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NEST SITE SELECTION AND NESTING SUCCESS IN SALTMARSH BREEDING SPARROWS: THE IMPORTANCE OF NEST HABITAT, TIMING, AND STUDY SITE DIFFERENCES

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Abstract. We examined nest-site selection and nesting success in Saltmarsh Sharp-tailed (*Ammodramus caudacutus*) and Seaside Sparrows (*A. maritimus*), at seven sites in Connecticut. We found 160 Saltmarsh Sharp-tailed Sparrow nests and 23 Seaside Sparrow nests, and compared characteristics of their locations to each other and to random locations. We tracked success of all nests, quantified nest productivity and causes of nest losses, and tested for habitat differences between successful and unsuccessful nests. Saltmarsh Sharp-tailed Sparrows nested in higher than average locations, where the vegetation was taller and more dense than at random locations, where there was a deep layer of thatch, and where salt-meadow cordgrass (*Spartina patens*) dominated the vegetation. There was little evidence that habitat characteristics influenced the success of nesting birds, but the timing of nest initiation relative to spring tides was important. Seaside Sparrow nests occurred in even taller vegetation, that was more sparse than average and dominated by the tall form of smooth cordgrass (*S. alterniflora*). Habitat influenced the success of Seaside Sparrow nests, but timing did not; on average, successful nests occurred in taller vegetation. Model comparisons suggest that vegetation structure influences site selection more than species composition or inherent differences among marshes. Overall, our results indicate that nest flooding is a major threat to successful reproduction in both species, but they have different strategies to avoid flooding. Saltmarsh Sharp-tailed Sparrows time their reproduction to avoid especially high tides, while Seaside Sparrows avoid flooding spatially by nesting in tall vegetation.

Key words: *Ammodramus*, *habitat selection*, *saltmarsh*, *Seaside Sparrow*, *Sharp-tailed Sparrow*, *reproductive success*.

Selección de Sitios de Nidificación y Éxito de Nidificación en *Ammodramus*: La Importancia del Hábitat de Nidificación, la Fecha y las Diferencias de los Sitios de Estudio

Resumen. Examinamos la selección de sitios de nidificación y el éxito de nidificación en *Ammodramus caudacutus* y *A. maritimus*, en siete sitios en Connecticut. Encontramos 160 nidos de *A. caudacutus* y 23 nidos de *A. maritimus* y comparamos las características de los lugares de localización de los nidos entre sí y con sitios elegidos al azar. Seguimos el éxito de todos los nidos, cuantificamos la productividad y las causas de pérdida de los nidos y evaluamos las diferencias de hábitat entre nidos exitosos y no exitosos. *A. caudacutus* nidificó a mayor altura que las localizaciones promedio, donde la vegetación fue más alta y más densa que los lugares al azar, donde hubo un estrato más profundo de materia orgánica no descompuesta, y donde *Spartina patens* fue la vegetación dominante. No encontramos evidencia fuerte de que las características del hábitat influenciaran el éxito de las aves nidificantes, pero la fecha de inicio de la nidificación fue importante en relación a las mareas de primavera. Los nidos de *A. maritimus* se ubicaron en vegetación aún más alta, la cual presentó una distribución más esparcida que el promedio, y estuvo dominada por la forma alta de *S. alterniflora*. El hábitat influenció el éxito de nidificación de *A. maritimus*, pero la fecha no lo hizo. En promedio, los nidos exitosos se ubicaron en vegetación más alta. Las comparaciones de modelos multivariados sugirieron que la estructura de la vegetación tuvo una mayor influencia sobre la selección del hábitat que la composición de especies o las diferencias inherentes entre marjales. En términos generales, nuestros resultados indican que la inundación de los nidos es una amenaza importante para la reproducción exitosa de ambas especies, pero éstas tienen estrategias diferentes para evitar las inundaciones. *A. caudacutus* programa temporalmente su reproducción para evitar las mareas particularmente altas, mientras que *A. maritimus* evita las inundaciones ubicando sus nidos en vegetación alta.

INTRODUCTION

Birds are expected to choose nest sites that maximize their reproductive success. For example, habitat features that conceal the nest from predators (Kelly 1993, Liebezeit and George 2002) or provide greater food abundance within the nesting area (Marshall and Cooper 2004) should be preferred over more exposed or poor quality sites if they increase the probability of producing fledglings. Birds may also choose sites based on the nesting location of conspecifics. For instance, birds may nest in colonies to decrease the chance that their nest will be depredated (Brown and Brown 1996), or to share information about the location of patchy food resources (Coulson 2002). In other cases, birds may be constrained as to where they can nest because of the territorial behavior of others (Fretwell and Lucas 1970). Nest-site selection may be similar throughout a species' range, or it may vary depending on habitat availability or constraints on nesting success among regions. Understanding the determinants of nest-site selection, and their subsequent consequences for nesting success, is not, therefore, straightforward. Nonetheless, this information can be critically important for guiding management activities, especially when considering vulnerable populations or species that breed in vulnerable habitats.

The Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*) is the world's only passerine that nests exclusively in salt marshes (R. Greenberg, pers. comm.), and the closely related Seaside Sparrow (*A. maritimus*) is also largely restricted to this habitat. The Saltmarsh Sharp-tailed Sparrow has been ranked as globally Vulnerable using IUCN Red List criteria (Birdlife International 2004), and Partners in Flight has identified it as being in need of immediate conservation action (Rich et al. 2004). Seaside Sparrows breed along the U.S. Atlantic coast from New Hampshire to northeastern Florida, as well as along the north coast of the Gulf of Mexico. Although more widespread than Saltmarsh Sharp-tailed Sparrows, Seaside Sparrows are often restricted to large marshes (Benoit and Askins 2002, Shriver et al. 2004) and have been identified as species of conservation concern in several regions (Post and Greenlaw 1994, Rich et al. 2004). Both species are on the National Audubon Society's WatchList of high conservation concern species (National Audubon So-

cety 2002) and are ranked by the U.S. Fish and Wildlife Service as national conservation priorities (U.S. Fish and Wildlife Service 2002).

Much of this concern centers on the limited extent and perceived vulnerability of the birds' saltmarsh habitat. Because salt marshes are located along the coast and at the mouths of large rivers, often in industrial areas, their inhabitants are considered to be especially vulnerable to pollution, habitat change due to development, and sea-level rise (Adam 1990). Moreover, because they are restricted to a very narrow strip along the coast, salt marshes as a whole have a small areal extent relative to many other habitat types (Mendelssohn and McKee 2000), exacerbating the potential impact of these problems.

Several studies have shown that both Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows are typically found in habitats dominated by native vegetation, such as saltmarsh cordgrass (*Spartina patens*), smooth cordgrass (*S. alterniflora*), and black grass (*Juncus gerardi*) (Woelfenden 1956, Reinert and Mello 1995, Brawley et al. 1998, Benoit and Askins 1999, Shriver et al. 2004). A few single-marsh studies have quantified nest-habitat requirements for Saltmarsh Sharp-tailed Sparrows, and suggest that this species selects sites with a deeper layer of accumulated dead plant material (Shriver 2002), higher elevations (Shriver 2002, DiQuinzio et al. 2002), and taller vegetation (DiQuinzio et al. 2002). Only a few studies have examined the breeding biology of Seaside Sparrows from the northern portion of the species' range. Seaside Sparrow nest sites could not be differentiated from random sites at a marsh in New York (Post et al. 1983), but tall *S. alterniflora* was chosen disproportionately for nest sites in a Massachusetts study (Marshall and Reinert 1990). In contrast, the vegetation surrounding Seaside Sparrow nests in a Florida study was shorter and less dense than at random points (Post et al. 1983).

Because prior studies of habitat use have been limited to single marshes, it is unclear whether the patterns seen, and especially the differences among studies, are representative of the species or due to idiosyncratic differences among sites. Evaluating the reasons for differences among studies is further complicated because not all variables were measured in every study. To address these concerns and provide a more detailed analysis of habitat selection in these two species,

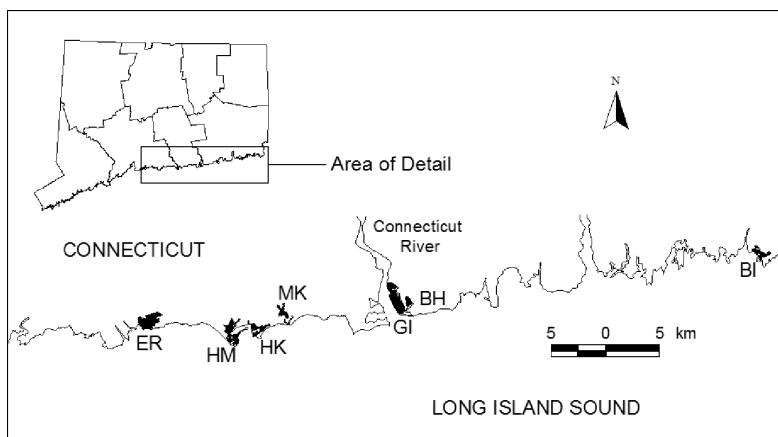


FIGURE 1. Location of saltmarsh study sites in Connecticut during 2002 and 2003. ER = East River Marsh, Guilford (289 ha); HM = Hammonasset State Park, Madison (209 ha); HK = Hammock River Marsh, Clinton (102 ha); MK = McKinney National Wildlife Refuge, Westbrook (68 ha); GI = Great Island Wildlife Management Area, Old Lyme (217 ha); BH = Black Hall River Marsh, Old Lyme (50 ha); BI = Barn Island Wildlife Management Area, Stonington (107 ha).

we examined nest-site selection and nesting success in sympatric populations of Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows at seven sites along the Connecticut coast. We compiled a list of habitat variables associated with nest-site selection in at least one previous study, or that were considered likely to influence selection but had not previously been studied. For each species, we tested whether habitat conditions differed between nest sites and non-nest sites, or between successful nests and those that failed. We then used an information-theoretic model selection approach to evaluate the relative influence of vegetation structure, plant species composition, and study site on nest-site selection and nesting success. Lastly, we determined how nest-site selection differed between these two closely related, syntopic, species.

We also conducted an analysis to compare alternative models describing variation in daily nest survival rates. Because spring tide flooding is a major source of nest failure in saltmarsh nesting sparrows (Shriver 2002; Greenberg et al., in press), we were especially interested in whether survival rates depended on the timing of nest initiation. In addition, we examined whether nest survival varied with nest age, between years, and among study sites.

METHODS

STUDY AREA

The study was conducted at seven sites along the Connecticut coast during the summers of

2002 and 2003 (Fig. 1). We collected most of our data in 40 one-hectare square study plots that had been created at these sites as part of a larger study. Although this one-hectare plot design provided our sampling frame, individual nests are the experimental units for our analyses. Sites were located at East River Marsh, Guilford (10 plots); Hammonasset State Park, Madison (8 plots); Hammock River Marsh, Clinton (2 plots); Stewart B. McKinney National Wildlife Refuge, Westbrook (5 plots); Great Island Wildlife Management Area, Old Lyme (8 plots); Black Hall River Marsh, Old Lyme (2 plots); and Barn Island Wildlife Management Area, Stonington (5 plots). Plot locations at each site were chosen by randomly selecting grid points placed within the marsh boundaries on U.S. Geological Survey topographic maps. Minimum distance between plots was 17 m (range: 17 m–1269 m). For logistical reasons, if a large, deep channel (>5 m wide) crossed the plot, we moved the location to the nearest point where we could reasonably access the entire plot without having to cross a channel.

NEST MONITORING

Each plot was visited five times at approximately two-week intervals, between late May and mid-August. On each visit, we conducted a thorough search of the plot to look for nests. In addition to these intensive searches, we looked for nests less exhaustively every three to five days

while visiting plots to check the status of known nests. All nests were marked with a flag 5 m away from the nest such that the nest lay on a line between the flag and the center of the plot; this system enabled us to relocate the nest easily, but reduced the risk of identifying the location to predators. Once a nest was found we visited it at three- to five-day intervals in order to determine its fate. Nests that were found incidentally outside of plots were also marked and monitored; because the analyses described in this paper are not based on our plot design, these additional nests are included in our analyses. Nests were considered successful if they produced at least one young. Failures were ascribed to flooding when at least one egg was found immediately outside of the nest cup and the female was no longer attending the nest, or when dead, wet chicks were found. Failures due to flooding always coincided with especially high tides. Failed nests were considered depredated when there were signs of predator activity (broken egg shells, disturbed nests, etc.), or when eggs or chicks that were too young to fledge (<8 days old) disappeared from the nest.

To calculate nest age, we assumed a 26-day nesting period for both species, because females lay an average of four eggs per clutch, incubate for 12 days, and feed the nestlings for another 10 days (Greenlaw and Rising 1994, Post and Greenlaw 1994). For nests found with an incomplete clutch, we assumed that females lay one egg a day and counted backwards in time to determine the nest initiation date. When the hatch date was not known, we estimated it as the midpoint between the last date eggs occurred in the nest and the first date chicks were present. Nests found during the nestling stage were aged based on the chicks' stage of development (Greenlaw and Rising 1994, Post and Greenlaw 1994). For the remaining 42 cases, when a nest that was found during incubation failed before the eggs hatched, we estimated the date that incubation began using the following formula (Martin et al. 1997):

First day of incubation

= date found

$$- \left(\frac{\text{incubation} - \text{number of days observed}}{2} \right).$$

This equation assumes that, on average, nests

are found exactly in the middle of the incubation period. To test this assumption, we used 56 nests for which the first day of incubation could be calculated, and determined whether nest discovery dates were biased towards either early or late in the incubation period. The mean (\pm SD) discovery date was 5.0 ± 3.3 days after incubation started, and there was no significant skew to the distribution (skewness = 0.21, $z = 0.7$, $P = 0.52$). Thus, we concluded that the assumption of the Martin et al. (1997) equation was reasonable.

HABITAT SAMPLING

We sampled habitat at 18 points within each plot (the center, the four corners, the mid-points of each side, and nine random locations) and at the site of each nest. Systematically and randomly located non-nest points were compared to assess whether complete randomization would be necessary in future work. A one-meter quadrat was placed around each sampling point. We measured the height of the vegetation at the corners of the quadrat, and the thatch depth (i.e., the depth of the accumulated dead plant material) near the center of the quadrat. Species composition was determined by estimating the proportionate abundance of each plant species within the quadrat. We counted the number of stems in five randomly located 100-cm² subquadrats to estimate vegetation density. At each sampling point we also determined the height of the ground relative to the center of the plot (i.e., relative elevation) using a surveying level. Habitat sampling occurred between mid-July and mid-August in both years.

STATISTICAL ANALYSES

First we tested whether there were habitat differences between our two types of non-nest data. We performed analyses of variance, in which plot was treated as a blocking factor, to compare habitat characteristics between quadrats placed systematically in reference to our plot boundaries, and those placed at random points.

To determine whether birds were selecting nest sites on the basis of habitat characteristics, we initially conducted univariate comparisons (t -tests or Mann-Whitney U -tests as appropriate) of vegetation height, vegetation density, thatch depth, and percent cover for the five most common vegetation types; *Spartina patens*, *S. alterniflora* (short form), *S. alterniflora* (tall form),

Distichlis spicata, and *Juncus gerardi*. We then used logistic regression (Hosmer and Lemeshow 2000) to compare habitat between nest and non-nest locations for both sparrow species, and an information-theoretic approach to select the model that best fit the data (Burnham and Anderson 2002, Johnson and Omland 2004, Stephens et al. 2005).

Measurements from all non-nest sites were used in our analyses for Saltmarsh Sharp-tailed Sparrows. Seaside Sparrows, however, nested in only four of the seven marshes, and the absence of this species from certain sites has been attributed to landscape-scale processes rather than within-site habitat selection (Benoit and Askins 1999, Shriver et al. 2004). Consequently, we used only those non-nest measurements taken from the marshes in which this species was present.

Based on our *a priori* assessment of earlier studies and our preconceptions of what might influence nesting behavior, we created a set of seven candidate models designed to examine the effects of vegetation structure, vegetation composition, and marsh site on sparrow nest-site selection. Models were compared by calculating Akaike's information criterion (AIC) for each model and determining the difference in AIC values (ΔAIC_i) compared to the model with the lowest AIC in the set of candidate models (Burnham and Anderson 2002). In all cases, variables were not highly correlated (i.e., $r < 0.7$) and thus could be used simultaneously in the same model (Hosmer and Lemeshow 2000).

Once we had identified the best models from our initial candidate set (i.e., those with $\Delta AIC_i < 2$; Burnham and Anderson 2002), we determined whether each could be reduced to provide a more parsimonious explanation of the data. This step involved the sequential removal of variables for which the likelihood-ratio statistic (G ; Hosmer and Lemeshow 2000) gave $P > 0.10$. Reduced models were preferred as long as they did not fit worse than the best model from the initial candidate set. Finally, for each set of analyses, we used Akaike weights (w_i) to evaluate the likelihood of each model (Burnham and Anderson 2002).

We could not include elevation in our multivariate analysis because we lacked a single reference point with which to compare elevations from different marshes. We did, however, test whether relative elevation differed between nest

sites and non-nest sites. For each plot, we calculated the mean elevation for all nest sites and the mean for all non-nest sites. We then compared these mean values across all plots using paired t -tests.

To investigate the effects of habitat variables on nest fates, we used univariate comparisons (two-tailed t -tests or Mann-Whitney U -tests as appropriate) to test the hypothesis that habitat conditions differed between successful and failed nests. Next, we compared the same set of models that we used to examine nest-site selection using Akaike's information criterion corrected for small sample sizes (AIC_c) to compare candidate models for explaining nest fates (Burnham and Anderson 2002). Because prior research has shown that flooding is a major source of nest failure in saltmarsh sparrows (Shriver 2002; Greenberg et al., in press), we also tested whether the number of days between the first day of incubation and the nearest spring tide differed among nests with different fates.

For each analysis, we present the likelihood ratio statistic (G) and associated P -value for the model with the lowest AIC or AIC_c . Goodness-of-fit for these best-fit models was evaluated using the Hosmer-Lemeshow test (Hosmer and Lemeshow 2000), where a nonsignificant value indicates a good fit between the model and the data. We also used the likelihood-ratio test to determine the significance of each independent variable in the model.

We used program MARK (White and Burnham 1999) to model daily nest survival, and calculated overall nest success as the product of daily survival rates across the 26-day nesting period (Dinsmore et al. 2002, Traylor et al. 2004). For Saltmarsh Sharp-tailed Sparrows, we compared seven models to examine the effects of year, daily nest age, site, nest initiation date relative to the timing of spring tides (when the high tide height peaks), and habitat. Our simplest model assumed daily nest survival was constant over the 26-day nesting cycle and across all nests. To test for annual and study site differences, we assumed daily nest survival was constant over the nesting cycle in each year (S_{year}) or at each site (S_{site}). Fourth, we modeled a linear decline in daily nest survival with nest age to test the hypothesis that survival decreases in older nests (S_{age} , Barash 1975). Fifth, we tested whether there was an effect of the nest's age combined with a year effect ($S_{\text{year+age}}$). Sixth, we

tested whether the tidal cycle influenced nest survival by using a quadratic function to relate survival to the number of days between nest initiation and the nearest spring tide ($S_{\text{tide}+\text{tide}}^2$). We included this model because Saltmarsh Sharp-tailed Sparrows are known to time their breeding so that nesting fits between the extreme high tides that can flood their nests (Shriver 2002). Therefore, we predicted lower daily survival rates for those nests initiated too early or too late in relation to the spring tide. Finally, we included the habitat model with the best explanatory power from the results of our logistic regressions to examine the relative effects of habitat characteristics on daily nest survival.

To examine nest survival in Seaside Sparrows, we used six of the seven models described for Saltmarsh Sharp-tailed Sparrows. Because Seaside Sparrows were absent from three of our seven sites, and sample sizes were small at the remaining sites, we were unable to test the global model for this species.

We used a logit-link function to transform all daily survival estimates to the interval (0, 1); individual covariates were standardized with a mean of zero and a range of ± 3 (Lebreton et al. 1992, Dinsmore et al. 2002). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to compare the set of candidate models (Burnham and Anderson 2002). We used program MARK (White and Burnham 1999) to model daily nest survival, and SYSTAT 8.0 (SPSS Inc. 1998) for all other analyses. We accepted significance at $\alpha = 0.05$ and summary statistics are presented as mean \pm SD, unless otherwise noted.

RESULTS

HABITAT CHARACTERISTICS

We measured habitat characteristics in 359 one-meter square quadrats located systematically, and 360 quadrats located randomly, within our study plots. There were no significant differences in relative elevation, vegetation height, thatch depth, or species composition between systematically and randomly located points ($P > 0.10$ in all comparisons). Statistical power for these tests indicated a good chance of detecting even a small difference between treatments ($1 - \beta = 0.51$ for an effect size of 0.1, $1 - \beta > 0.99$ for an effect size of 0.2; Cohen 1988). Random points had higher stem density counts on aver-

age (mean difference = 4 stems, $P = 0.02$), however, the difference was not statistically significant after controlling for Type I error rates for multiple tests (Rice 1989). Perhaps more importantly, a difference of four stems is small (12%) relative to the average stem density in plots, and two and a half to six times smaller than the differences between nest sites and non-nest sites (Table 1). Thus, it seems unlikely that the difference is large enough to be biologically significant. Given these results, we pooled the habitat data taken at systematically and randomly selected locations.

Vegetation in our plots was dominated by *Spartina patens*, followed by *S. alterniflora* (short form), *S. alterniflora* (tall form), spike grass (*Distichlis spicata*), and *Juncus gerardi*. Interspersed were small amounts of the herbaceous sea lavender (*Limonium carolinianum*), glasswort (*Salicornia europaea*) and seaside gerardia (*Gerardia maritime*). Habitat variables are summarized in Table 1.

NEST SITE SELECTION

We compared habitat characteristics at 160 Saltmarsh Sharp-tailed Sparrow nest sites found across all seven marshes to 719 non-nest sites. Univariate analyses indicated that nest sites had taller, more dense vegetation, a deeper layer of thatch, and higher elevations compared to non-nest sites (Table 1). In addition, *S. patens*, tall *S. alterniflora*, and *J. gerardi* were significantly more common at nest sites than at non-nest sites, and *D. spicata* was less common at nest sites.

Of the initial candidate models, the global model, which included all structural variables, species composition variables, and marsh site, provided the best explanation of the differences between Saltmarsh Sharp-tailed Sparrow nest sites and non-nest sites (Table 2). Removing vegetation height ($G = 1.2$, $P = 0.27$) slightly improved this model ($\Delta AIC_c = 0.77$; Table 2). Thus, our analysis suggests that the preferred model includes marsh site, vegetation density, thatch depth, and the relative amounts of all the major plant types (log-likelihood = -351.86 , $G = 123.5$, $P < 0.001$; Hosmer-Lemeshow statistic = 13.1, $df = 7$, $P = 0.07$).

We compared habitat measurements at 23 Seaside Sparrow nest sites to the 503 non-nest sites from the four marshes where the species occurred. Univariate tests suggest that nest sites had taller, less dense, vegetation than non-nest

TABLE 1. Univariate comparisons (mean \pm SD, range) of habitat variables at nest sites and non-nest sites for Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows. Asterisks indicate tests that remain significant after using the sequential Bonferroni test, with $\alpha = 0.05$ and tests $n = 9$ (Rice 1989).

Habitat variable	Non-nest site ($n = 719$)	Saltmarsh Sharp-tailed Sparrow nest sites ($n = 160$)	Seaside Sparrow nest sites ($n = 23$)	Saltmarsh Sharp-tailed Sparrow nest sites compared to non-nest sites	Seaside Sparrow nest sites compared to non-nest sites ^a	Saltmarsh Sharp-tailed Sparrow nest sites compared to Seaside Sparrow nest sites
Vegetation height (cm) ^b	39.9 \pm 16.4 (0–112)	44.9 \pm 10.2 (21–81)	64.3 \pm 16.1 (38–97)	$t_{367.0} = 4.9, P < 0.001^*$	$t_{24.0} = 6.5, P < 0.001^*$	$t_{24.6} = 5.6, P < 0.001^*$
Vegetation density (#stems/100 cm ²) ^b	37.1 \pm 26.3 (0–108)	52.7 \pm 26.2 (7–128)	26.1 \pm 20.8 (5–71)	$t_{235.8} = 6.9, P < 0.001^*$	$t_{24.5} = -2.9, P = 0.01^*$	$t_{31.8} = 5.6, P < 0.001^*$
Thatch depth (cm) ^b	5.5 \pm 0.2 (0–34)	8.8 \pm 0.4 (0–22)	9.3 \pm 7.8 (0–31)	$t_{248.3} = 7.8, P < 0.001^*$	$t_{22.8} = 2.1, P = 0.04$	$t_{24.3} = 0.3, P = 0.76$
Percent <i>Spartina patens</i> ^c	38.9 \pm 40.4 (0–100)	54.2 \pm 35.2 (0–100)	21.2 \pm 32.1 (0–85)	$U = 69,097, P < 0.001^*$	$U = 4163, P = 0.02$	$U = 911, P < 0.001^*$
Percent <i>S. alterniflora</i> (short) ^c	20.6 \pm 35.1 (0–100)	10.4 \pm 20.6 (0–100)	0.0 (0)	$U = 53,891, P = 0.14$	$U = 4163, P < 0.01^*$	$U = 1242, P < 0.01^*$
Percent <i>S. alterniflora</i> (tall) ^c	10.9 \pm 26.6 (0–100)	14.6 \pm 26.3 (0–100)	47.0 \pm 44.7 (0–100)	$U = 64,716, P < 0.01^*$	$U = 8894, P < 0.001^*$	$U = 2692, P < 0.001^*$
Percent <i>Distichlis spicata</i> ^c	10.0 \pm 22.0 (0–100)	5.9 \pm 14.4 (0–80)	7.4 \pm 15.7 (0–50)	$U = 52,224, P < 0.001^*$	$U = 5169, P = 0.30$	$U = 1796, P = 0.81$
Percent <i>Juncus gerardi</i> ^c	8.8 \pm 23.8 (0–100)	12.2 \pm 25.8 (0–100)	14.3 \pm 24.7 (0–85)	$U = 62,162, P = 0.02^*$	$U = 6395, P = 0.21$	$U = 1948, P = 0.55$
Mean difference in elevation (cm) ^d	—	—	—	2.5 \pm 5.0	0.3 \pm 6.4	3.1 \pm 5.8
				$t_{34} = -2.9, P < 0.01^*$	$t_{10} = 0.2, P = 0.87$	$t_9 = -0.1, P = 0.12$

^a Habitat at nest sites compared to 503 non-nest sites that were measured at the same four marshes.

^b t -test comparisons with separate variance.

^c Mann-Whitney U -test comparisons.

^d The mean differences in elevation between nest sites and non-nest sites, and between Seaside and Saltmarsh Sharp-tailed Sparrow nest sites, were calculated for each plot and compared using a paired t -test.

sites, but we found no evidence that there was any difference in elevation among sites (Table 1). Seaside Sparrow nest sites also had a much higher percentage of tall *S. alterniflora* than non-nest sites, but no short *S. alterniflora* (Table 1). The best model, from our candidate set, for the difference between Seaside Sparrow nest sites and non-nest sites included vegetation height, density, and thatch depth (log-likelihood = -73.37 , $G = 35.9$, $P < 0.001$; Hosmer-Lemeshow statistic = 4.8 , $df = 5$, $P = 0.44$). Removing the thatch depth variable ($G = 0.6$, $P = 0.43$) resulted in an equally good ($\Delta AIC_i = 0.92$; Table 2), yet simpler, model.

Nest-site selection differed between Saltmarsh Sharp-tailed and Seaside Sparrows in several ways. Seaside Sparrows used sites with taller and more sparse vegetation. *S. patens* and short form *S. alterniflora* were less common near Seaside Sparrow nests than at Saltmarsh Sharp-tailed Sparrow nests, but tall form *S. alterniflora* was more abundant. We found no evidence that thatch depth or the amounts of *D. spicata* and *J. gerardi* differed between the nest sites of the two species (Table 1).

NEST SUCCESS

Of the 160 Saltmarsh Sharp-tailed Sparrow nests that we found, 136 had known outcomes, and 125 had sufficient information for use in our nest survival analyses. Eighty (59%) failed to produced fledglings. Flooding was the major cause of nest failure, accounting for 60% ($n = 48$) of all failed nests. Another 31% ($n = 25$) of failed nests were depredated. We also found evidence for partial nest losses; 17 of the 136 nests (13%) fledged at least one chick but not a complete clutch. Flooding caused the loss of at least one egg or chick in seven of these nests, and at least one egg or chick went missing in the other ten nests. Partial failure, however, was relatively uncommon, with 87% of flooding events and 71% of predation events causing total nest failure.

When we compared habitat variables using univariate tests, we found no significant differences between successful and failed nests, nor between successful and flooded nests ($P > 0.19$ in all comparisons). Repeating this analysis to compare nests that lost no eggs or chicks to those that suffered at least partial losses also found no differences. Of the models that we considered, the one that included vegetation height, vegetation density, and thatch depth had

TABLE 2. Ranking of models considered to explain Saltmarsh Sharp-tailed Sparrow and Seaside Sparrow nest site selection. Ranking is based on the smallest AIC value; k is the number of parameters in the model; w_i is the Akaike weight.

Model ^a	Log-likelihood	k	ΔAIC_i^b	w_i
Saltmarsh Sharp-tailed Sparrow				
REDUCED1	-351.86	15	0.00	0.59
ALLVAR	-351.25	16	0.77	0.40
VEGST	-368.90	5	14.09	0.00
VEGSTSI	-364.96	11	18.20	0.00
VEGCOMP	-388.32	7	56.91	0.00
VEGCOMPSI	-383.59	13	59.46	0.00
INTERCEPT	-413.62	2	97.53	0.00
SITE	-424.74	8	131.76	0.00
Seaside Sparrow				
VEGST	-73.37	5	0.00	0.58
REDUCED2	-74.83	4	0.92	0.36
VEGSTSI	-72.81	8	4.89	0.05
ALLVAR	-69.23	13	7.72	0.01
VEGCOMP	-79.47	7	16.20	0.00
VEGCOMPSI	-78.39	10	20.04	0.00
INTERCEPT	-91.32	2	29.92	0.00
SITE	-88.47	5	30.20	0.00

^a Models are defined as INTERCEPT = intercept only; VEGST = vegetation structure, including vegetation density, height, and thatch depth; SITE = marsh site only; VEGSTSI = vegetation structure with site; VEGCOMP = vegetation composition, including relative percent of *S. patens*, *S. alterniflora* (short and tall forms), *D. spicata*, and *J. gerardi*; VEGCOMPSI = vegetation composition with site; ALLVAR = all structural and compositional variables with site; REDUCED1 = all variables except vegetation height; REDUCED2 = vegetation height and density only.

^b The lowest AIC values for Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows were 733.72 and 156.73, respectively.

the best explanatory power (Table 3). None of the individual variables, however, were significant ($P > 0.35$ for all variables), suggesting that although this is the best model it is not an especially good one (log-likelihood = -87.58, $G = 1.3$, $P = 0.73$; Hosmer-Lemeshow statistic = 0.6, $df = 2$, $P = 0.74$).

The daily nest survival rate calculated from the intercept-only model was 0.94 ± 0.01 SE, suggesting an overall nest success of 0.20 (95% CL = 0.13, 0.29) across the 26-day nesting cycle. Incorporating the timing of nesting relative to the occurrence of spring tides substantially improved the model's fit, by accounting for reduced survival at the beginning and end of the nesting period. In contrast, incorporating the

TABLE 3. Ranking of models relating Saltmarsh Sharp-tailed Sparrow and Seaside Sparrow nest success to habitat variables. Ranking is based on the smallest AIC_c value; k is the number of parameters in the model; w_i is the Akaike weight.

Model ^a	Log-likelihood	k	ΔAIC_{ci}^b	w_i
Saltmarsh Sharp-tailed Sparrow				
VEGST	-87.58	5	0.00	0.69
INTERCEPT	-92.14	2	2.72	0.18
VEGCOMP	-87.12	7	3.51	0.12
VEGSTSI	-85.14	11	8.86	0.01
SITE	-89.76	8	11.06	0.00
VEGCOMPSI	-84.55	13	12.59	0.00
ALLVAR	-84.22	16	19.61	0.00
Seaside Sparrow ^c				
INTERCEPT	-14.42	2	0.00	0.56
VEGST	-10.09	5	0.67	0.40
SITE	-12.67	5	5.84	0.03
VEGCOMP	-11.62	6	7.72	0.01
VEGSTSI	-9.28	8	13.05	0.00
VEGCOMPSI	-9.30	9	19.45	0.00

^a See Table 2 for explanations of model names.

^b The lowest AIC_c values for Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows were 185.65 and 33.51, respectively.

^c We were unable to evaluate the global model due to small sample size.

year, the age of the nest, the study site at which the nest occurred, or vegetation structure all resulted in substantially worse models (Table 4).

Incubation of successful nests was initiated 5.3 days later in the season on average than failed nests (t -test: $t_{129} = -1.9$, $P = 0.06$). The number of days between the beginning of incubation and the nearest spring tide was an even better indicator of a nest's fate, however, with clear differences among nests that were successful, those that were flooded during incubation, and those that were flooded during chick rearing ($F_{2,97} = 31.2$, $P < 0.001$; Fig. 2a). Incubation of nests that failed due to flooding during incubation began 5.7 ± 7.6 days prior to the spring tide, compared to 4.0 ± 5.4 days after the spring tide for nests that successfully raised at least one fledgling. Incubation of nests that were flooded during chick rearing began 6.2 ± 3.6 days after the spring tide.

We were able to determine the outcome for only 22 Seaside Sparrow nests, and of these, 20 had sufficient information for use in our nest survival analyses. Four nests were depredated, three were flooded during incubation, and for

TABLE 4. Summary of model selection results for the daily nest survival of Saltmarsh Sharp-tailed Sparrow and Seaside Sparrow.

Model ^a	Deviance	<i>k</i>	ΔAIC_{ci} ^b	<i>w_i</i>
Saltmarsh Sharp-tailed Sparrow				
$S_{\text{tide}+\text{tide}^2}$	324.35	3	0.00	0.99
S_{age}	337.75	2	11.38	0.00
$S_{\text{year}+\text{age}}$	337.47	3	13.12	0.00
$S_{\text{.}}$	341.69	1	13.32	0.00
S_{year}	341.58	2	15.22	0.00
$S_{\text{veg. structure}}$	337.87	4	15.53	0.00
S_{site}	339.85	7	23.58	0.00
Seaside Sparrow				
$S_{\text{veg. structure}}$	32.69	4	0.00	0.59
$S_{\text{.}}$	41.55	1	2.61	0.16
$S_{\text{tide}+\text{tide}^2}$	38.18	3	3.37	0.11
S_{age}	41.45	2	4.56	0.06
S_{year}	41.51	2	4.62	0.06
$S_{\text{year}+\text{age}}$	41.38	3	6.58	0.02

^a See the text for explanation of model names.

^b The lowest AIC_c values for Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows were 330.38 and 40.96, respectively.

one the cause of failure could not be determined. No Seaside Sparrow nests were found partially flooded, but one egg went missing in two of the 14 successful nests.

Based on individual tests, successful Seaside Sparrow nests were placed in taller, less dense, vegetation with less *S. patens* and more tall *S. alterniflora* than failed nests (Table 5), although none of these findings were significant after sequential Bonferroni adjustments to control for Type I errors (Rice 1989). Our best-fit model contained only an intercept term, although the model that included structural variables (vegetation height, density, and thatch depth) was not substantially worse ($\Delta AIC_{ci} = 0.67$). Both models received relatively high Akaike weights (Table 3). We did not include percent *S. alterniflora* (short form) in our model set because it did not occur at any of our nest sites (Table 1), and we could not compare flooded Seaside Sparrow nests to those that survived because so few were flooded. We were also unable to evaluate the global model due to small sample size.

Daily nest survival for Seaside Sparrows, calculated from the intercept-only model, was 0.95 ± 0.02 SE, resulting in an overall survival estimate of 0.27 (95% CL = 0.08, 0.52) across the nesting period. The model that included vegetation height, vegetation density, and thatch

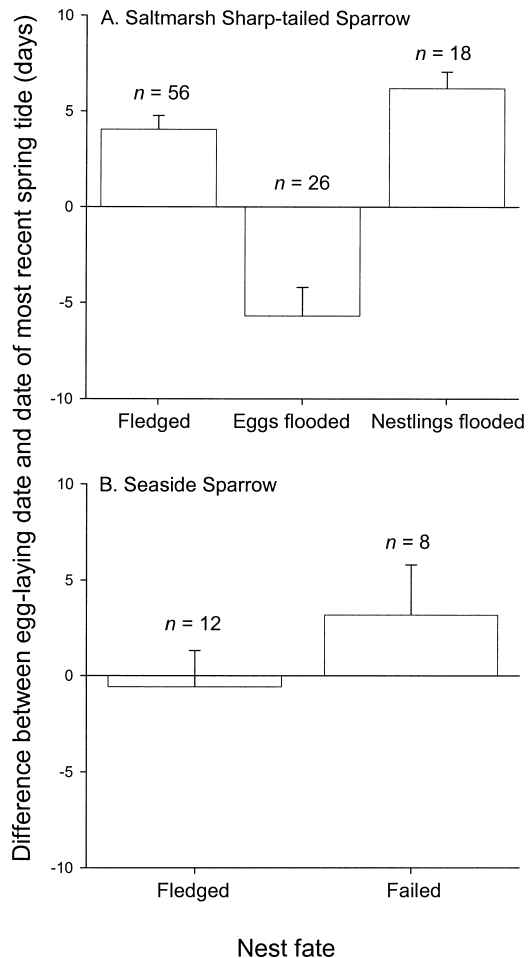


FIGURE 2. The number of days (mean \pm SE) after the last spring tide that female Saltmarsh Sharp-tailed Sparrows (A.) and Seaside Sparrows (B.) initiated incubation for nests that suffered different fates. Negative values indicate nests that were initiated prior to the spring tide. Sample sizes for each group are indicated above the bar.

depth provided the best fit among our candidate set (Table 4). For Seaside Sparrows, the timing of nesting did not differ between successful and failed nests either when viewed in strict chronological terms ($t_{18} = 1.1$, $P = 0.28$), or when the number of days between the beginning of incubation and the nearest spring tide was used ($t_{18} = 1.2$, $P = 0.25$; Fig. 2b).

DISCUSSION

Nest-site selection has been well studied in birds, and many studies have shown that micro-habitat structure and plant species composition

TABLE 5. Comparisons between the habitat characteristics (mean \pm SD) at successful ($n = 14$) and failed ($n = 8$) Seaside Sparrow nests.

Habitat variable	Successful	Failed	Successful vs. failed ^a
Vegetation ht. (cm)	70.3 \pm 13.2	53.5 \pm 16.8	$t_{20} = -2.6, P = 0.02$
Vegetation density (#stems/100 cm ²)	20.1 \pm 17.3	38.2 \pm 20.2	$U = 78, P = 0.06$
Thatch depth (cm)	9.5 \pm 9.1	9.1 \pm 6.2	$U = 56, P = 0.97$
Percent <i>S. patens</i>	10.7 \pm 25.9	42.3 \pm 34.6	$U = 86, P = 0.02$
Percent <i>D. spicata</i>	5.7 \pm 15.0	5.0 \pm 9.3	$U = 60, P = 0.69$
Percent <i>S. alterniflora</i> (tall)	61.8 \pm 44.3	23.8 \pm 38.9	$U = 25, P = 0.03$
Percent <i>J. gerardi</i>	14.6 \pm 26.9	12.5 \pm 27.8	$U = 54, P = 0.86$

^a Comparisons from t -test with pooled variance and Mann-Whitney U -tests.

are related to both nest placement and success (Misenhelter and Rotenberry 2000, Lusk et al. 2003, Pidgeon et al. 2003). Our ability to investigate these links, however, has improved with the growing use of model-selection techniques (Burnham and Anderson 2002, Dinsmore et al. 2002), which have enhanced our ability to distinguish among alternative explanatory models and identify those variables that have the greatest influence on nesting behavior.

Understanding the nature of these relationships is especially important for habitat specialists, because they are particularly vulnerable to changing conditions and are often species of conservation concern. A comprehensive understanding of nest-site selection and success in Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows is therefore valuable both because these species have been identified as top conservation priorities (U.S. Fish and Wildlife Service 2002, Rich et al. 2004), and because both are restricted to a very narrow range of habitats (Greenlaw and Rising 1994, Post and Greenlaw 1994). Moreover, our comparison between these particular species is interesting because, although closely related and living side by side in the same areas, they respond quite differently to the tidal marsh environment.

Saltmarsh Sharp-tailed Sparrows chose sites where the vegetation was taller and more dense than at random locations, where there was a deep layer of thatch, where the vegetation community was dominated by *S. patens*, and where the marsh was higher in elevation than average. Seaside Sparrows selected even taller vegetation than Saltmarsh Sharp-tailed Sparrows, choosing nest sites that were dominated by tall form *S. alterniflora*, and where the vegetation was less dense than average.

Our results broadly match those of previous studies (Marshall and Reinert 1990, Reinert and Mello 1995, DiQuinzio et al. 2002, Shriver 2002), although support for specific variables varied among studies resulting in somewhat different conclusions about habitat selection. These differences no doubt arose through some combination of different sampling techniques, differences in the variables measured and sample sizes, or different sparrow behavior when faced with subtle differences in marsh habitats at different sites. Evidence for facultative behavioral responses to different habitat conditions comes in two forms. First, the elevation difference between Saltmarsh Sharp-tailed Sparrow nest sites and random locations was much larger in the Gulf of Maine (~ 15 cm; Shriver 2002) than in Long Island Sound (~ 2 cm; DiQuinzio et al. 2002, this study), where there is a much smaller tidal range. Second, in one study, Saltmarsh Sharp-tailed Sparrows selected sites with significantly taller vegetation and deeper thatch following a marsh restoration project that resulted in deeper tidal flooding and thus greater flooding risk (DiQuinzio et al. 2002).

Although univariate tests from our study and those conducted by others collectively suggest that vegetation structure, plant species composition, and study site differences all have some influence on nest site selection, our multivariate models suggest that both species respond more strongly to vegetation structure than to other variables. For Seaside Sparrows, this result was clear: models that included only vegetation structure were substantially better than the alternatives considered. For Saltmarsh Sharp-tailed Sparrows, plant species composition and marsh site differences appeared to play some role because the global model provided the best fit. Re-

removal of the structural variables, however, resulted in far worse models than did removal of the compositional or site variables, suggesting similarities to the results for Seaside Sparrows.

Although we found that both species selected certain habitat characteristics over others when choosing nest locations, the evidence that vegetation characteristics influenced nest success was weak. For Saltmarsh Sharp-tailed Sparrows, our best model did include vegetation structure, but individual variables were not significant. For Seaside Sparrows, univariate tests suggested that successful nests were more likely to be in taller vegetation with more *S. alterniflora* and less *S. patens*, but there was a high risk that Type I statistical errors accounted for some of these differences. In our model comparisons for this species, both the model relating success to vegetation structure and that which assumed that successes were randomly distributed received support, but the latter provided the better fit. In our analysis of daily nest survival, however, the model that included vegetation structure received the most support.

Our analysis of nest fates matched results from studies elsewhere (DeRagon 1988, Shriver 2002), and from closely related species (Burhans et al. 2002, Swanson et al. 2004, Winter et al. 2005). One explanation for the lack of a strong relationship between habitat and nest success is that nest-site selection is sufficiently effective that most birds simply avoid building nests where the habitat is likely to result in failure. Such nonrandom nest-site selection would make the detection of a habitat effect difficult. Contrary to the predictions of this hypothesis, however, the amount of variation in each habitat characteristic was similar at nest sites and random sites, and the range of nest situations broadly overlapped with what was available. Other explanations may be that characteristics of the nest itself (e.g., height and concealment) may influence success more than the habitat in which it is placed, or that nest construction is modified to compensate for placement in an otherwise vulnerable location. A separate study of nest construction in Saltmarsh Sharp-tailed Sparrows, however, did not support the notion that construction differences affect nest success (S. Humphries, unpubl. data).

Although habitat did not obviously affect the nesting success of Saltmarsh Sharp-tailed Sparrows, timing of breeding was very important.

Salt marshes are flooded during high tides, and can be completely covered during especially high spring tides. Saltmarsh Sharp-tailed Sparrows apparently time their breeding so that nesting fits between these extreme tides (Shriver 2002). Because egg laying, incubation, and the nestling stage together take 22–27 days (DeRagon 1988, Greenlaw and Rising 1994), nest initiation must be timed just right to avoid flooding. Thus, it is not surprising that flooding was the major cause of nest failure in most studies of Saltmarsh Sharp-tailed Sparrows, causing approximately 60% of nest failures (DeRagon 1988, Shriver 2002, this study). DiQuinzio et al. (2002) found that predation was the primary source of nest loss in their study, but the restoration of natural tidal flows at the study site resulted in a shift to match the pattern of the other studies.

In contrast to Saltmarsh Sharp-tailed Sparrows, timing of reproduction did not have a strong affect on nesting success in Seaside Sparrows, presumably because their nests are built in taller vegetation and thus a far smaller proportion of nests fail due to flooding. Nelson's Sharp-tailed Sparrows also do not synchronize their breeding to match the tidal cycles, resulting in reduced nesting success compared to Saltmarsh Sharp-tailed Sparrows (Shriver 2002). We did not find such a difference in overall nest survival between Seaside and Saltmarsh Sharp-tailed Sparrows. In fact, although precision was low, our estimate of survival rate for Seaside Sparrows (0.27) was not only higher than that for Saltmarsh Sharp-tailed Sparrow (0.20) but close to the upper limit of the 95% confidence interval for that species (0.29).

The importance of vegetation structure makes sense if birds are selecting sites based primarily on their suitability for avoiding flooding (i.e., by raising nests above the tide) or predation (i.e., by concealing nests). That marsh site does not feature prominently in most models is important because it suggests that it is reasonable to use the results from single study sites to extrapolate more broadly. The occurrence of our marsh site variable in the best-fit model for Saltmarsh Sharp-tailed Sparrow nest-site selection, however, indicates that the features of individual sites can have some influence on breeding behavior (see also Rogers et al. 1997, Braden 1999, Chase 2002).

Overall, our results suggest that Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows have two very different strategies for reproducing successfully in salt marshes. Saltmarsh Sharp-tailed Sparrows apparently cope with the challenge of living in an environment that floods regularly by timing their reproductive behavior in such a way as to reduce the frequency with which nesting coincides with flooding events. In contrast, Seaside Sparrows have solved the same problem by nesting in taller vegetation where they can escape even the highest of tides.

Despite adaptations to avoid nest losses to flooding tides, large-scale phenomena such as rising sea levels or smaller-scale alterations of tidal flow will have a direct effect on nesting saltmarsh sparrows. For example, after restoring tidal flow to a salt marsh in Rhode Island, Saltmarsh Sharp-tailed Sparrows began nesting where the vegetation was taller but still lost over 90% of their nests to flooding (DiQuinzio et al. 2002). At other sites, increased tidal flooding with low marsh accretion rates, due to rising sea levels, resulted in the replacement of *Spartina patens* and *Juncus gerardi* by the short form of *S. alterniflora* (Warren and Niering 1993), which is not favored for nesting by either species. The replacement of typical saltmarsh vegetation by the invasive *Phragmites australis* due to tidal restriction is yet another example of coastal areas becoming unsuitable for breeding saltmarsh sparrows (Benoit and Askins 1999).

Mosquito ditching, agriculture, waterfowl management, and tidal restriction for the construction of roads, bridges, and causeways have resulted in the disappearance of more than 50% of the tidal wetland area in the United States (Tiner 1984). In Connecticut, it has been estimated that 30% of tidal marshes were lost in the last century (Rozsa 1995). Our work, and that of others, suggests that both Saltmarsh Sharp-tailed and Seaside Sparrows have highly specialized habitat needs and are constrained in their ability to adapt to new conditions. Saltmarsh Sharp-tailed Sparrows are limited to areas of marsh in which the length of their nesting period can coincide with flooding frequency, and Seaside Sparrows are limited to areas where vegetation is tall enough to avoid flooding. The long-term viability of these species, therefore, will depend on the maintenance of sufficient areas of salt marsh that meet these conditions.

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