there was no clear relationship at the suburban site (Fig. 3).

DISCUSSION

We found that Saltmarsh and Seaside Sparrows can have breeding seasons that are successful or at least comparable to range-wide nest success rates, even in degraded environments experiencing high rates of tidal flooding, by nesting in tall vegetation at high elevations. Nest site selection for both sparrows was best explained by models containing *S. alterniflora*, a tall and sturdy but low-elevation species of cordgrass. A significant positive relationship between nest site selection and proportion of *S. alterniflora* was detected at the urban site, but only in areas of higher elevation. On the island, the mediating effect of proximity to the gull colony on the relationship between nest site selection and the combination of elevation and *S. alterniflora* suggests a role for the perceived threat of predators in choosing nest vegetation at particular elevations. However, without a gull-free reference island of similar elevation to our island site, we cannot conclude with certainty how important the presence of gulls was compared to flooding risk in determining patterns in nest site selection. The strength of selection for areas dominated by *S. alterniflora* appears to contradict previous studies in which Saltmarsh Sparrow nests were associated with the high-elevation marsh zones dominated by *S. patens* and tall thatch, although selection in these studies did often include low proportions of a mosaic of other tall vegetation types, including *S. alterniflora* (Gjerdrum et al. 2005, Shriver et al. 2007, Greenlaw et al. 2020).

The tall rigid structure of *S. alterniflora* may allow sparrows to build their nests higher off the ground to mitigate flooding risk while also providing cover from predators. Our prediction that sparrows nesting in close proximity to the gull colony would place their nests lower to the ground and with greater woven canopy cover to reduce risk of predation (Hunter et al. 2016) was not supported by our observations. Canopy cover did not differ significantly between nests near and far from gulls and although nest heights on the island were significantly lower than at our other two sites they were well within the expected range for these species (Greenlaw et al. 2020, Kocek et al. 2022). At our island site, there was little evidence of birds intentionally attempting to distance themselves from the gull colony. In a similar study on an island off the coast of New Brunswick, Canada, Wheelwright et al. (1997) found that Herring Gulls opportunistically predated Savannah Sparrow (*Passerculus sandwichensis*) nests, and sparrows nesting among the gulls were found to make microhabitat selections (taller and denser vegetation), coupled with increased cryptic behaviors, which allowed them to successfully nest among gulls relatively undetected. In this study, sparrows nesting near gulls had lower rates of chick predation and comparable overall nest survival to sparrows nesting away from gulls. Our results could similarly indicate that the tall structure of *S. alterniflora* within this undisturbed marsh provided sparrow nests not only the height needed to avoid flooding, but also cover from nearby predators.

At the urban site, nests were significantly higher off the ground than at the other two sites. The urban marsh experienced higher maximum tide heights than the island and suburban sites; therefore, we believe sparrows had to build their nests both high

Table 4. Model structure and information-theoretic model selection criteria for Saltmarsh Sparrow (n = 252), Seaside Sparrow (n = 127) nest site selection models in New York, 2018–2019. Models with a ΔAICc less than 2 are shown. *k* is the number of parameters in a model, ΔAICc is the difference between the top-supported model and a given model in AICc units, and *wi* is the model weight, relative likelihood is the likelihood ratio between a given model and the top model, and deviance is a measure of error between observations and predictions.

Species	Model	*k*	ΔAICc	*wi*	Relative likelihood	Deviance
Saltmarsh Sparrow	Elevation × Proportion cover *S. alterniflora*[†] × Site + Elevation × Thatch Height × Site + Proportion cover *S. alterniflora* × Distance to Gull (Island) + Elevation × Distance to Gull (Island) + Elevation × Proportion cover *S. alterniflora* × Distance to Gull (Island)	19	0.00	0.36	1.00	519.28
	""[‡] + Elevation × Thatch Height × Distance to Gull (Island) + Horizon Under 50 m YN × Horizon Max Angle × Site Suburban	23	0.89	0.23	0.64	514.95
	"" + Thatch Height × Distance to Gull (Island)	20	1.98	0.14	0.37	519.09
	Elevation × Site (Null)	3	604.77	0.00	0.00	839.25
Seaside Sparrow	Elevation × Proportion cover *S. alterniflora*[§] × Site + Elevation × Thatch Height × Site + Elevation × Distance to Gull (Island) + Elevation × Proportion cover *S. alterniflora* × Distance to Gull (Island)	14	0.00	0.48	1.00	206.60
	""[‡] + Elevation × Thatch Height × Distance to Gull (Island) + Horizon Under 50 m × Horizon Max Angle × Urban Site	18	1.12	0.27	0.57	201.82
	"" + Thatch Height × Distance to Gull (Island)	15	1.99	0.18	0.37	206.30
	Elevation × Site (Null)	2	440.10	0.00	0.00	440.53

[†] Top models that included average vegetation height and proportion cover of *S. patens* or *D. spicata* (instead of *S. alterniflora*) had a ΔAICc from the top Saltmarsh Sparrow of 43.52, 42.18, 47.38, respectively.
[‡] "" = all model terms from the top model.
[§] Top models that included average vegetation height and proportion cover of *S. patens* or *D. spicata* (instead of *S. alterniflora*) had a ΔAICc from the top Seaside Sparrow model of 38.26, 37.25, 42.00, respectively.

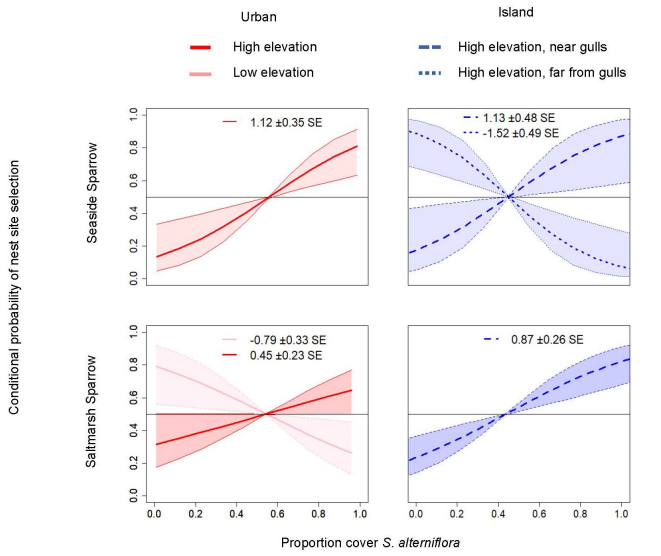


Fig. 1. Conditional probability of nest site selection versus proportion cover of *S. alterniflora* of Seaside Sparrows and Saltmarsh Sparrows at low elevation (0.65 m, pink) and high elevation (0.75 m, red) at an urban site, and at high elevation (0.75 m) near a gull colony (−1 SD from mean distance to colony center, blue long dash) and far from a gull colony (+1 SD from mean distance to colony center, blue short dash) at an island site in New York, 2018–2019. Derived main effects (regression parameters) at each elevation displayed in legends. Horizontal line at 0.5 indicates no selection. Prediction lines for levels of the interaction with a slope not different from 0 are not displayed. Shaded areas are 95% confidence intervals. Sample sizes: Saltmarsh Sparrows (urban n = 77, island n = 136), Seaside Sparrows (urban n = 61, island n = 66).

off the ground and at higher elevations than at other sites to have any chance of avoiding nest flooding. These observations of taller nest heights at the most urbanized site are consistent with results reported in Kocek et al. (2022), who found sparrows in NYC marshes had significantly taller nest heights than those observed in other parts of the species' range, partially attributed to overall taller marsh vegetation heights in NYC. Salt marshes in NYC are experiencing increased inundation frequency and are known to be sinking because of sediment starvation (Peteet et al. 2018), causing increased flooding on *S. patens*–dominated areas (Hill and Anisfeld 2015) and making them potentially risky sites for nesting. Additionally, it appears possible that the elevation at all three of our study sites may not be high enough to allow large patches of high-quality *S. patens* to dominate, requiring birds to seek alternate nesting habitat and intensifying the importance of *S. alterniflora* as nesting habitat.

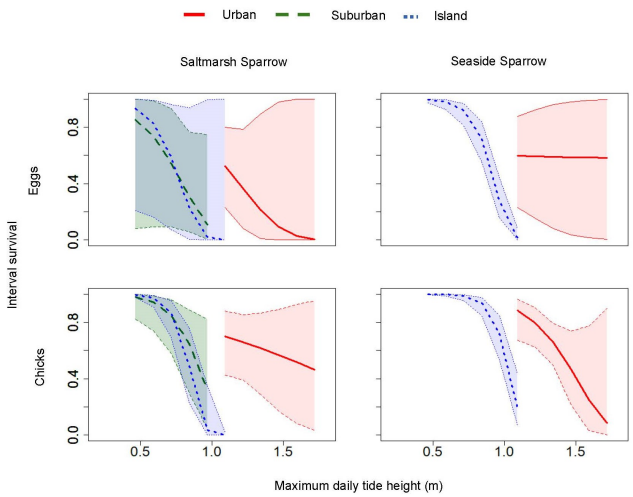
Although elevation appeared to play a role in nest site selection, we did not detect a strong relationship between elevation and nest survival at any site, with the suburban site even showing a negative relationship between elevation and nest survival. At the latter site, high elevations potentially provided easy access to nesting areas by predators. These results contradicted our hypotheses and previous studies showing a strong benefit of elevation to nest success (Shriver et al. 2007, Benvenuti et al. 2018). Elevation at our sites may already be below optimal thresholds for high-marsh specialists like the Saltmarsh Sparrow, making the effect of elevation less observable than at other sites. Nest survival was instead best explained by average vegetation height, suggesting that in marshes with suboptimal elevations for nesting, the only option for sparrows to mitigate flood risk may be to build their nests high off the ground in tall vegetation. Mean daily nest survival estimates for Saltmarsh Sparrows at the island site in both years were greater than other studies in the species' ranges, including in Connecticut (0.94 ± 0.01 SE, Gjerdrum et al. 2005), Maine (0.967 ± 0.006, Shriver et al. 2007), predation-prone sites

Table 5. Daily (1 d) and interval (21 d) nest survival estimates of Saltmarsh Sparrow and Seaside Sparrow nests in 2018 and 2019 in New York. Mean nest survival was estimated from logistic exposure models with all predictor variables set to mean values averaged across the entire study (for continuous variables that did not interact with categorical variables) or within levels of categorical variables (for those continuous variables that interacted with categorical variables).

		Saltmarsh Sparrow						Seaside Sparrow					
		2018			2019			2018			2019		
Site	Exposure days	n	Estimate	SE	n	Estimate	SE	n	Estimate	SE	n	Estimate	SE
Urban	1	20	0.924	0.076	46	0.87	0.148	21	0.970	0.011	38	0.882	0.036
Suburban	1	13	0.394	0.328	8	0.783	0.27	NA[†]	NA	NA	NA	NA	NA
Island	1	57	0.977	0.01	79	0.975	0.02	24	0.994	0.003	21	0.985	0.006
Urban	21	20	0.189	0.326	46	0.054	0.191	21	0.525	0.130	38	0.071	0.062
Suburban	21	13	0.000	0.000	8	0.006	0.042	NA	NA	NA	NA	NA	NA
Island	21	57	0.612	0.130	79	0.594	0.262	24	0.881	0.063	21	0.726	0.097

[†] Not applicable (species did not use the site).

Fig. 2. Interval survival of Saltmarsh Sparrow and Seaside Sparrow in the egg stage (12 d) and chick stage (9 d) versus daily maximum tide height at an urban site, a suburban site, and an island site in New York, 2018–2019. Shaded areas are 95% confidence intervals. Sample sizes: Saltmarsh Sparrows (urban n = 68, suburban n = 22, island n = 136), Seaside Sparrows (urban n = 59, suburban n = 65).



in New Jersey (0.94, calculated from regression coefficients in Roberts et al. 2017), and the mean range-wide estimate (0.938 ± 0.006, Ruskin et al. 2015). Seaside Sparrows at both the island and urban site had greater daily nest survival than was found by a study in Connecticut (0.94 ± 0.02 SE, Gjerdrum et al. 2005). Daily nest survival probabilities of Saltmarsh and Seaside Sparrow nests at the urban site in 2018 were similar to results from other non-urban locations (Gjerdrum et al. 2005, Roberts et al. 2017). Thus, even under the difficult conditions faced at our urban site and variation in typical nest selection strategies, the nesting success of both species was comparable to other locations within the range, in at least one year. But in 2019 in the urban marsh, nest survival of Saltmarsh Sparrows was much lower than observed in other studies. We note that even though sparrows at our sites were able to achieve similar nest survival to locations with higher quality habitat, reproductive success range-wide is not considered sufficient for a sustainable population.

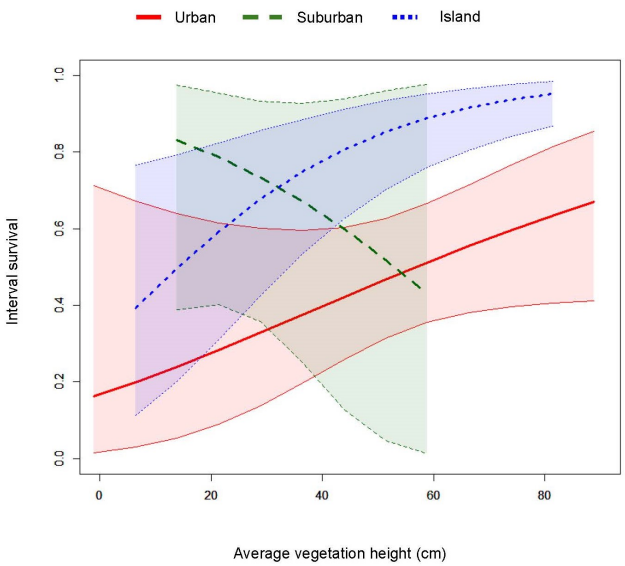
Although nest survival was positively correlated with vegetation height at the urban and island sites, predictions of nest survival at maximum vegetation heights at the urban site remained significantly lower than predicted nest survival for the island site at the same vegetation heights. These results indicate that simply placing nests in tall vegetation and high off the ground at the urban site was not sufficient to mitigate nest failure risk. Tide height was another strong predictor of nest survival, as seen in other studies (Shriver et al. 2007, Bayard and Elphick 2011, Ruskin 2015, Benvenuti et al. 2018). However, we observed variation among sites in the strength of the effect of tide height on nest survival. Nest survival at the suburban and island sites had a strong negative relationship with maximum tide height and daily survival was nearly 100% at the lowest tide height. In contrast, at the urban site nest survival at locally low maximum tide heights remained low, and the effect of tide height was weaker. Both of these findings suggest that another factor besides flooding exerted a strong effect on nest survival at the urban site, with the primary candidate being predation, as starvation in tidal systems is rare and was not observed (Post and Greenlaw 2006). Although we did not have adequate sample sizes of predation events across all sites and years to model the probabilities of specific nest fates, the majority of confirmed nest predation events occurred at the urban site and mammalian predator sign at the urban site was common. We hypothesize that these predation events occurred during periods of lower tidal flow that provide easier access to terrestrial mammals. Such a pattern would explain our model results and those of other studies (Jobin and Picman 1997), but this hypothesis remains untested.

Altering nest height is one strategy sparrows have to mitigate risk of nest loss. We found that the interaction between nest height, tide height, species, stage, and site improved our nest survival models and illuminated variations of the effects of nest height at different development stages (eggs versus chicks) and tide heights. The strong negative effect of nest height on nest survival for

Table 6. Derived main effect (regression parameter) of nest height (cm) on nest survival at different daily tide heights (m) relative to the study wide mean for Saltmarsh Sparrow and Seaside Sparrow nests at the egg and chick stage in New York, 2018–2019. Sample sizes: Saltmarsh Sparrows (urban n = 68, suburban n = 22, island n = 136), Seaside Sparrows (urban n = 59, island n = 65).

Relative tide height	Saltmarsh Sparrow eggs		Saltmarsh Sparrow chicks		Seaside Sparrow eggs		Seaside Sparrow chicks	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
−1 SD (low)	1.014	0.347	−0.965	0.468	−0.647	0.556	0.319	0.933
Mean	0.572	0.215	0.027	0.251	0.201	0.310	0.637	0.569
+1 SD (high)	0.129	0.194	1.018	0.366	1.049	0.356	0.955	0.345

Fig. 3. 21-d interval nest survival estimates with sparrow species pooled versus average vegetation height in 1-m quadrats around the nest at an urban site (n = 127), suburban site (n = 22), and an island site (n = 201) in New York, 2018–2019. Shaded dashed lines are 95% confidence intervals.



Saltmarsh Sparrows during the chick stage and Seaside Sparrows during the egg stage that our models predicted at low tide heights could again indicate predators were causing nest failure during times of lower tidal flow. In addition to access being easier during lower tides, nests higher off the ground in sparse vegetation and nests that contain moving and vocalizing chicks can be more visible and at greater risk of predation than nests lower to the ground or nests with eggs. However, nests higher off the ground that are able to avoid predation until chicks hatch should have an enhanced probability of avoiding inundation during higher tides because chicks can climb out of their nest to escape flooding (Hunter 2016, Apgar 2023). Conversely, in the egg stage, nest height only had a positive effect on Saltmarsh Sparrow nest survival during low and mean tides, but not at high tides. It is likely that nests cannot be built at a suitable height above the ground to completely avoid flooding during the periods of highest tidal flow, and only nests in the chick stage can survive these tides because chicks can climb even higher off the ground into the vegetation above the nest.

Although variation in nesting strategies can allow species to cope with changing environmental conditions (Forstmeier and Weiss 2004), tidal marsh sparrow studies have concluded that these types of shifts in habitat selection or behavior may not be able to outpace the rapid and large-scale changes caused by climate change (Correll et al. 2017, Benvenuti et al. 2018). Our case study, which included two sites with conditions that would be considered suboptimal, provides insights and suggests hypotheses as to how sparrows may respond to changing conditions over time and how they might maintain reproductive output. These hypotheses can be tested through replication at other locations in the species' range where habitat conditions are, or may soon become, suboptimal, as most studies of these species to date have occurred in less degraded sites.

Suboptimal habitat conditions are likely to become more widespread as climate change and human development of coastlines continue. Results from our study suggest the importance of planting or maintaining tall vegetation along the elevational gradient during marsh restoration projects. Our results also suggest, but do not confirm, that predation can have a heavy impact on nest survival at lower tides. Therefore, studying predation risk and surrounding predator communities when implementing restoration to support tidal marsh sparrows is suggested. In urban areas, predation by human commensal predators (Kristan and Boarman 2003, Oro et al. 2013, Newsome and Van Eeden 2017) can act as an extra stressor to already small habitat patches, which in conjunction with high-water levels may make it increasingly difficult for tidal marsh birds to succeed in degraded marshes. Because it can take many years before desired habitat conditions develop post-restoration (Warren et al. 2002), it would be prudent for managers restoring marshes with active sparrow nesting populations to consider the role of tall vegetation in providing escape cover from predators and flooding. As tidal marshes across our coastlines degrade because of the impacts of sea level rise, tidal marsh restoration projects will become more necessary and likely more commonplace. Finding ways to maintain active sparrow nesting populations while restoration projects occur will be critical to the persistence of the species, and our results suggest important facets of nest cover for such endeavors.

Author Contributions:

Author contributions: JBC acquired funding. JBC and ARK designed the study. AMC and ARK supervised and collected data. AMC, JBC and ARK analyzed data. AMC, JBC and ARK wrote the manuscript.

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Supplemental Table 1. Top ranking Saltmarsh Sparrow habitat selection model coefficient estimates, standard error (SE), upper 95% confidence limit (UCL) and lower 95% confidence limit (LCL), New York, 2018-2019.

Model term	Coefficient estimate	SE	LCL	UCL
Proportion *S. alterniflora*	-0.02	0.17	-0.35	0.30
ThatchHeight	0.96	0.12	0.74	1.19
Elevation	0.03	0.30	-0.57	0.62
Proportion *S. alterniflora*×Suburban	0.53	0.35	-0.16	1.23
Proportion *S. alterniflora*×Island	0.21	0.29	-0.36	0.78
ThatchHeight×Suburban	1.84	0.50	0.86	2.83
ThatchHeight×Island	0.55	0.21	0.13	0.96
Island(DistancetoGull)	0.32	0.18	-0.03	0.67
Elevation×Island	1.39	0.37	0.66	2.12
Elevation×Suburban	1.69	0.54	0.63	2.75
Proportion *S. alterniflora*×Elevation	0.96	0.35	0.27	1.65
ThatchHeight×Elevation	0.09	0.22	-0.34	0.51
Proportion *S. alterniflora*×DistancetoGull(Island)	-0.25	0.18	-0.61	0.10
Proportion *S. alterniflora*×Elevation×Island	-0.64	0.41	-1.46	0.17
Proportion *S. alterniflora*×Elevation×Suburban	-1.02	0.50	-2.00	-0.05
ThatchHeight×Elevation×Island	1.03	0.28	0.47	1.58
ThatchHeight×Elevation×Suburban	1.63	0.42	0.80	2.45
Elevation×Island×DistancetoGull	0.03	0.22	-0.39	0.46
Proportion *S. alterniflora*×Elevation×DistancetoGull(Island)	-0.54	0.22	-0.97	-0.12

Supplemental Table 2. Top ranking Seaside Sparrow habitat selection model coefficient estimates, standard error (SE), upper 95% confidence limit (UCL) and lower 95% confidence limit (LCL), New York, 2018-2019.

Model term	Coefficient estimate	SE	LCL	UCL
Proportion *S. alterniflora*	0.98	0.29	0.41	1.55
ThatchHeight	1.06	0.14	0.79	1.32
Elevation	0.32	0.46	-0.58	1.21
Proportion *S. alterniflora*×Island	-1.60	0.53	-2.65	-0.56
ThatchHeight×Island	1.65	0.38	0.91	2.38
DistancetoGull(Island)	-0.25	0.34	-0.92	0.41
Elevation×Island	0.73	0.60	-0.44	1.90
Proportion *S. alterniflora*×Elevation	0.28	0.47	-0.64	1.20
ThatchHeight×Elevation	0.22	0.24	-0.25	0.69
Proportion *S. alterniflora*×DistancetoGull(Island)	-0.64	0.34	-1.31	0.03
Proportion *S. alterniflora*×Elevation×Island	0.57	0.62	-0.64	1.78
ThatchHeight×Elevation×Island	0.96	0.40	0.18	1.75
Elevation×DistancetoGull(Island)	-0.24	0.36	-0.93	0.46
Proportion *S. alterniflora*×Elevation×DistancetoGull(Island)	-1.39	0.40	-2.16	-0.61

Supplemental Table 3. Derived main effects (regression parameters) and standard errors of parameters of interest in top habitat selection models at an urban site, suburban and island site in New York, 2018-2019.

		Urban		Suburban		Island	
Species	Variable	Main effect	SE	Main effect	SE	Main effect	SE
Saltmarsh Sparrow	Average vegetation height	0.10	0.17	-0.39	0.65	0.53	0.30
	Proportion cover *S. alterniflora*	-0.02	0.17	0.51	0.31	0.19	0.24
	Proportion cover *D. spicata*	-0.19	0.26	-0.70	0.63	0.18	0.19
	Proportion cover *S. patens*	0.26	0.13	0.17	0.24	0.43	0.21
	Thatch height	0.96	0.12	2.81	0.49	1.51	0.18
Seaside Sparrow	Average vegetation height	0.70	0.20	NA[†]	NA	-0.17	0.36
	Proportion cover *S. alterniflora*	0.98	0.57	NA	NA	-0.62	0.65
	Proportion cover *D. spicata*	-0.04	0.26	NA	NA	-0.08	0.36
	Proportion cover *S. patens*	-0.93	0.60	NA	NA	1.19	0.71
	Thatch height	1.06	0.14	NA	NA	2.70	0.35

Supplemental Table 4. Top ranking sparrow nest survival model coefficient estimates, standard error (SE), upper 95% confidence limit

(UCL) and lower 95% confidence limit (LCL), New York, 2018-2019.

Model term	Coefficient estimate	SE	LCL	UCL
(Intercept)	5.07	0.68	3.74	6.40
Incubating	-1.16	0.41	-1.95	-0.36
Species	-1.33	0.48	-2.27	-0.39
Island	-0.93	0.62	-2.14	0.28
Suburban	-2.76	1.05	-4.81	-0.71
Average vegetation height	0.26	0.17	-0.06	0.59
MaxTide	-1.64	0.48	-2.58	-0.71
NestHeight	0.64	0.57	-0.48	1.75
CanopyCover	-0.17	0.13	-0.43	0.09
Elevation	0.15	0.10	-0.05	0.35
Year	-1.46	0.41	-2.26	-0.66
Island×Average vegetation height	0.34	0.22	-0.10	0.77
Suburban×Average vegetation height	-0.78	0.66	-2.07	0.51
Island×MaxTide	-1.71	0.48	-2.66	-0.76
Suburban×MaxTide	-0.73	0.74	-2.17	0.71
MaxTidexNestHeight	0.32	0.41	-0.49	1.13
SpeciesxMaxTide	0.61	0.46	-0.29	1.50
SpeciesxNestHeight	-0.61	0.60	-1.79	0.56

Stage×MaxTide	0.54	0.49	-0.42	1.50
Stage×NestHeight	-0.44	0.61	-1.63	0.76
Stage×Species	0.94	0.49	-0.03	1.91
Stage×CanopyCover	0.09	0.16	-0.22	0.40
Island×Year	0.53	0.38	-0.22	1.28
Suburban×Year	2.31	0.93	0.48	4.13
Species×Year	0.87	0.41	0.07	1.66
Species×MaxTide×NestHeight	0.67	0.53	-0.36	1.71
Stage×MaxTide×NestHeight	0.53	0.53	-0.50	1.56
Stage×Species×MaxTide	-0.21	0.57	-1.33	0.91
Stage×Species×NestHeight	0.98	0.67	-0.34	2.30
Stage×Species×MaxTide×NestHeight	-1.96	0.64	-3.22	-0.70