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Research Paper

Imperiled sparrows can exhibit high nest survival despite atypical nest site selection in urban saltmarshes

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ABSTRACT. Understanding habitat selection and its fitness consequences in remnant populations of birds in fragmented and urbanized habitat may provide guidance to land managers for imperiled species conservation. We studied Saltmarsh Sparrow, *Ammospiza caudacuta*, and Seaside Sparrow, *A. maritima*, nest site selection and nest survival at five sites in New York City (NYC) and one site on western Long Island, New York in 2012 and 2013. We compared marsh vegetation and nest structure characteristics between our study sites and other studied sites for these species in the Northeastern United States. Saltmarsh Sparrows in NYC selected nest sites with the tall form of low-elevation marsh grass (at two sites this was above the proportion available), which is atypical for this species, and Seaside Sparrows selected an upland shrub species at one site, possibly to compensate for a lack of tall low-elevation marsh grasses. Daily nest survival at New York sites increased with nest height above the ground for both species, contrary to previous studies for Saltmarsh Sparrows in intact habitat. Mean nest height for both species was found to be taller in NYC than at other studied locations, and NYC sites may have had taller than average vegetation available, indicating that these sparrows may be able to adapt to some changing marsh characteristics. The difference in nest site selection observed in NYC populations from published studies did not appear to have a cost to nest survival in at least one year. Although high-elevation marsh is the optimal habitat restoration target for Saltmarsh Sparrows, it may be difficult to create in small, urbanized marshes, and our results suggest that other approaches may be successful. A mix of substrates and vegetation heights may allow sparrows to exhibit variation in nest site selection and promote nest survival in the face of changing limiting factors.

Des bruants en péril présentent un taux élevé de survie au nid malgré une sélection atypique de sites de nidification dans des marais salants urbains

RÉSUMÉ. La compréhension de la sélection de l’habitat et de ses conséquences sur la condition physique des populations résiduelles d’oiseaux dans un milieu fragmenté et urbanisé peut fournir aux gestionnaires de territoire des orientations en matière de conservation d’espèces en péril. Nous avons examiné la sélection des sites de nidification et la survie des nids du Bruant à queue aiguë, *Ammospiza caudacuta*, et du Bruant maritime, *A. maritima*, à cinq sites dans la ville de New York (NYC) et à un site dans l’ouest de Long Island, New York, en 2012 et en 2013. Nous avons comparé les caractéristiques de la végétation des marais et de la structure des nids entre nos sites d’étude et d’autres sites étudiés pour ces espèces dans le nord-est des États-Unis. Les Bruants à queue aiguë de New York ont choisi des sites de nidification où se trouvaient des graminées de grande taille en bas terrain (sur deux sites, la taille était supérieure à la proportion disponible), choix qui est atypique pour cette espèce, et les Bruants maritimes ont choisi une espèce d’arbuste en terrain élevé sur un site, peut-être pour compenser le manque de grandes graminées en bas terrain. La survie quotidienne des nids aux sites de New York a augmenté avec la hauteur du nid pour les deux espèces, contrairement aux études précédentes sur les Bruants à queue aiguë dans un habitat naturel. La hauteur moyenne des nids des deux espèces s’est avérée plus élevée à New York qu’aux autres endroits étudiés, et les sites de New York présentaient peut-être une végétation plus haute que la moyenne, résultat qui indique que ces bruants sont peut-être capables de s’adapter à certaines caractéristiques différentes des marais. La différence entre la sélection des sites de nidification observée dans les populations de NYC et celle tirée d’études publiées n’a pas semblé avoir un coût pour la survie des nids pendant au moins une année. Bien que le marais situé en terrain élevé soit la cible optimale de restauration de l’habitat pour le Bruant à queue aiguë, il peut être difficile à créer dans les petits marais urbanisés, et nos résultats indiquent que d’autres approches peuvent être fructueuses. Un mélange de substrats et de hauteurs de végétation peut permettre aux bruants d’avoir le choix de leur site de nidification et favoriser la survie des nids face à des facteurs limitatifs changeants.

Key Words: *Ammospiza caudacuta; Ammospiza maritima; biological conservation; habitat restoration; habitat selection; nest site selection; nest survival; saltmarsh; Saltmarsh Sparrow; Seaside Sparrow; tidal marsh birds; urban ecosystem*

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INTRODUCTION

The relationship between avian nest survival and habitat selection has important implications for species distributions and for conservation planning (Jones 2001). Nest site selection is expected to be shaped by fitness within a particular ecosystem. When these two factors are no longer positively correlated, an ecological trap may result (Misenhelter and Rotenberry 2000). For altricial birds, fledgling production is often most influenced by availability of food for provisioning nestlings (Martin 1987, Holmes et al. 1992, Marshall and Cooper 2004, Post and Greenlaw 2006), coverings that conceal nests from predators (Martin and Roper 1988, Liebezeit and George 2002), or nest placement and structures that protect nestlings from abiotic factors (Post and Greenlaw 1982, Martin 2001). High quality habitat features are not always available to all individuals because of competition for limited nest sites by native (Dobkin et al. 1995) or introduced species (Schlaepfer et al. 2005, McChesney and Anderson 2015), or because of habitat fragmentation or degradation (Stephens et al. 2004, Berger-Tal and Saltz 2016). Self-sustaining populations may persist in patches of abject habitat if individuals can adjust their breeding strategies to novel habitat arrangements over time (Yeh et al. 2004, Salinas-Melgoza et al. 2013) or densely cluster in space in the highest quality portions of the habitat (Fretwell and Lucas 1969) while reproducing successfully.

Tidal marshes provide habitat for a suite of specialist nesting birds (Correll et al. 2016) and are experiencing rapid ecological change that could affect nest survival. Between the 1950s and 1970s, over 50% of tidal marshes along the Atlantic Coast of the United States were destroyed due to draining and filling for habitation and agriculture or channelized and treated with chemicals for mosquito reduction (Tiner 1984, Dahl 1990). These impacts were especially acute on Western Long Island, in which parts of New York City (NYC) lie. Here, marshes suffered losses of over 75% between 1900 and 1970 and continued to decline at rates of 0.5-3% per year (Hartig et al. 2002). These continued losses are due to a combination of factors including sea level rise (Gornitz et al. 2001, Hartig et al. 2002), increased tidal range (Swanson and Wilson 2008), and urban development, which has hardened shorelines and starved marshes of inorganic sediment making them fragile and prone to fragmentation (Peteet et al. 2018).

For tidal marsh specialist songbird species in northeastern North America, the largest reported influence on breeding failure is tidal inundation of ground nests (Gjerdrum et al. 2005, 2008, Shriver et al. 2007, Ruskin et al. 2017a), which often leads to multiple nesting attempts per season (Post and Greenlaw 1983, Shriver 2002). Because sea level rise amplifies tides and intensifies flooding, the nest building behavior of the tidal marsh obligate Saltmarsh Sparrow, *Ammospiza caudacuta*, and is put at great risk of extinction because of flooding-induced nesting failure (Bayard and Elphick 2011, Correll et al. 2017).

Saltmarsh Sparrow nest survival in large, relatively intact saltmarshes has been found to be positively correlated with ground elevation (DeRagon 1988, Shriver et al. 2007) and to benefit from nest initiation immediately following high spring tides (DeRagon 1988, Gjerdrum et al. 2005, Shriver et al. 2007, Walsh et al. 2016). Seaside Sparrows, *A. maritima*, found along the northeastern Atlantic Coast are also largely restricted to tidal marshes and nest sympatrically with Saltmarsh Sparrows from New Hampshire to Virginia. Seaside Sparrow nest survival has also been found to benefit from rapid re-nesting following loss to spring tides in some studies (DeRagon 1988, Marshall and Reinert 1990) and by height and density of the vegetation surrounding the nest in other studies (Gjerdrum et al. 2005, Hunter et al. 2016). Seaside Sparrows are potentially afforded greater variability in nest height selection than Saltmarsh Sparrows because of their propensity to nest among taller, more rigid, low-elevation, *Spartina alterniflora*, grasses. Seaside Sparrows are also likely to have access to suitable nest vegetation later into the progression of sea level rise than Saltmarsh Sparrows (Field et al. 2016) because low-marsh vegetation is expected to increase in prevalence on the landscape as the climate changes because of its ability to survive tidal flooding. High-marsh zones selected by nesting Saltmarsh Sparrows may not persevere because marsh migration into current uplands may not be able to keep up with the rate of sea level rise in some areas (Watson et al. 2016). Although in many areas, high-marsh vegetation is likely to be prevented from landward migration by urban or forested borders (Field et al. 2016) or steeply sloping uplands (Kirwan et al. 2016). This combination will result in the conversion of much high marsh to low marsh, without concomitant replacement in the uplands.

Previous studies of nesting habitat used for these species have primarily taken place in broad expanses of marsh surrounded by low densities of human development, which is thought to be optimal for these birds (Benoit and Askins 2002). Large contiguous patches of habitat are known to have positive associations with species richness and abundance in forests (Ambuel and Temple 1983, Askins et al. 1990), and this relationship also holds true for tidal marshes (Benoit and Askins 2002). In urban environments, tidal marshes often get caught between sea level rise and urban borders causing marshes to be reduced in overall area. When urban saltmarshes maintain a wide expanse, the benefit of area could be undermined by fragmentation and degradation often associated with human development. This constraint may lead to reduced avian abundance and biodiversity (Friesen et al. 1995) and negative demographic consequences for specialist species (Chace and Walsh 2006).

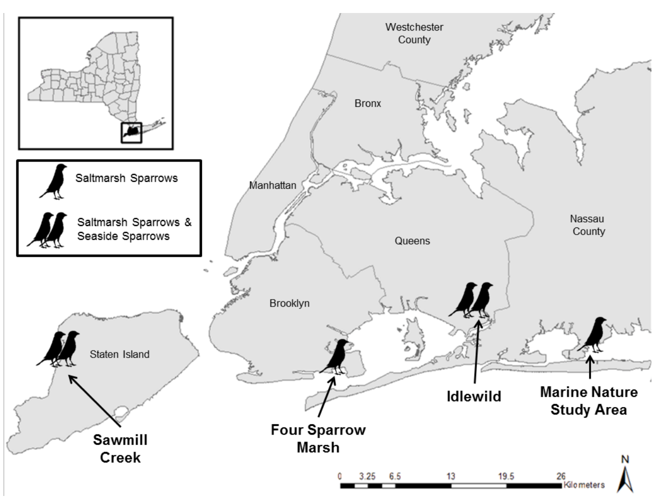
As small, urbanized marsh patches become more frequent on the landscape, determining whether such patches could be managed to keep species of conservation concern within them will aid in proper use of limited resources (Bayard and Elphick 2010). We aimed to determine if the urban landscape of NYC is indeed suitable for tidal marsh specialist songbirds by studying nest site selection and factors affecting nest survival of Saltmarsh and Seaside Sparrows in NYC. We predicted that to persist in this distinctive environment, these birds may nest in alternate habitat (taller low-marsh habitat or upland habitat) or alter their nest building strategies (use taller vegetation or nest higher off the ground) from individuals living in larger, less urbanized marshes throughout the species' ranges. We also sought to provide new insights into the ecology of saltmarsh obligate birds in small, human-impacted patches and aid in the management of these birds in urban tidal marsh systems.

METHODS

Study area

We identified tidal marsh sparrows nesting in five locations throughout NYC in 2012 and a sixth location was added just outside NYC in neighboring Nassau County on Long Island, New York in 2013 (Fig. 1). Study sites included: Sawmill Creek (SA1, SA2, 40°36′36.227″N, -74°11′32.982″W) on Staten Island; Four Sparrow Marsh (FS, 40°35′58.772″N, -73°54′24.390″W) in Brooklyn; Idlewild (ID, 40°39′9.140″N, -73°45′7.729″W) in Queens; and Marine Nature Study Area (MN, 40°37′16.050″ N, -73°37′19.542″W) in Oceanside, Nassau County. We designated 1-ha to 4-ha (depending on total patch size) study plots at each site, centered at the densest known sparrow nest site locations. For analysis, two sites were designated at Sawmill Creek, i.e., Sawmill Creek East (SA1) and Sawmill Creek West (SA2), because these sites were separated by train tracks, differed in vegetation composition, and Seaside Sparrows were only observed at the western site. Study marshes ranged from consisting of predominantly high marsh (*S. patens* interspersed with *Juncus effusus*, SA2), to predominantly low marsh (*S. alterniflora*, ID), to a mixture of both (FS, MN, SA1) vegetation types, and no marshes contained *Juncus gerardii*, a high-marsh grass found to typically be used by nesting Saltmarsh Sparrows (Greenlaw et al. 2020). Sawmill Creek West (SA2) contained a large patch of upland *Iva frutescens* shrubs in the center of the marsh, but this shrub was only present in the upland periphery at the other study marshes, as is typical. Study marshes were generally small (5 ha to 35 ha) and had a highly urbanized periphery of commercial industry (SA1), urban transportation (highways, railways, and airports; FS, SA1, SA2, and ID), and/or residential areas (MN, ID). Saltmarsh Sparrows were found nesting at all five sites, and Seaside Sparrows were only observed nesting at SA2 and ID. We included these specific sites in the study because they represented a range of marsh-level characteristics and because they were the only accessible sites within and near the NYC area with confirmed nesting by tidal marsh sparrows.

Fig. 1. Location of study sites for Saltmarsh Sparrow (*Ammospiza caudacuta*) and Seaside Sparrow (*A. maritima*) nest survival study in New York City and Long Island, New York, 2012-2013.



Field methods

Nest searching was performed twice weekly from mid-May to mid-August at each site according to methods described in Ruskin et al. (2017b). Three to four observers stood two-arm lengths apart and walked transects across the marsh through all possible nesting habitat, watching for birds flushing from a nest and checking under thatch and overhanging vegetation for nests. Checks of known nests were performed every three to four days. The status of the nest (active, failed, or fledged) was recorded, as were the number of eggs or chicks and the cause of failure (flooding, depredation) if applicable (Ruskin et al. 2017b).

Nest-specific data were collected either at the time of discovery, if eggs were present, or once eggs were first observed in the nest to reduce the likelihood of research activity causing nest abandonment. The height of the bottom of the nest to the ground, rim of the nest to the ground, and the depth of the nest cup were measured to the nearest 0.5 cm using a meter stick. Percent vegetative cover over the nest was estimated by placing a round, white disc (the same diameter as the mean nest cup diameter for these species) into the nest and recording the percent of the disc that was visible from above, following Saltmarsh Habitat and Avian Research Program (SHARP) protocols (Roberts et al. 2017). Percent ground cover in the 1 m^2 around each nest was estimated using a vegetation sampling frame within one week of the failure or fledging of a nest. The PVC frame contained two sets of parallel lengths of twine, perpendicular to each other, to create 64 evenly spaced intersections. We recorded the type of stem emerging from the ground beneath each intersection or other type of ground cover as appropriate (bare ground, water, wrack), for the estimation of percent of basal ground cover. We also visually assessed the proportion of foliar cover within the 1 m^2. Additionally, we recorded the mean and tallest height of vegetation at five points (one at the mid-point of each side of the frame, and one at the center of the frame) within the vegetation frame.

We generated random points within each site, at least 5 m apart, in ArcMap 10.0 (ESRI 2012) to compare vegetation characteristics at nest sites to unused available habitat. We measured proportion ground cover and vegetation height within 1-m^2 quadrats as described for nests. Random points were paired temporally but not spatially with nest points. This design was used to ensure a useful distribution of random points throughout the study period for comparison with nest habitat data. In late July to August, 6 to 50 additional random points were sampled at each site for vegetation composition comparisons among marshes. The sample size in 2012 was small (6-14 samples per study site) and was used to plan an optimal sampling design in 2013 (25-50 samples depending on the area of the study site).

Analytical methods

Nest site selection

We tested for differences in proportion of basal vegetative cover between nests and random points at each study site using multi-response permutation procedures (MRPP) in the Blossom Package (Talbert and Cade 2005) for R version 3.4.3 (R Core Team 2013) at $\alpha = 0.05$. A non-parametric analog to MANOVA, MRPP is useful for small sample sizes and data that do not follow a multivariate normal distribution (Cade and Richards 2006). We

Table 1. Summary of published nest height (mean ± SE bottom to ground and rim to ground) data for Saltmarsh Sparrow, *Ammospiza caudacuta* (breeding from Maine to North Carolina) and Seaside Sparrow, *A. maritima*.

Species	Nest height, bottom to ground (cm)	Nest height, rim to ground (cm)	n	Location	Study date	Paper
Saltmarsh Sparrow	8.4 ± 0.4		65	Rhode Island	1981	DeRagon 1988
		13.3 ± 0.3†	173	Rhode Island	1981-1982	DeRagon 1988
		12.9 ± 1.8	27	Connecticut	2003	Humphereys et al. 2007
	6.3 ± 2.7	10.5 ± 3.0	57	New York (not NYC)	Not specified	Greenlaw et al. 2020
	8.58 ± 0.32		186	New Jersey	2011-2013	Kern 2015
	8.1 ± 0.8	12.6 ± 1.1		All (mean)		
Seaside Sparrow		18.7 ± 4.4†	60	Massachusetts	1985-1986	Marshall and Reinert 1990
		18.4 ± 0.9	32	Rhode Island	1981-1982	DeRagon 1988
	14.2 ± 5.8		94	New York (not NYC)	Not specified	Greenlaw et al. 2022
	14.12 ± 0.42		205	New Jersey	2011-2013	Kern 2015
Seaside Sparrow	14.1 ± 2.1	18.7 ± 4.4		All (mean)		

†Data combined from a table provided within the manuscript containing mean, SE, and n.

had low nest sample sizes for Seaside Sparrows at some sites, so we only conducted the analysis for sites with six or more nests per year (SA2 in 2012 and ID in 2013).

Collecting habitat data at the time the fate of a nest is determined can bias the interpretation of nest site selection results because the fate of failed nests occurs earlier in the breeding cycle than that of successful nests (McConnell et al. 2017). Although our design did not account for such bias because of frequent re-nesting of sparrows throughout the study period, the distribution of collection dates for vegetation data was similar between plots.

Nest success

We estimated daily nest survival rates using the logistic-exposure method (Shaffer 2004) that accommodates varying exposure periods and does not require knowledge or guesses of when nest losses occur in an interval between nest checks. We included site, year, and nest stage (incubation or brooding) in all models to account for likely sources of heterogeneity (Mayfield 1961). Nest fate was then modeled as a function of several predictor variables related to nest structure, i.e., nest height (bottom to ground, cm), nest depth (cm), proportion of vegetative cover over nest, species, and all biologically significant interactions with species. All models, including a null intercept-only model, were run using the glm function in R with a custom logit link function to account for exposure days.

We used an information-theoretic approach to evaluate support for the models (Burnham and Anderson 2002). We assessed the candidate models using Akaike's Information Criterion (AIC) corrected for small sample sizes, including ΔAIC_c, Akaike weights (w_i), and deviance. We generated estimates of daily survival rates using the best-supported model, or model-averaged predictions if there was not a single best model based on a $\Delta AIC_c < 2$ (Burnham and Anderson 2002) or deviance > 1.

Region-wide comparisons

We compared vegetation (composition and structure) and nest structure characteristics between our urban NYC marshes (FS, ID, MN, SA1, and SA2), our Long Island site (MN), 12 SHARP locations outside of New York, i.e., other sites; Maine (4 sites), New Hampshire (2), Connecticut (3), and New Jersey (3), which were sampled with the same protocol as ours and during the same timeframe (2012-2013 pooled), and from the popular literature (nest height comparison only, Table 1). For our vegetation composition comparison, we separately modeled the proportion cover of four common grasses (*S. alterniflora*, *D. spicata*, *S. patens*, and *J. effusus*), mean vegetation height within 1 m² around the nest and tallest vegetation height within 1 m² around the nest by location (NYC, Long Island, other), and study year, with a random effect of site using linear regression models in R (R Core Team 2013). We separately modeled our nest structure characteristic nest height (rim to ground and bottom to ground; cm) by location (NYC, Long Island, other, i.e., literature, and other, SHARP) using a linear mixed-effects model with site as a random effect in the R package lme4 (Bates et al. 2015).

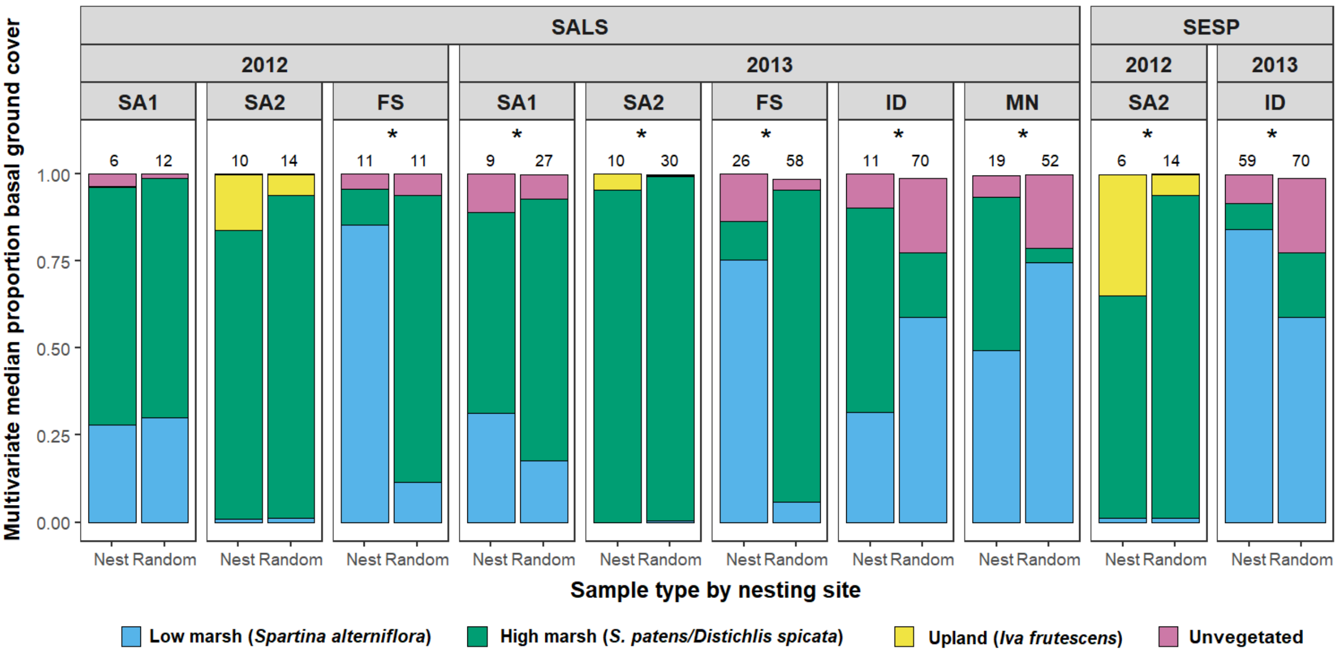
RESULTS

We found 114 Saltmarsh Sparrow nests (2012: 29 nests, 2013: 85 nests) and 65 Seaside Sparrow nests (2012: 6 nests, 2013: 59 nests) during the span of this study. Known fates (fledged or failed) were assigned to 73 Saltmarsh Sparrow nests and 64 Seaside Sparrow nests. Seventy-two nests had a known cause of failure, of which 0.86 were lost due to flooding (Saltmarsh Sparrow: 28 nests, Seaside Sparrow: 34 nests) and 0.14 due to depredation (Saltmarsh Sparrow: 8 nests, Seaside Sparrow: 2 nests).

Nest site selection

In 2012, we found no difference in percent basal vegetative cover between Saltmarsh Sparrow nests and random points at Sawmill Creek plots (SA1: MRPP, Pearson Type III statistic = 0.62, P = 0.697; SA2: statistic = -0.39, P = 0.290) but Saltmarsh Sparrows at Four Sparrow Marsh used tall-form *S. alterniflora* out of proportion to its availability (FS: statistic: -3.91, P = 0.004; ID and MN were not sampled; Fig. 2). Marsh vegetation converted to bare ground at many sites between years at a rate of 5-25% (except at SA2) likely due to the effects of Hurricane Sandy, October 2012 (Fig. 2). Saltmarsh Sparrows at all five nesting sites used some vegetation types out of proportion to their availability in 2013, including tall-form *S. alterniflora* at SA1 and FS, the woody shrub *Iva frutescens* at SA2, and *S. patens* at ID and MN (SA1: MRPP, Pearson Type III statistic: -10.74, P < 0.001; SA2: statistic: -3.33, P = 0.011; FS: statistic: -7.52, P < 0.001; ID: statistic: -3.11, P = 0.012; MN: statistic: -4.63, P = 0.003; Fig. 2). Seaside Sparrows used *I. frutescens* at SA2 in 2012 and *S.*

Fig. 2. Multivariate median proportion basal ground cover at Saltmarsh Sparrow (*Ammospiza caudacuta*, SALS) and Seaside Sparrow (*A. maritima*, SESP) nests and random points at study marshes in New York City, New York, 2012-2013 and Long Island, New York, 2013. Rarely occurring plants (< 5% of total ground cover) are excluded. Significantly different pairs of bars† are indicated with an asterisk. Sample sizes are shown above bars.



†2012 SALS: SA1: MRPP, Pearson Type III Statistic: 0.6, $P = 0.697$; SA2: Statistic:-0.4, $P = 0.290$; FS: Statistic: -3.9, $P = 0.004$; 2013 SALS: SA1: MRPP, Pearson Type III Statistic: -10.7, $P < 0.001$; SA2: Statistic: -3.3, $P = 0.011$; FS: Statistic: -7.5, $P < 0.001$; ID: Statistic: -3.1, $P = 0.012$; MN: Statistic: -4.6, $P = 0.003$; SESP: 2012 SA2: MRPP, Pearson Type III Statistic: -6.7, $P < 0.001$; 2013 ID: Statistic: -12.5, $P < 0.001$). Results remain the same when comparing vegetation only (i.e., unvegetated cover excluded; 2012 SALS: SA1: MRPP, Pearson Type III Statistic: 0.2, $P = 0.451$; SA2: Statistic: -1.0, $P = 0.148$; FS: Statistic: -3.0, $P = 0.019$; 2013 SALS: SA1: MRPP, Pearson Type III Statistic: -2.0, $P < 0.001$; SA2: Statistic: -5.2, $P = 0.002$; FS: Statistic: -15.6, $P < 0.001$; ID: Statistic: -2.7, $P = 0.026$; MN: Statistic: -11.2, $P < 0.001$; SESP: 2012 SA2: MRPP, Pearson Type III Statistic: -2.8, $P < 0.017$; 2013 ID: Statistic: -12.0, $P < 0.001$.

alterniflora at ID in 2013 out of proportion to their availability (2012 SA2: MRPP, Pearson Type III statistic: -6.71, $P < 0.001$; 2013 ID: statistic: -12.53, $P < 0.001$; Fig. 2).

Nest success

Controlling for differences among sites and between years and nesting stages, we found evidence that nest survival increased with nest height (bottom to the ground, mean estimate 0.072 ± 0.025 SE) above the substrate because it appeared in all of the top models (Table 2). The 95% confidence intervals for the effects of nest height, stage, year, and some sites in the top three models did not contain zero (Table 3). No model structure was unequivocally best, although there was no support for the null model. Additional covariates (nest depth, percent cover, and species) appeared in some of the top models; however, inclusion of these variables did not lower deviance by more than one (Table 2) and 95% confidence limits on the regression parameters of these covariates contained zero (Table 3), so we considered them to be non-informative parameters (Arnold 2010) and used the top model (containing only nest height and our control variables) for further inference.

Nest survival increased with nest height (bottom to ground) above the ground at all sites, in both years, and at both egg and chick stage (Fig. 3). Nests at the brooding stage had an average trend of approximately 5-10% higher survival than nests at the incubation stage. The smallest site, Four Sparrow Marsh, had higher nest survival than the other sites, although there was broad overlap of 95% confidence bounds across the trend lines. Nests in 2012 had an average trend of approximately 13-25% higher survival than nests in 2013 (Fig. 3).

Table 2. Models, parameter counts (K), and information-theoretic model selection results for factors affecting nest survival of sparrows in New York in 2012-2013, including: species (Saltmarsh Sparrow, *Ammospiza caudacuta*, and Seaside Sparrow, *A. maritima*), year (2012, 2013), site, stage (incubation of eggs, brooding of chicks), nest height (bottom of cup to ground), depth of nest cup, and % cover over the nest cup (N = 125 nests). Models with $\Delta AICc$ values < 2 and the null model are shown. We tested 128 models with year, site, and stage included in all models.

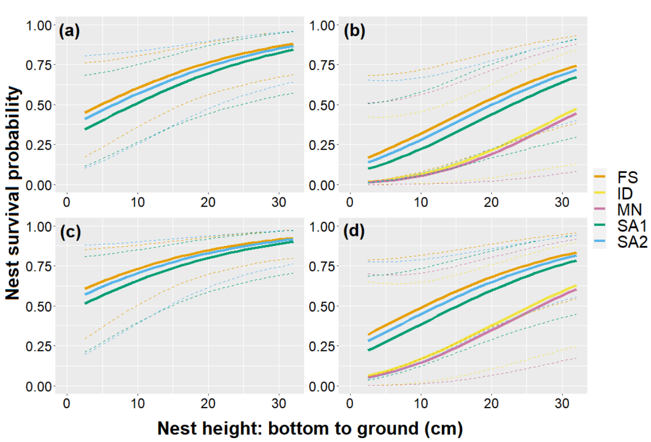
Model	ΔAIC_c†	K	Model weight (w_i)	Deviance
Year + site + stage + nest height	0	9	0.343	403.72
Year + site + stage + nest height + depth	1.917	10	0.132	403.55
Year + site + stage + nest height + species	2.041	10	0.124	403.67
Year + site + stage + nest height + % cover	2.089	10	0.121	403.72
Null	21.087	2	0.000	439.15

†AIC_c for the top model was 420.072.

Table 3. Model parameter estimates, standard errors (SE), and lower 2.5% (LCL) and upper 97.5% confidence limits (UCL) for the top three models predicting Saltmarsh Sparrow (*Ammospiza caudacuta*) and Seaside Sparrow (*A. maritima*) daily nest survival in New York City in 2012 and 2013. The covariate nest depth in model 2 and species Saltmarsh Sparrow in model 3 have confidence bounds that surround 0.

Model	Parameter	Estimate	SE	LCL	UCL	P-value
1	Intercept	1.764	0.675	0.470	3.127	0.009
	Site: ID	-1.031	0.402	-1.891	-0.302	0.010
	Site: MN	-1.095	0.535	-2.149	-0.061	0.041
	Site: SA1	-0.305	0.523	-1.352	-0.738	0.559
	Site: SA2	-0.110	0.587	-1.255	1.092	0.851
	Egg stage	-0.522	0.256	-1.038	-0.036	0.042
	2012	0.984	0.471	0.028	1.902	0.037
	Nest height	0.072	0.025	0.025	0.121	0.003
2	Intercept	2.100	1.059	0.052	4.200	0.047
	Site: ID	-1.027	0.401	-1.885	-0.298	0.010
	Site: MN	-1.094	0.535	-2.147	-0.059	0.041
	Site: SA1	-0.302	0.524	-1.351	0.744	0.564
	Site: SA2	-0.134	0.591	-1.290	1.076	0.821
	Egg stage	-0.517	0.257	-1.034	-0.029	0.044
	2012	0.956	0.478	-0.015	1.885	0.045
	Nest height	0.073	0.025	0.025	0.122	0.003
	Nest depth	-0.062	0.150	-0.351	0.237	0.678
3	Intercept	1.659	0.828	0.031	3.291	0.045
	Site: ID	-0.948	0.551	-2.053	0.141	0.086
	Site: MN	-1.087	0.537	-2.143	-0.051	0.043
	Site: SA1	-0.302	0.524	-1.349	0.743	0.564
	Site: SA2	-0.089	0.596	-1.248	1.134	0.881
	Egg stage	-0.525	0.257	-1.042	-0.038	0.041
	2012	0.975	0.474	0.014	1.897	0.039
	Nest height	0.074	0.026	0.025	0.125	0.004
	Saltmarsh Sparrow	0.090	0.407	-0.681	0.945	0.825

Fig. 3. Predicted probability of interval nest survival for Saltmarsh Sparrow (*Ammospiza caudacuta*) and Seaside Sparrow (*A. maritima*; species pooled) during the (a) incubation stage (12 days) in 2012 (n = 10 nests), and (b) 2013 (n = 90 nests), and (c) brooding stage (9 days) in 2012 (n = 12 nests), and (d) 2013 (n = 54 nests) vs. nest height, New York. 95% confidence intervals are shown.

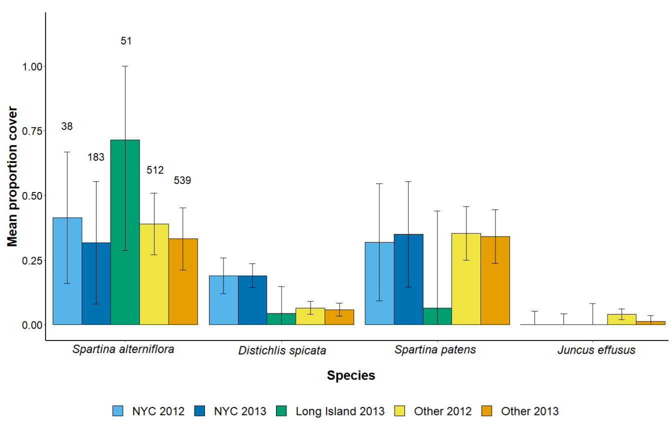


Regional Comparisons

Marsh level

Mean proportion cover of *D. spicata* was higher at NYC sites than all other sites in the species range in both study years (NYC 2012: 0.188 ± 0.035 SE, 2013: 0.189 ± 0.024; other 2012: 0.065 ± 0.013, 2013: 0.058 ± 0.013; Long Island 2013: 0.043 ± 0.053), and no difference in cover by *J. effusus* was detected between sites. Our Long Island site appeared to have an overall higher mean proportion cover of *S. alterniflora* and a lower mean proportion cover of *S. patens* than all other study sites, whereas proportion cover of these two vegetation types at NYC sites did not differ from sites outside of New York (Fig. 4). Tallest vegetation height around the nest was greater at NYC sites, although the difference was not statistically significant based on wide confidence intervals for sites outside of New York (Fig. 5). Tallest vegetation height around the nest at our Long Island site appeared lower than at NYC sites (Fig. 5).

Fig. 4. Mean proportion cover of four common vegetation types at study sites containing nesting Saltmarsh Sparrows (*Ammospiza caudacuta*) in New York City, New York in 2012 and 2013; on Long Island, New York in 2013; and at other sites throughout the Northeast, i.e., Maine, New Hampshire, Connecticut, and New Jersey, in 2012 and 2013, with 95% confidence intervals shown. Sample sizes above bars on *Spartina alterniflora* are reflective of the sample sizes for the other vegetation types.



Nest level

We found mean nest heights (both bottom to ground and rim to ground) of both sparrow species in NYC to be taller than nest heights for each species in all other locations and in the popular literature ($P < 0.001$). Saltmarsh Sparrow nest heights at our Long Island site did not differ from nest heights at other SHARP sites outside of New York (bottom to ground: $P = 0.985$, rim to ground: $P = 0.822$) or in the popular literature (Fig. 6).

DISCUSSION

Nest site selection by Saltmarsh and Seaside Sparrows in NYC was different than is typically recorded elsewhere in their ranges. Sparrows used vegetation in atypical marsh zones out of proportion to their availability, and both species nested higher off the ground

Fig. 5. Mean vegetation height and tallest vegetation height collected 1 m^2 around Saltmarsh Sparrow (*Ammospiza caudacuta*) and Seaside Sparrow (*A. maritima*) nests at study sites in New York City, New York in 2012 and 2013; on Long Island, New York in 2013; and at other sites throughout the Northeast, i.e., Maine, New Hampshire, Connecticut, and New Jersey, in 2012 and 2013, with 95% credible intervals shown. Sample sizes above bars of mean vegetation height are reflective of the sample sizes for tallest vegetation height.

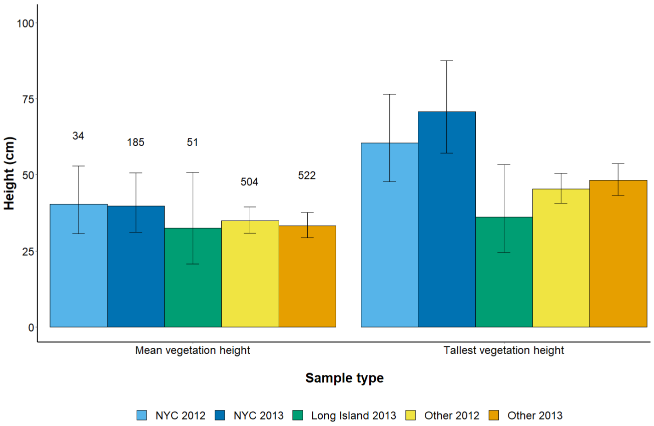
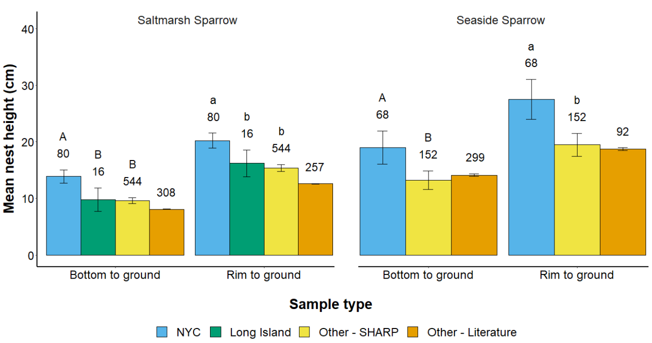


Fig. 6. Mean nest heights (rim to ground and bottom to ground) of Saltmarsh Sparrow (*Ammospiza caudacuta*) and Seaside Sparrow (*A. maritima*) nests in this study (New York City, New York, 2012 and 2013 combined and Long Island, New York, 2013), from literature (Table 3), and from Saltmarsh Habitat and Avian Research Program (SHARP) study sites throughout the Northeast, i.e., Saltmarsh Sparrows: Maine, New Hampshire, Massachusetts, Connecticut, and New Jersey; Seaside Sparrows: Connecticut, and New Jersey; 2012 and 2013 combined, with standard errors shown. Sample sizes above bars. Within sparrow species, rim to ground means with the same capital letter are not significantly different and bottom to ground means with the same lowercase letter are not significantly different. Heights from literature were not included in the statistical comparative analysis.



in NYC than at other locations throughout the sparrows' northeastern range. Nest height (bottom to ground) was positively associated with nest survival for Saltmarsh Sparrows, which has not previously been documented as a significant predictor of nest survival for this species. New York City marshes appear to contain on average taller vegetation than other tidal marsh sparrow breeding sites in the northeast Atlantic, although the great variation in vegetation height in non-New York marshes affected our ability to detect statistical significance. New York City marshes had higher than average proportions of *D. spicata*, an indicator species for transition from high marsh to low marsh (Lonard et al. 2013). Thus, atypical nest site selection in our small, urbanized marshes may reflect ecological differences between degraded and pristine habitat or a bias in sampling nest sites in only expected habitat.

Selection of low-elevation marsh plants by Saltmarsh Sparrows in NYC for nesting afforded them the ability to place their nests higher off the ground than has typically been observed for this species. Seaside Sparrows using similar habitat also built nests higher off the ground than has been recorded for the northeastern breeding population. This difference may be due to the greater than average vegetation heights observed in NYC, which would provide more opportunity for sparrows to select taller grasses for nesting. Both species had similar nest survival rates that were higher than the published average (0.38, Table 4) at 0.55 in 2012 but dropped substantially to 0.25 in 2013. It is difficult to interpret the drop in 2013 because it occurred just after Hurricane Sandy altered the habitat in our study area. However, our results demonstrate that in at least some years, atypical nest habitat selection may not have negative nest survival consequences.

The positive relationship we found between Saltmarsh Sparrow nest survival and nest height contrasts with the Gjerdrum et al. (2005) finding of no effect of nest height on nest survival for Saltmarsh Sparrows and the Kern (2015) finding that the hypervolume niche space of Saltmarsh Sparrows in New Jersey covered a region with below-average nest height and above-average high-marsh cover. Our results are consistent with findings by Benvenuti et al. (2018) that the mean nest height for Saltmarsh Sparrow nests that survive to fledging is higher than nests lost to flooding in Maine, Massachusetts, and New Hampshire. Nest height may be more important for nest survival in NYC than at other sites throughout the birds' range due to a combination of limited available habitat and marsh subsidence (in Idlewild in particular) causing birds to be forced to nest in marshes with higher than normal tidal flows (Cook 2019) because they don't have nearby alternate locations to move to and exhibit strong site fidelity. The response of nesting higher off the ground appears to allow some nests to successfully avoid flooding without inordinately increasing detection and loss to predators. This result may be because of the taller than average vegetation present in NYC that likely aided in concealing higher nests.

Below rangewide average nest survival at New York sites (NYC and Long Island combined) were predicted by Ruskin et al. (2017a) based on a model of flooding characteristics of marshes from Maine to New Jersey. When only a site effect, and no covariates were included in their model, however, nest survival in New York was estimated as below the rangewide average. The inclusion of nest height in our nest survival model may explain this discrepancy and suggests that Saltmarsh Sparrows may be able to perform well in taller marsh vegetation if the birds do not have other options. Sea level rise is expected to lead to population

Table 4. Summary of published nest survival data for Saltmarsh Sparrows, *Ammospiza caudacuta* and Seaside Sparrows, *A. maritima* (breeding from Maine to North Carolina).

Species	Interval Nest Survival	Location	Study Date	Paper
Saltmarsh Sparrow	0.46[†]	ME to NJ	2011-2013	Ruskin et al. 2017b
	0.55	ME, NH	2011-2013	Walsh et al. 2016
	0.404	RI	1993-1998	DiQuinzio et al. 2002
	0.2	CT	2002-2003	Gjerdrum et al. 2005
	0.46	ME	1999-2001	Shriver 2002
	0.36	MD	unknown	Greenberg et al. 2006
	0.44	RI	1981-1982	DeRagon 1988
	0.27	NY	1977-1980	Post and Greenlaw 1982
Saltmarsh Sparrow mean	0.383			
Seaside Sparrow	0.283	NJ	2012-2016	Roberts et al. 2017
	0.35	NY	1977-1980	Post and Greenlaw 1982
	0.64	CT	unknown	Greenberg et al. 2006
	0.37	MD	unknown	Greenberg et al. 2006
	0.29	MA	1985-1986	Marshall and Reinert 1990
Seaside Sparrow mean	0.387			

[†]Successful broods per female. Not from a direct nest survival analysis.

declines in this species to the point of extinction by mid-century (Field et al. 2017, 2018). Vegetation height may therefore be a valuable consideration in addition to marsh zone when planning restoration, especially at smaller, urbanized, or otherwise degraded sites.

We provide evidence that Saltmarsh Sparrows may be able to vary their nest site selection tactics more readily than previously suspected because we found that Saltmarsh Sparrows at all five study marshes selected *S. alterniflora* (primarily in its taller low-elevation marsh form except at our Long Island site) and did so out of proportion to its occurrence at two of our smallest marshes (Four Sparrow Marsh and Sawmill Creek East). This result contrasts with many prior studies that documented use of predominantly (80% +) high-elevation marsh vegetation, sometimes interspersed with short-form *S. alterniflora* (DeRagon 1988, DiQuinzio et al. 2002, Shriver 2002, Gjerdrum et al. 2005, Humphreys et al. 2007, Meiman et al. 2012), but has been suggested anecdotally in earlier studies from New York (Greenlaw et al. 2020). Use of tall *S. alterniflora* grasses may be related to the importance of nest height in determining nest survival in these NYC sparrow populations.

Previous studies in New York found that Seaside Sparrows often used tall enough grasses that most individuals did not lose nests to flooding, except early in the season when tidal marsh grasses are still short and when seasonally high tides are coupled with extreme storm events (Post et al. 1983). Our findings support that Seaside Sparrows in NYC are searching out tall grasses, but perhaps not tall enough grasses because flooding was the primary cause of nest loss for these birds. Seaside Sparrows at Idlewild nested in typical habitat, whereas at Sawmill Creek West, where low-elevation marsh was lacking, Seaside Sparrows primarily nested at the base of tall upland shrubs (*I. frutescens*). Substrate switching to *I. frutescens* bushes in the absence of plentiful low-marsh substrate is uncommon but was also observed by Woolfenden (1956) in New Jersey and also likely occurred because tall grasses were limited.

Our smallest marsh, Four Sparrow Marsh, had the highest nest survival rates in both years, although not significantly so. This result was surprising because only 1.2 ha of the 5.2 ha marsh was used by nesting sparrows, and the site had a highly urbanized fringe including a major highway. Birds at this site predominantly selected low-marsh *S. alterniflora* for nesting despite the marsh's predominant high-marsh composition. In contrast, Marine Nature Study, our Long Island site, had what appeared to be the lowest nest survival rate in 2013 (it was not surveyed in 2012), and this site was found to be more similar to other nest sites throughout the Northeast than NYC (shorter overall grass heights and nests built lower to the ground). The higher mean nest survival at Four Sparrow Marsh, a small, urbanized patch, in comparison to Marine Nature Study area, a more typical sparrow nesting marsh, suggests that the typical way we characterize habitat requirements for Saltmarsh Sparrows and other tidal marsh birds (i.e., low-marsh or high-marsh obligates) may be too simplistic, and may therefore obscure potential conservation strategies.

We demonstrated variation in nest site selection within populations of two tidal marsh obligate sparrows. Whether or not the responses we observed were due to population-level or individual-level processes, they suggest potential conservation strategies in small, urbanized marshes. Habitat restoration that provides a heterogeneous matrix of high- and low-elevation zones and marsh plant species, while maintaining an above average availability of high-marsh vegetation, would mimic the conditions at our sites where birds were successful while providing continued habitat options as sea level rise progresses.

By focusing study on the largest or densest populations of species of conservation concern, researchers may miss critical phenotypes that may inform management (Hunter and Hutchinson 2002) and introduce sampling bias. Smaller populations on the edge of the realized niche may be more likely to exhibit adaptive plasticity and evolutionary rescue (Ghalambor et al. 2007) and can easily go undetected. These small populations are especially important to not miss in the study of declining species such as the Saltmarsh Sparrow, which require immediate intervention to persist. Focusing on these small populations and understanding how individuals within them are using habitat at their niche's edge will provide insight for habitat restoration that may not create the most ideal conditions but can keep imperiled species present on the landscape until those conditions can be met.

Author Contributions:

C. S. E., T. P. H., A. I. K., B. J. O., K. J. R., and W. G. S. designed the long-term study methods. J. B. C., and A. R. K. formulated the study questions. A. R. K. conducted the field research, supervised field assistants, analyzed the data, and wrote the paper. J. B. C., C. S. E., T. P. H., A. I. K., B. J. O., K. J. R., and W. G. S. provided edits to the paper.

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LITERATURE CITED

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64(5):1057-1068. https://doi.org/10.2307/1937814

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74(6):1175-1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Askins, R. A., J. F. Lynch, and R. Greenburg. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7:1-57.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48. https://doi.org/10.18637/jss.v067.i01

Bayard, T. S., and C. S. Elphick. 2010. How area sensitivity in birds is studied. Conservation Biology 24(4):938-947. https://doi.org/10.1111/j.1523-1739.2010.01480.x

Bayard, T. S., and C. S. Elphick. 2011. Planning for sea-level rise: quantifying patterns of Saltmarsh Sparrow (*Ammodramus caudacutus*) nest flooding under current sea-level conditions. Auk 128(2):393-403. https://doi.org/10.1525/auk.2011.10178

Benoit, L. K., and R. A. Askins. 2002. Relationship between habitat area and the distribution of tidal marsh birds. Wilson Bulletin 114(3):314-323. https://doi.org/10.1676/0043-5643(2002)114[0314:RBHAAT]2.0.CO;2

Benvenuti, B., J. Walsh, K. M. O'Brien, and A. I. Kovach. 2018. Plasticity in nesting adaptations of a tidal marsh endemic bird. Ecology and Evolution 8(22):10780-10793. https://doi.org/10.1002/ece3.4528

Berger-Tal, O., and D. Saltz. 2016. Introduction: the whys and the hows of conservation behavior. Pages 3-35 in O. Berger-Tal and D. Saltz, editors. Conservation behavior: applying behavioral ecology to wildlife conservation and management. Cambridge University Press, New York, New York, USA. https://doi.org/10.1017/CBO9781139627078.003

Burnham K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Cade, B. S., and J. D. Richards. 2006. A permutation test for quantile regression. Journal of Agricultural, Biological, and Environmental Statistics 11:106-126. https://doi.org/10.1198/108571106X96835

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Cook, A. M. 2019. Habitat selection and nest survival of tidal marsh birds in NYC and Long Island: implications for restoration. Thesis. State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA.

Correll, M. D., W. A. Wiest, T. P. Hodgman, W. G. Shriver, C. S. Elphick, B. J. McGill, K. M. O'Brien, and B. J. Olsen. 2017. Predictors of specialist avifaunal decline in coastal marshes. Conservation Biology 31:172-182. https://doi.org/10.1111/cobi.12797

Correll, M. D., W. A. Wiest, B. J. Olsen, W. G. Shriver, C. S. Elphick, and T. P. Hodgman. 2016. Habitat specialization explains avian persistence in tidal marshes. Ecosphere 7(11): e01506. https://doi.org/10.1002/ecs2.1506

Dahl, T. E. 1990. Wetlands losses in the United States, 1780's to 1980's. Report to the Congress. Technical Report PB-91-169284/XAB. https://www.fws.gov/wetlands/documents/Wetlands-Losses-in-the-United-States-1780s-to-1980s.pdf

DeRagon, W. R. 1988. Breeding ecology of Seaside and Sharp-tailed Sparrows in Rhode Island salt marshes. Thesis. University of Rhode Island, Kingston, Rhode Island, USA. https://web.uri.edu/rhodeislandwoods/files/DeRagon-1988.pdf

DiQuinzio, D. A., P. W. C. Paton, and W. R. Eddleman. 2002. Nesting ecology of Saltmarsh Sharp-tailed Sparrows in a tidally restricted salt marsh. Wetlands 22:179-185. https://doi.org/10.1672/0277-5212(2002)022[0179:NEOSST]2.0.CO;2

Dobkin, D. S., A. C. Rich, J. A. Pretare, and W. H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the Northwestern Great Basin. Condor 97(3):694-707. https://doi.org/10.2307/1369178

Environmental Systems Research Institute (ESRI). 2012. ArcMap for ArcGIS 10.1. Environmental Systems Research Institute, Redlands, California, USA.

Field, C. R., T. Bayard, C. Gjerdrum, J. M. Hill, S. Meiman, and C. S. Elphick. 2017. High-resolution tide projections reveal extinction threshold in response to sea-level rise. Global Change Biology 23(5):2058-2070. https://doi.org/10.1111/gcb.13519

Field, C. R., C. Gjerdrum, and C. S. Elphick. 2016. Forest resistance to sea-level rise prevents landward migration of tidal marsh. Biological Conservation 201:363-369. https://doi.org/10.1016/j.biocon.2016.07.035

Field, C. R., K. J. Ruskin, B. Benvenuti, A. Borowske, J. B. Cohen, L. Garey, T. P. Hodgman, R. A. Kern, E. King, A. R. Kocek, A. I. Kovach, K. M. O'Brien, B. J. Olsen, N. Pau, S. G. Roberts, E. Shelly, W. G. Shriver, J. Walsh, and C. S. Elphick. 2018. Quantifying the importance of geographic replication and representativeness when estimating demographic rates, using a coastal species as a case study. Ecography 41:971-981. https://doi.org/10.1111/ecog.02424

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36. https://doi.org/10.1007/BF01601953

Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling neotropical migrant songbirds. Conservation Biology 9(6):1408-1414. https://doi.org/10.1046/j.1523-1739.1995.09061408.x

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21(3):394-407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Gjerdrum, C., C. S. Elphick, and M. Rubega. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: the importance of nest habitat, timing, and study site differences. Condor 107(4):849-862. https://doi.org/10.1093/condor/107.4.849

Gjerdrum, C., K. Sullivan-Wiley, and E. King. 2008. Egg and chick fates during tidal marsh flooding of Saltmarsh Sharp-tailed Sparrow nests. Condor 110(3):579-584. https://doi.org/10.1525/cond.2008.8559

Gornitz, V., S. Couch, and E. K. Hartic. 2001. Impacts of sea level rise in the New York City metropolitan area. Global and Planetary Changes 32:61-88. https://doi.org/10.1016/S0921-8181(01)00150-3

Greenberg, R., C. S. Elphick, J. C. Nordby, C. Gjerdrum, H. Spautz, G. Shriver, B. Schmeling, B. Olsen, P. Marra, N. Nur, and M. Winter. 2006. Flooding and predation: trade-offs in the nesting ecology of tidal-marsh sparrows. Studies in Avian Biology 32 (32):96–109. https://www.researchgate.net/publication/257306148_Flooding_and_predation_Trade-offs_in_the_nesting_ecology_of_tidal-marsh_sparrows

Greenlaw, J. S., C. S. Elphick, W. Post, and J. D. Rising. 2020. Saltmarsh Sparrow, *Ammospiza caudacuta*. Version 1.0. In P. G. Rodewald, editor. Birds of the World. Cornell Lab of Ornithology, Ithica, New York, USA. https://doi.org/10.2173/bow.sstspa.01

Greenlaw, J. S., W. G. Shriver, and W. Post. 2022. Seaside Sparrow, *Ammospiza maritima*. Version 2.0. In P. G. Rodewald and B. K. Keeney, editors. Birds of the World. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.seaspa.02

Hartig, E. K., V. Gornitz, A. Kolker, F. Mushacke, and D. Fallon. 2002. Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City. Wetlands 22:71-89. https://doi.org/10.1672/0277-5212(2002)022[0071:AACCIO]2.0.CO;2

Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. Auk 109(2):321-333. https://doi.org/10.2307/4088201

Humphreys, S., C. S. Elphick, C. Gjerdrum, and M. Rubega. 2007. Testing the function of the domed nests of Saltmarsh Sharp-tailed Sparrows. Journal of Field Ornithology 78(2):152-158. https://doi.org/10.1111/j.1557-9263.2007.00098.x

Hunter, E. A., N. P. Nibbelink, and R. J. Cooper. 2016. Threat predictability influences Seaside Sparrow nest site selection when facing trade-offs from predation and flooding. Animal Behaviour 120:135-142. https://doi.org/10.1016/j.anbehav.2016.08.001

Hunter, Jr., M. L., and A. Hutchinson. 2002. The virtues and shortcoming of parochialism: conserving species that are locally rare, but globally common. Conservation Biology 8 (4):1163-1165. https://doi.org/10.1046/j.1523-1739.1994.08041163.x

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118(2):577-562. https://doi.org//10.1093/auk/118.2.557

Kern, R. A. 2015. Conservation ecology of tidal marsh sparrows in New Jersey. Dissertation, University of Delaware, Newark, Delaware, USA. https://udspace.udel.edu/bitstream/handle/19716/17143/2015_KernRebecca_PhD.pdf?isAllowed=y&sequence=1

Kirwan, M. L., S. Temmerman, E. E. Skeehan, G. R. Guntenspergen, and S. Fagherazzi. 2016. Overestimation of marsh vulnerability to sea level rise. Nature Climate Change 6:253-260. https://doi.org/10.1038/nclimate2909

Liebezeit, J. R., and T. L. George. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. Condor 104(3):507-517. https://doi.org/10.1093/condor/104.3.507

Lonard, R. I., F. W. Judd, and R. Stalter. 2013. The biological flora of coastal dunes and wetlands: *Distichlis spicata* (C. Linnaeus) E. Greene. Journal of Coastal Research 29(1):105-117. https://doi.org/10.2112/JCOASTRES-D-12-00018.1

Marshall, M. R., and R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. Ecology 85(2):432-445. https://doi.org/10.1890/02-0548

Marshall, R. M., and S. E. Reinert. 1990. Breeding ecology of Seaside Sparrows in a Massachusetts salt marsh. Wilson Bulletin 102(3):501-513. https://sora.unm.edu/sites/default/files/journals/wilson/v102n03/p0501-p0513.pdf

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453-487. https://doi.org/10.1146/annurev.es.18.110187.002321

Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? Ecology 82(1):175-188. https://doi.org/10.1890/0012-9658(2001)082[0175:avbioh]2.0.co;2

Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90(1):51-57. https://doi.org/10.2307/1368432

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261. http://webhome.auburn.edu/~grandjb/wildpop/readings/Nesting/mayfield_1961.pdf

McChesney, H. M., and J. T. Anderson. 2015. Reproductive success of Field Sparrows (*Spizella Pusilla*) in response to invasive Morrow's honeysuckle: does Morrow's honeysuckle promote population sinks? Wilson Journal of Ornithology 127(2):222-232. https://doi.org/10.1676/wils-127-02-222-232.1

McConnell, M. D., A. P. Monroe, L. W. Burger, Jr., and J. A. Martin. 2017. Timing of nest vegetation measurement may obscure adaptive significance of nest-site characteristics: a simulation study. Ecology and Evolution 7(4):1259-1270. https://doi.org/10.1002/ece3.2767

Meiman, S., D. Civeo, K. Holsinger, and C. S. Elphick. 2012. Comparing habitat models using ground-based and remote sensing data: Saltmarsh Sparrow presence versus nesting. Wetlands 32:725-736. https://doi.org/10.1007/s13157-012-0306-8

Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology 81(10):2892-2901. https://doi.org/10.1890/0012-9658(2000)081[2892:CACOHO]2.0.CO;2

Peteet, D. M., J. Nichols, T. Kenna, C. Chang, J. Browne, M. Reza, S. Kovari, L. Liberman, and S. Stern-Protz. 2018. Sediment starvation destroys New York City marshes' resistance to sea level rise. Proceedings of the National Academy of Sciences 115 (41):10281-10286. https://doi.org/10.1073/pnas.1715392115

Post, W., and J. S. Greenlaw. 1982. Comparative costs of promiscuity and monogamy: a test of reproductive effort theory. Behavioral Ecology and Sociobiology 10:101-107. https://doi.org/10.1007/BF00300169

Post, W., and J. S. Greenlaw. 2006. Nestling diets of coexisting Saltmarsh Sparrows: opportunism in a food-rich environment. Estuaries and Coasts 29:765-775. https://doi.org/10.1007/BF02786527

Post, W., J. S. Greenlaw, T. L. Merriam, and L. A. Wood. 1983. Comparative ecology of northern and southern populations of the Seaside Sparrow. Pages 123-136 in L. T. Quay, editor. The seaside sparrow: its biology and management. Occasional papers of the North Carolina biological survey. The Survey, Raleigh, North Carolina, USA. https://doi.org/10.5962/bhl.title.141714

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, S. G., R. A. Longenecker, M. A. Etterson, K. J. Ruskin, C. S. Elphick, B. J. Olsen, and W. G. Shriver. 2017. Factors that influence vital rates of Seaside and Saltmarsh Sparrows in coastal New Jersey, USA. Journal of Field Ornithology 88(2):115-131. https://doi.org/10.1111/jofo.12199

Ruskin, K. J., M. A. Etterson, T. P. Hodgman, A. C. Borowske, J. B. Cohen, C. S. Elphick, C. R. Field, R. A. Kern, E. King, A. R. Kocek, A. I. Kovach, K. M. O'Brien, N. Pau, W. G. Shriver, J. Walsh, and B. J. Olsen. 2017b. Seasonal fecundity is not related to geographic position across a species' global range despite a central peak in abundance. Oecologia 183:291-301. https://doi.org/10.1007/s00442-016-3745-8

Ruskin, K. J., M. A. Etterson, T. P. Hodgman, A. C. Borowske, J. B. Cohen, C. S. Elphick, C. R. Field, R. A. Longenecker, E. King, A. R. Kocek, A. I. Kovach, K. M. O'Brien, N. Pau, W. G. Shriver, J. Walsh, and B. J. Olsen. 2017a. Demographic analysis demonstrates systematic but independent spatial variation in abiotic and biotic stressors across 59 percent of a global species range. Auk 134(4):903-916. https://doi.org/10.1642/auk-16-230.1

Salinas-Melgoza, A., V. Salinas-Melgoza, and T. F. Wright. 2013. Behavioral plasticity of a threatened parrot in human-modified landscapes. Biological Conservation 159:303-312. https://doi.org/10.1016/j.biocon.2012.12.013

Schlaepfer, M. A., P. W. Sherman, B. Blossey, and M. C. Runge. 2005. Introduced species as evolutionary traps. Ecology Letters 8(3):241-246. https://doi.org/10.1111/j.1461-0248.2005.00730.x

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121(2):526-540. https://academic.oup.com/auk/article/121/2/526/5562433

Shriver, W. G. 2002. Conservation ecology of salt marsh birds in New England. Dissertation. State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA. https://doi.org/10.21926/aeer.2104026

Shriver, W. G., P. D. Vickery, T. P. Hodgman, and J. P. Gibbs. 2007. Flood tides affect breeding ecology of two sympatric sharp-tailed sparrows. Auk 124(2):552-560. https://doi.org/10.1093/auk/124.2.552

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115(1):101-110. https://doi.org/10.1016/S0006-3207(03)00098-3

Swanson, R. L., and R. E. Wilson. 2008. Increased tidal ranges coinciding with Jamaica Bay development contribute to marsh flooding. Journal of Coastal Research 246:1565-1569. https://doi.org/10.2112/07-0907.1

Talbert, M. K., and B. S. Cade. 2005. User manual for Blossom statistical package for R. U.S. Geological Survey Open-File Report 2005-1353. U.S. Geology Survey, Reston, Virginia, USA. https://doi.org/10.3133/ofr20051353

Tiner, Jr., R. W. 1984. Wetlands of the United States: current status and recent trends. U.S. Fish and Wildlife Service National Wetlands Inventory, Washington, D.C., USA. https://doi.org/10.5962/bhl.title.4097

Walsh, J., B. J. Olsen, K. R. Ruskin, W. G. Shriver, K. M. O'Brien, and A. I. Kovach. 2016. Extrinsic and intrinsic factors influence fitness in an avian hybrid zone. Biological Journal of the Linnean Society 119(4):890-903. https://doi.org/10.1111/bij.12837

Watson, E. B., K. Szura, C. Wigand, K. B. Raposa, K. Blount, and M. Cencer. 2016. Sea level rise, drought and the decline of *Spartina patens* in New England marshes. Biological Conservation 196:173-181. https://doi.org/10.1016/j.biocon.2016.02.011

Woolfenden, G. E. 1956. Comparative breeding behavior of *Ammospiza caudacuta* and *A. maritima*. University of Kansas, Museum of Natural History 10:45-75. https://www.gutenberg.org/files/36285/36285-h/36285-h.htm

Yeh, P. J., T. D. Price, and A. E. R. B. Huey. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist 164(4):531-542. https://doi.org/10.1086/423825

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