SALTMARSH-BREEDING SPARROWS IN LONG ISLAND SOUND: STATUS AND PRODUCTIVITY OF GLOBALLY IMPORTANT POPULATIONS

Final Report

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EXECUTIVE SUMMARY

During the summers of 2002-03 we studied the biology of saltmarsh breeding birds along the Connecticut coast of Long Island Sound. We paid particular attention to two species of high conservation concern – saltmarsh sharp-tailed sparrow and seaside sparrow – in order to improve our ability to monitor and manage populations of these species. Over the course of our study we collected data from 40 study plots situated in seven marshes. We captured and banded 1042 saltmarsh sharp-tailed sparrows and 183 seaside sparrows. We also found and monitored 167 and 24 nests, respectively, for these two species. In this executive summary we highlight the key results from our work during these two years. Each of these points is elaborated upon in more detail in the main body of this report. The work included herein also is in the process of being prepared for submission to peer reviewed scientific journals, and the report includes appendices that provide the first manuscripts to be submitted. These manuscripts present the work in a somewhat broader scientific context, and thus complement the primary report text, which focuses specifically on Long Island Sound. Readers wishing to receive peer-reviewed publications that emanate from this study should contact the lead author.

This study also represents the beginning of a longer term research program designed to better understand the ecology and conservation of salt marsh birds in New England. This work has provided valuable insights into the ecology of these globally important bird populations, and resulted in the species being recognized as globally vulnerable to extinction (BirdLife International, 2004), but additional work remains. Our research group has initiated further research along several avenues and we expect to expand greatly our understanding of salt marsh bird conservation over the next few years. Results from these future studies will be posted on the internet as they are completed (see http://www.eeb.uconn.edu/faculty/Elphick/).

MAIN RESULTS AND RECOMMENDATIONS

Population size estimates

- All seven of our study sites support sufficiently large populations of saltmarsh sharp-tailed sparrows to be considered globally important bird areas under current criteria. This result suggests that other salt marsh sites in Connecticut and adjacent states will also meet these criteria and supports the hypothesis that Long Island Sound marshes play a critical role in the global persistence of this species.

- Point count data provide an index of saltmarsh sharp-tailed sparrow and seaside sparrow population size that could be used to rank sites in terms of their sparrow population sizes and to monitor population trends.

- Point counts cannot be used to identify areas with high densities of saltmarsh sharp-tailed sparrow nests, and thus cannot be used to identify or evaluate local habitat quality for saltmarsh sharp-tailed sparrows. In contrast, point counts can be expected to provide an adequate proxy for identifying good quality habitat for seaside sparrows.

Habitat selection

- *Juncus gerardi* is a good indicator of the very best saltmarsh sharp-tailed sparrow habitat, providing the resolution needed to distinguish among areas of high marsh that differ in the abundance of birds and, to a lesser extent, nests. At a grosser level, the presence of *Spartina patens* also indicates good areas for saltmarsh sharp-tailed sparrows, but this grass is so common that it lacks the resolution provided by *J. gerardi* and is therefore not as good an indicator.

- Marsh size, and perhaps associated landscape features, have a large effect on seaside sparrow abundance and are perhaps more important than local habitat features. The presence of tall vegetation, however, is also a good indicator of seaside sparrow abundance, and it is possible that interactions between vegetation height and landscape features account for discrepancies in the relationship between marsh area and seaside sparrow abundance. Areas with abundant short-form *Spartina alterniflora* are avoided by nesting seaside sparrows.

- Although perhaps counterintuitive, even highly significant habitat use models with good internal consistency may not provide good predictions when applied beyond the original set of sites. Combining our information on habitat use with a more detailed understanding of the effects of landscape features and movement behavior is likely to improve the quality of the predictive models.

Nest site selection and demographic parameters

- Saltmarsh sharp-tailed sparrows chose relatively high elevation nest sites, where the vegetation was taller and denser than at random locations, where there was a deep layer of thatch, and where the habitat was dominated by *S. patens*. Although vegetation characteristics influenced where birds built nests, they did not affect nest success.

- Seaside sparrow nests were placed where the vegetation was very tall, relatively sparse, and dominated by the tall form of *S. alterniflora*, largely to the exclusion of *S. patens*. Short *S. alterniflora* was avoided by nesting seaside sparrows. Nests were most successful when placed in taller, less dense vegetation where there was more *S. alterniflora* and less *S. patens*.

- Saltmarsh sharp-tailed sparrows cope with the challenge of living in an environment that floods regularly by adjusting their reproductive behavior temporally, such that most nesting does not coincide with high tides that could flood nests. In contrast, seaside sparrows have solved the same problem by nesting in taller vegetation where they can escape even the highest of tides.

- Of the 1042 saltmarsh sharp-tailed sparrows banded, 30% were recaptured at least once and 8% were captured on at least two plots. In contrast, we recaptured 37% of the 183 seaside sparrows that we banded, with all but 6 recaptures in the same one-hectare plot in which the bird was originally captured.

Indicators of avian community health

- Saltmarsh sparrows were easy to detect in our study plots suggesting that it is not difficult to monitor these species directly and that there is little need to develop indirect indicators of their presence or abundance.

- Saltmarsh bird communities were significantly nested in our study. The species of greatest conservation concern, however, were the most commonly detected species, and many of the "rare" species in our surveys are common in nearby habitats. Nestedness, therefore, might not be a good basis for identifying indicators in this system.

- Abundance of either sparrow species significantly predicted the total abundance of all other state-listed species, although model-fit was low. Sparrow surveys, therefore, could provide a good general proxy for the abundance of state-listed saltmarsh species, but the precision of such an index is likely to be low for individual sites.

- Our conclusions about indicators should be tempered by the knowledge that our study was limited to some of the state's largest and best salt marsh sites. The on-going expansion of our work to encompass smaller marshes will allow us to verify our conclusions.

INTRODUCTION

Saltmarsh sharp-tailed and seaside sparrows are two of the highest priority species for bird conservation in New England. Saltmarsh sharp-tailed sparrows in particular are thought to have internationally important numbers in the marshes of Long Island Sound, with perhaps half of the world's population in southern New England (Dettmers and Rosenberg, 2000). Both species are on the National Audubon Society's WatchList of high conservation concern species (National Audubon Society, 2002) and are ranked by the US Fish and Wildlife Service as priorities both nationally and regionally (U.S. Fish and Wildlife Service, 2002). Saltmarsh sharp-tailed sparrow is considered globally Vulnerable using IUCN Red List criteria (BirdLife International, 2004). Although globally more widespread than saltmarsh sharp-tailed sparrows, seaside sparrows are found only in large marshes, making them locally less common in some areas (Benoit and Askins, 2002; Shriver et al., 2004), and populations in several regions have been identified as species of conservation concern (Post and Greenlaw, 1994; Rich et al., 2004). Despite the concerns, relatively little is known about the status of either species, especially in northeastern North America, and methods for measuring abundance are not well developed.

In this study we compared a variety of methods for estimating saltmarsh sparrow abundance, ranging from simple traditional methods that have previously been used to describe the distribution and abundance of these birds in the region, to much more labor intensive methods. As a key component of this analysis, we developed habitat models, which attempt to explain variation in sparrow abundance, nest density, and reproductive success. Finally, as a by-product of our attempts to quantify the size of sparrow populations, we collected data on the abundance of other marsh birds to test whether there are particular bird species that can be used as indicators of the state of the avian community found in Long Island Sound salt marshes.

The main objectives of this study were to (1) assess the population size of saltmarsh sharp-tailed sparrows and seaside sparrows at key coastal marshes in Connecticut in order to fully understand the global significance of this region for both sparrow species, (2) compare traditional methods for indexing population size with more complex, time consuming, methods that give absolute population sizes, in order to calibrate the traditional indices and facilitate the calculation of regional population estimates, (3) determine within and among marsh variation in sparrow abundance in order to evaluate the consequences of habitat change, marsh management, and sea-level rise, (4) obtain estimates of breeding productivity, and (5) identify suitable indicators of saltmarsh health.

HYPOTHESES

H_1: Key coastal marshes along the Connecticut shore are globally important bird areas, primarily because of the numbers of saltmarsh sharp-tailed sparrows and seaside sparrows they support.

H_2: Sparrow density varies as a function of within-marsh characteristics, which can be modeled to predict population size, evaluate threats, and guide management.

H_3: Sparrow productivity varies as a function of within-marsh characteristics, and these relationships can be used to understand the mechanisms underlying variation in occurrence and density of saltmarsh-breeding sparrows.

H_4: Identifying good indicators of avian community health in Long Island Sound salt marshes will require an accurate understanding of the numbers of birds present in the marshes and how they relate to conservation priorities.

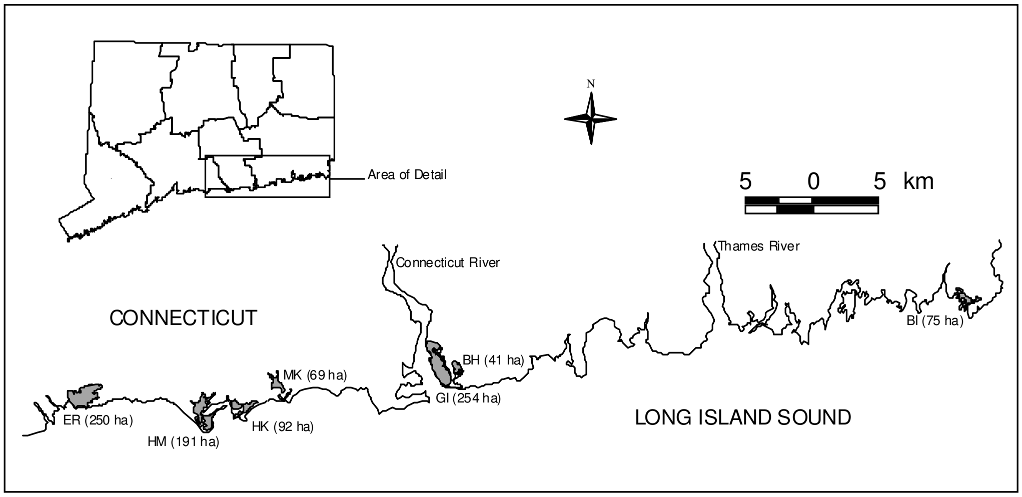
METHODS

STUDY AREA

Data were collected from seven marsh sites along the Connecticut coast during the summers of 2002 and 2003 (Figure 1). These sites included three of the largest marshes in the state (East River Marsh, Guilford; Stewart B. McKinney National Wildlife Refuge, Westbrook; Hammonasset State Park, Madison), which previous studies have shown to support especially high densities of saltmarsh sharp-tailed sparrows (Lori Benoit, unpublished data). Seaside sparrows are also known to occur at each of these sites. We also added an additional four sites (Hammock River Marsh, Clinton; Great Island Wildlife Management Area, Old Lyme; Black Hall River Marsh, Old Lyme; Barn Island Wildlife Management Area, Stonington), which vary in size, to broaden the geographical scope of the study.

We set up a total of 40 one-hectare square study plots across all sites in which we focused our research activities. We originally proposed to conduct our research in four-hectare study plots, but plots of this size were too large to fit into smaller marshes or among the meandering channels of the larger sites. Moreover, we found that the nesting density was high enough that one-hectare plots were sufficiently large to achieve our goal of encompassing the nests of at least several nesting birds per plot, yet small enough for us to be confident that we were finding almost all of the nests present within the plot. Plot locations at each site were chosen by randomly selecting grid points placed within the marsh boundaries on USGS topographic maps. If a large, deep channel (> 5 m wide) crossed the plot, we adjusted the location slightly so that we could access the entire plot without having to cross a channel.

Figure 1. Location of saltmarsh study sites in Connecticut during 2002 and 2003. ER = East River Marsh, Guilford (10 plots); HM = Hammonasset State Park, Madison (8 plots); HK = Hammock River Marsh, Clinton (2 plots); MK = McKinney National Wildlife Refuge, Westbrook (5 plots); GI = Great Island Wildlife Management Area, Old Lyme (8 plots); BH = Black Hall River Marsh, Old Lyme (2 plots); BI = Barn Island Wildlife Management Area, Stonington (5 plots).



SAMPLING POPULATION SIZE WITHIN PLOTS

We used a combination of intensive banding, nest searches, and point counts to determine the size of breeding populations at each site. Each plot was visited five times at approximately two-week intervals. On each visit, we set up an array of six 12 m long mist nets across the plot in order to capture birds present within the plot's boundaries. The location of nets was changed on each visit to maximize coverage within each plot. We flushed birds into the nets by walking along channel edges and through the vegetation towards the nets. Mist-netting occurred in the mornings and each visit lasted approximately four hours. All birds captured were fitted with a standard USFWS metal leg band and up to three plastic color bands, to allow for individual recognition. We determined sex of adult birds by the presence of a brood patch (females) or an enlarged cloacal protuberance (males), and we distinguished juvenile birds from adults by plumage features and by the extent of skull ossification.

We augmented our banding efforts by determining the number of nests in each saltmarsh plot. On each date that banding occurred in a plot, we also conducted a thorough search of the plot to look for nests. In addition to these intensive searches, we looked for nests every three to five days when checking the status of known nests. All nests were marked with a flag 5 m away such that the nest lay on a line between the flag and the center of the plot; this system enabled us to refind the nest easily, but reduced the risk of identifying nest locations to predators. Once a nest was found we visited it at three to five day intervals in order to determine the nest's fate. Nests that were incidentally found outside of plots were also marked and monitored. These additional nests were included in analyses designed to test questions about nests per se, but not in those tests that were based on our plot design. Nests were considered to have failed due 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. Failure due to flooding always coincided with especially high tides. 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 disappeared from the nest. A nest was considered successful if at least one nestling fledged from it.

In the two years combined we found 167 saltmarsh sharp-tailed sparrow nests, 134 of which we could estimate the date on which egg laying finished (see section *Estimating reproductive success)*. We found 84% (113) of these nests during the incubation phase of the nesting cycle, when nests are typically more difficult to find, and just 16% (21) during the chick-rearing phase (Figure 2). Thus, we concluded that our intensive nest-searching efforts successfully located almost all of the active nests in our study plots.

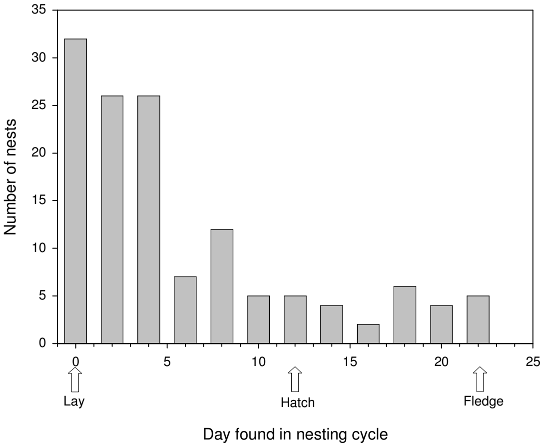


Figure 2. Histogram of the day in the nesting cycle on which each nest was found (*n* = 134). Clutch completion is Day 0 and chicks fledge on Day 22. Nests found during laying (before Day 0) were considered to have been found on Day 0 (*n* = 18).

In order to relate our population estimates to those obtained in other studies, we also conducted point counts in each plot. On each day that we mist netted we conducted a 5 minute point count from the center of the focal plot. Timing of point counts was standardized to occur soon after sunrise, when singing rates peak (e.g., Post and Greenlaw, 1994), and before other research activities occurred on the plot. During these point counts we recorded the total number of birds detected and the approximate distance from the point to each bird (within 25 m; between 25 and 50 m; beyond 50 m).

SAMPLING MARSH CHARACTERISTICS

Within each plot, we sampled the habitat at nine grid points (the center, the four corners, and the mid-points of each side) and at the site of each nest. We also sampled at nine randomly selected points within each plot to determine whether our grid points produced biased estimates of available habitat. By comparing habitat at each nest site to non-nest sites we determined whether habitat features influenced nest site selection in saltmarsh sparrows. A one-meter quadrat was placed around each sampling point. We measured the height of the vegetation at the corners of the quadrat, and 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 plant stems in five randomly located 10 x 10 cm sub-quadrats 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. We used a GPS to locate the center of each plot, and determined the distance from the center of each plot to the nearest marsh edge and total marsh area using Arcview GIS 3.2 (Environmental Systems Research Institute, Inc.) and scanned USGS Topographic Quadrangle Map Images (CT State Plane 1927).

DATA QUALITY OBJECTIVES FOR MEASUREMENT DATA

For many types of data, quality assurance requires calibrating measurements to a common standard (e.g., by systematically comparing measurements taken by different individuals and calculating statistical correction factors where necessary). The data collected in this study were limited to field counts of bird numbers, measurements of vegetation characteristics and marsh elevation, counts of plant abundance, and identifications of both birds and plants. At the end of the first summer's field season, we conducted a series of data quality tests to identify areas where data collection could be improved in subsequent field seasons. The results of the data quality assessments are detailed in Appendix 1.

STATISTICAL ANALYSES

Comparing methods for estimating population size. Data from our banding efforts, nest searching and point counts were used to obtain measures of population size for each plot. Because birds are mobile and plots are relatively small, the population size in any given area varied over the course of the breeding season. Moreover, there are several different ways in which one can define the population of interest, each of which has different relevance to the ecology and conservation of these birds. We initially defined the population size as the number of birds that use the plot over the course of the breeding period, and used the total number of birds captured in a plot as a minimum estimate of this number. Since, reproductive success is generally more limited by the number of females than by the number of males, we also determined the number of females captured as a measure of the breeding population of each plot.

Breeding activity was also estimated from our nest monitoring data. We used the number of nests as an alternative measure of the size of the breeding population (recognizing that the number of nests does not equate directly to the number of females, since females can lay multiple clutches over the course of a breeding season). We also used the number of fledglings produced in a plot as a measure of the local population's breeding success. Finally, we used our point counts to index sparrow abundance by averaging the number of detections over all five counts conducted at a plot. These different indices were compared to one another to determine the level of agreement among methods, and to formally test whether point counts can be used to estimate the number of birds and breeding attempts in an area.

Estimating total population size at study marshes. We estimated the total population size at each of our marshes using three different methods. First, we used our banding data to extrapolate from the numbers of birds captured in our study plots to the entire marsh. Both our recapture data (see section *Survival, dispersal, and short-term movements*), and our analyses of the relationship between bird abundance and nesting activity (Figure 3), suggest that birds may move around a lot within individual marshes and are not necessarily confined to the area of a plot. Thus, we could not simply multiply the average density of birds in a plot by the area of a marsh. Instead, we estimated a correction factor to adjust for the proportion of a bird's time that was spent in a plot, and incorporated this correction factor into our estimate of an area's population size: $N = pDA$, where N is the estimated number of birds in a marsh, D is the mean number of birds captured in a one hectare plot during the breeding season, p is the average proportion of the five capture occasions on which an individual was caught on a plot, and A is the area of the marsh. To account for potential differences in movement between males and females, we calculated the value of N separately for each sex and summed the two values for an estimate of the total population size.

Our correction factor (p) provides only a very approximate estimate of how much time each sparrow spent in the plot in which it was caught. Improved estimates of this parameter would be possible if we had more detailed data on the movement behavior and home range sizes of individual birds. We are consequently developing plans to collect such data. We are also seeking to use the results of our habitat analysis (see section *Linking habitat to sparrow abundance*) to refine our estimates of the area of suitable habitat over which extrapolations should be made.

Second, we estimated the size of the breeding population by extrapolation from our estimates of nest density in each marsh. Given that the location of a nest is fixed in space, we did not need to correct these estimates in the same manner as for the number of birds captured in each plot. We did, however, need to correct for the incidence of renesting, as some females build more than one nest over the course of the breeding season. To make this correction, we used nest data collected in 2004 to determine the proportion of nests that were renesting attempts. Data from 2004, rather than those collected during the LISS-funded years, were used for this analysis because we were able to spend more time identifying the female attending each nest in 2004, thus giving us more accurate information on the renesting rate than in previous years. We multiplied the corrected nest density value by 2 to estimate the total population size, assuming a 1:1 sex ratio (Greenlaw and Rising, 1994).

Lastly, we used an incidence-based estimator (Chao2: Chao, 1987), for our final estimate of sparrow population size. Chao2 was computed using the EstimateS software (Version 7, R.K. Colwell, http://purl.oclc.org/estimates). This method uses information about the number of times each individual is recaptured to estimate the number of individuals that are present but have not yet been marked, thereby allowing one to estimate total population size.

Initially, we also proposed to use our recapture and resighting information in a mark-recapture model to estimate the overall population size. As our data gathering proceeded, however, it became apparent that our sample populations were extremely open (i.e., there was considerable movement of birds in and out of the areas sampled). Given this level of mobility, we could not be confident that such models would have sufficient precision to make informative population estimates. We therefore abandoned this approach to estimating population size for the current study. As we improve our understanding of movement patterns in these birds, through future studies, we intend to reassess the potential use of mark-recapture models to improve on current population estimates.

Linking habitat to sparrow abundance. To determine the effects of habitat features on sparrow abundance and productivity, we constructed multiple regression models that link abundance to each of the marsh characteristics measured. We used data collected from 30 plots across five marsh sites to develop the habitat models (East River Marsh, Guilford; Hammonasset State Park, Madison; McKinney National Wildlife Refuge, Westbrook; Great Island Wildlife Management Area, Old Lyme; and Barn Island Wildlife Management Area, Stonington; Figure 1). We chose these sites as they were known to have high densities of nesting saltmarsh sparrows. To validate the models, we collected new data from an additional 10 plots, six from sites that were used for model building (two plots each in East River Marsh, Hammonasset State Park, and Great Island Wildlife Management Area) and four from new marsh sites (Hammock River Marsh, Clinton and Black Hall River Marsh, Old Lyme; Figure 1).

We used four measures of sparrow abundance in a plot as dependent variables in our analyses for saltmarsh sharp-tailed sparrows: (1) the total number of birds captured over the course of a breeding season, (2) the number of females captured, (3) the number of nests found, and (4) the number of young birds fledged from those nests. We included a separate analysis of the number of females because males are nonterritorial, polygynous, and provide little parental care (Greenlaw and Rising, 1994), meaning that their abundance in an area may bear little relationship to the amount of reproductive activity in the area (see Figure 3). The number of females on a particular plot, therefore, may better reflect the productivity of the site than the total number of birds, since females occupy small home ranges within which they nest and provide all parental care

(Greenlaw and Rising, 1994). The number of nests and the number of fledglings produced provide direct measures of where females choose to nest and where they are most successful.

The predictor variables of interest included the distance from the center of the plot to the nearest point on the edge of the marsh, vegetation height, vegetation density, thatch depth, and percent cover for the five most common vegetation types; *Spartina patens*, short form *S. alterniflora* (< 50 cm), tall form *S. alterniflora* (> 50 cm), *Distichlis spicata*, and *Juncus gerardi*. For each plot, we used the mean value for each habitat variable across the 18 sampling points. The standard deviations of vegetation height and vegetation density were also included to test whether the structural heterogeneity of the habitat was important.

We first made univariate comparisons (Pearson or Spearman rank correlation coefficients, as appropriate) of predictor variables and sparrow abundance, and included all variables with $P > 0.25$ in an initial multivariate model (Hosmer and Lemeshow, 2000). To account for any site effects on sparrow abundance, or seasonal variation in the structure or composition of the habitat, we evaluated the effects of plot location (i.e., the marsh in which the plot lay) and habitat sampling date on each of the predictor variables. Plot location had a strong significant effect on the habitat variables measured ($P < 0.0001$ in all comparisons), but the date on which we measured the vegetation did not ($P > 0.05$ in all comparisons). Therefore, we included plot location, but not habitat sampling date, in the initial multivariate model for each measure of sparrow abundance.

From our initial model, we systematically removed each variable one at a time. The set of reduced models were compared by calculating Akaike's Information Criterion for small sample sizes (AIC_c) for each model and determining the difference in AIC_c values (Δ_i) compared to the model with the lowest AIC_c in the set of candidate models (Burnham and Anderson, 2002). All models with $\Delta_i < 2$ were considered to be equally as good as the best model (the one with the lowest AIC_c) and were retained as plausible models. We then took the reduced set of models and repeated the process of systematically eliminating each variable one at a time from each of them to create a new set of candidate models, which were then compared to each other using Δ_i as described above. This process continued until we had a set of models from which it was not possible to reduce the number of variables without producing $\Delta_i > 2$ in all reduced models (i.e. all reduced models were significantly worse than the current set).

For seaside sparrows, we defined our first dependent variable as the total number of birds that used a plot over the course of a breeding season. We did not separately analyze the number of females banded because we had no *a priori* reason to expect that this measure would provide information different from the total number of birds in this territorial and socially monogamous species. All variables with $P > 0.25$ in univariate comparisons between predictor variables and the number of sparrows were included in an initial multivariate model. We used the same procedure described for saltmarsh sharp-tailed sparrows to determine which predictor variables to include in the final multivariate model describing the variation in the number of sparrows captured.

Due to the small number of plots in which seaside sparrow nests were found, we transformed this dependent variable to reflect presence/absence and used logistic regression to evaluate nest-habitat associations. Wherever nests were found, fledglings were produced, so we did not separately analyze the relationship between habitat and the presence of fledglings as this analysis would have been identical to that for nests. For the logistic regressions we used the same model-building strategy that we used for our linear regression models. To determine the significance of the best-fit model (i.e. model with the lowest AIC_c), we calculated the likelihood ratio statistic (LRS) and associated *P*-value. Goodness-of-fit was evaluated using the Hosmer-Lemeshow test, where a non-significant value indicates a good fit between the model and the data. We also used the Likelihood Ratio Test to test for the significance of each independent variable in the model and report its associated statistic, the LRS. We also report the Akaike weights (*w*) for all selected models as a measure of the relative likelihood of the selected model given the data and the set of models evaluated (Burnham and Anderson, 2002).

We used SYSTAT 8.0 (SPSS Inc. 1999) to develop all abundance and presence/absence models (GLM, multiple and logistic regressions). To meet the assumptions of multiple regression, we first transformed several variables to reduce skewness, reduce the number of outliers, and improve the normality, linearity, and homoscedasticity of residuals (Tabachnick and Fidell, 2001). Logarithmic transformations ($\log_{10}(y + 1)$) were used for the distance to the marsh edge, percent cover of *Distichlis spicata*, percent cover of tall form *Spartina alterniflora*, and total number of seaside sparrows captured. We used square-root transformations for the number of saltmarsh sharp-tailed sparrow nests and fledglings produced. No transformation improved the distribution for percent cover of *Juncus gerardi* (skewness: 1.51 ± 0.43; kurtosis: 0.98 ± 0.83) and so these data were not transformed. We did not transform any of the predictor variables for the logistic regression as this procedure makes no assumptions about their distributions (Hosmer and Lemeshow, 2000).

Validating model predictions. We estimated the validity of the four final model equations resulting from the model-building procedure for saltmarsh sharp-tailed sparrows in two ways. First, we used a jackknife approach in which we sequentially, one plot at a time, removed one of the 30 plots from the data set, estimated the model coefficients with the remaining data, and then obtained a predicted value for the plot that had been dropped. This process was repeated for each plot, and the predicted values were compared to observed values. Second, we used our final models to predict sparrow abundance at 10 validation plots that were not used during the model-building procedure, and again compared the predicted sparrow abundance to the observed values obtained from those plots. For both the jackknife and cross-validation approaches, we examined the fit between the observed and predicted values with paired *t*-tests for which a significant value indicates a bad fit (i.e., rejection of the null hypothesis that the two groups are equal). We also examined the significance and resulting *r* from a correlation between the observed and predicted values, which gives us a measure of the strength of their association. We used the same two approaches to test model performance for the number of seaside sparrows captured.

To assess the prediction performance of the best-fit logistic regression model describing the presence/absence of seaside sparrow nests, we compared the distribution of predicted outcomes to actual observations to determine the proportion of cases that were classified correctly. We also examined the 'success index', which measures the gain the model shows over a purely random model (SPSS Inc., 1999). We then applied the best-fit regression model to our validation data set to determine its prediction success when applied to the new data.

Nest site selection. To determine whether birds were selecting nest sites on the basis of habitat characteristics, we used logistic regression to compare habitat between nest and non-nest locations for both sparrow species. 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*. Within each plot, we also compared the elevation between nest sites and non-nest sites using paired *t*-tests. Using the results of our univariate tests, we built an initial multivariate model for each species using only those variables that were significant at $P < 0.25$ (Hosmer and Lemeshow, 2000). We used the same model building strategy described in *Linking habitat to sparrow abundance* to determine which predictor variables to include in the final multivariate models.

Estimating reproductive success. We used the Mayfield method (Mayfield, 1975) to determine daily nest survival rates with variance calculated according to Johnson (1979). We assumed a 22-day nesting period for both species (Greenlaw and Rising, 1994; Post and Greenlaw, 1994). To estimate the date incubation began for nests found with an incomplete clutch, we assumed that females lay one egg a day and determined the number of additional days until the clutch was complete. For nests where hatch date was known, we assumed a 12 day incubation period (Greenlaw and Rising, 1994; Post and Greenlaw, 1994) and counted backwards in time to determine when incubation began. For the remaining 42 cases, when a nest that was found during incubation failed before hatching, we estimated the first date of incubation using the following formula (Martin et al., 1997):

$$\text{First day of incubation} = \text{date found} - \left(\left(\text{incubation period} - \text{number of days observed} \right) \div 2 \right)$$

This equation assumes that, on average, nests are found exactly in the middle of the incubation period. To test this assumption, we used 54 nests for which the first day of incubation was known and determined whether nest discovery dates were biased towards either early or late days in the incubation period. The mean discovery date was 5.4 days (SD 3.6) after incubation started, and there was no significant skew to the distribution (skewness = 0.13, $z = 0.35$, $P = 0.73$). Thus we concluded that the assumption of the Martin et al. (1997) equation was reasonable. We compared nest survival estimates between years using a *Z*-test (Johnson, 1979).

To predict nest fates we used logistic regression following the same model building procedure described in *Linking habitat to sparrow abundance*. Because prior research has shown that flooding is a major source of nest failure in saltmarsh sparrows (Shriver, 2002), we conducted two tests for each species. First, we compared habitat variables for successful versus failed nests; second, we determined whether there were differences between successful nests and those that failed due to flooding. For each nest, we also calculated the number of days between the egg-laying date and the nearest full moon tide (when the height of the high tide reached its maximum) and used analysis of variance to test whether nest fate was related to the timing of the full moon tide. All analyses were performed using SYSTAT 8.0 (SPSS Inc., 1999).

Indicators of avian community health. During point count surveys designed to estimate the size of sparrow populations, we also collected data for the entire avian community at each of our study plots and used two methods to test whether it is possible to identify appropriate indicator species. First, we used a nested subset analysis, which determines the degree to which the collection of species found at species-poor sites is a nested subset of those found at increasingly species-rich sites. The *Nestedness Calculator* (http://aics-research.com/nestedness/tempcalc.html) measures the extent to which the presence/absence species matrix is ordered and describes the degree of nestedness in thermodynamic terminology (Atmar and Patterson, 1995). A perfectly nested matrix is described as "cold" with a temperature of 0°, and one that is completely random is maximally "hot" at 100°. The temperature obtained from the data matrix is compared to the average temperature of 1000 randomly generated matrices to estimate where on the temperature scale the observed data set lies. If salt marsh communities exhibit a nested pattern, then one could use the presence of rare species to indicate the presence of a full complement of salt marsh species.

Our second method used regression analyses to determine whether the abundance of saltmarsh sharp-tailed sparrows or seaside sparrows detected on point counts is related to either species richness (i.e., the total number of species detected on each plot) or the total number of individuals of Connecticut State listed species. Salt marsh species that are currently on the State List are saltmarsh sharp-tailed sparrow, seaside sparrow, great egret (*Ardea alba*), snowy egret (*Egretta thula*), and glossy ibis (*Plegadis falcinellus*). We excluded the proposed "indicator" (i.e., saltmarsh sharp-tailed sparrow or seaside sparrow) in regressions on State listed species. These analyses were conducted because both sparrows are easy to detect with point counts, and are already the subject of much monitoring interest. If these birds proved to be good surrogates for the entire saltmarsh avifauna then monitoring the health of marsh bird communities could be subsumed under work directed specifically at these sparrow species. Moreover, the ease with which sparrows can be detected could remove the need for the more intensive work required to detect secretive species (e.g., rails) or species that use a particular spot in a marsh infrequently (e.g., some wading birds).

RESULTS and DISCUSSION

1. ESTIMATING POPULATION SIZE

Comparing methods for estimating population size

Current knowledge of sparrow population sizes is based on extrapolation from point-count surveys, which rely heavily on the detection of singing birds. It has been suggested, however, that these methods are inappropriate and can be misleading, especially for saltmarsh sharp-tailed sparrow, because this species is not territorial and has a polygynous mating system (Greenlaw and Rising, 1994). Thus, estimates of the number of singing birds do not necessarily relate directly to the number of breeding females. Indeed, even in socially monogamous birds high detection rates on point counts may be a poor indicator of reproductive success, because the highest singing rates may occur in situations where males are unable to find mates and hence reproduce (Gibbs and Wenny, 1993), or because successfully mated males may cease singing altogether (Tyler and Green, 1996). Thus it is necessary to determine actual population numbers at key sites, and to calibrate traditional point count estimates, if one is to estimate regional population sizes or evaluate the relative importance of different sites for management.

For each plot, we obtained multiple measures of population size using a variety of methods of varying logistical difficulty. Using these indices, we were able to estimate the number of birds and breeding attempts in each of our study marshes. Comparing multiple methods also allowed us to determine the most cost effective method for estimating population size at other sites and to investigate the potential for calibrating existing data derived from point count surveys.

For saltmarsh sharp-tailed sparrows, the total number of birds caught in a plot, the number of females caught, and the average number of birds detected during a point count were all highly correlated (Table 1). Not surprisingly, the total number of nests found on a given plot was significantly and positively correlated with the number of fledglings produced (Table 1). Neither the number of birds caught, females caught, nor the number of birds detected on point counts, however, were related to the number of nests or fledglings in a plot (Table 1). For seaside sparrows, all indices of population size were positively and significantly correlated with each other (Table 2).

Table 1. Correlation matrix of population size indices for saltmarsh sharp-tailed sparrows.

Variable	Females caught	Point count detections	Number of nests	Number of fledglings
Total caught	$r = 0.80$, $P < 0.0001$	$r = 0.62$, $P < 0.0001$	$r = 0.21$, $P = 0.19$	$r = 0.11$, $P = 0.51$
Females caught	--	$r = 0.60$, $P < 0.0001$	$r = 0.22$, $P = 0.16$	$r = 0.06$, $P = 0.72$
Point count detections	--	--	$r = 0.08$, $P = 0.60$	$r = -0.01$, $P = 0.96$
Number of nests	--	--	--	$r = 0.73$, $P < 0.0001$

Table 2. Correlation matrix of population size indices for seaside sparrows.

Variable	Females caught	Point count detections	Number of nests	Number of fledglings
Total caught	*r* = 0.85, ***P* < 0.0001**	*r* = 0.66, ***P* < 0.0001**	*r* = 0.62, ***P* < 0.0001**	*r* = 0.38, ***P* = 0.01**
Females caught	--	*r* = 0.59, ***P* = 0.0001**	*r* = 0.63, ***P* < 0.0001**	*r* = 0.43, ***P* = 0.006**
Point count detections	--	--	*r* = 0.69, ***P* < 0.0001**	*r* = 0.60, ***P* < 0.0001**
Number of nests	--	--	--	*r* = 0.79, ***P* < 0.0001**

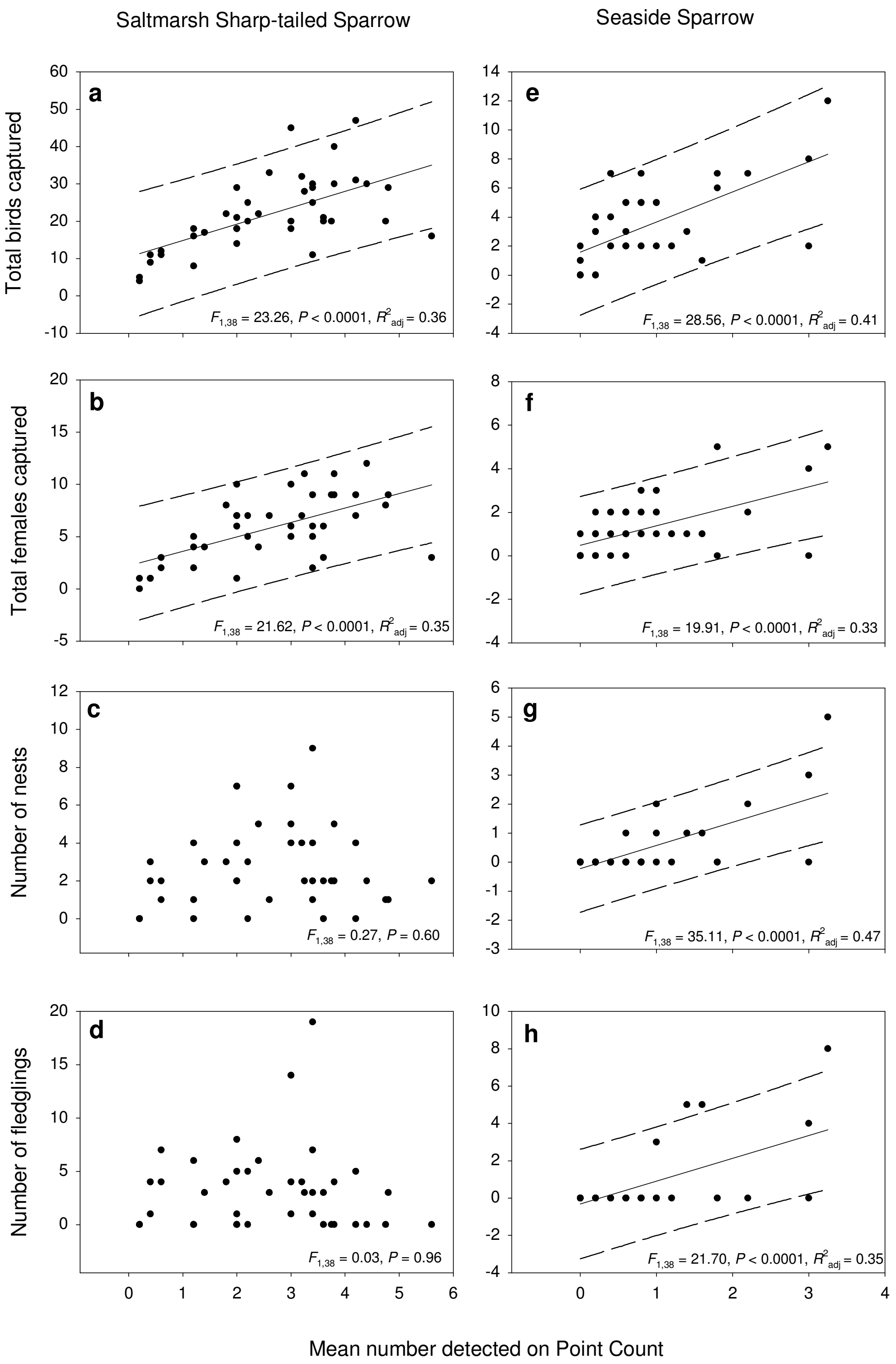
These results do not support the hypothesis that point counts are poor predictors of sparrow densities. For both species, population size indices derived from point count data could be used to predict both the total number of sparrows caught in a plot and the number of females. Using these relationships we can estimate the minimum number of birds that use a plot as (10.5 + 4.4x) and the minimum number of females as (2.2 + 1.4x), where x is the average number of point count detections. The prediction intervals associated with these regression equations, however, are relatively wide, potentially limiting the precision with which bird use of a site could be estimated (Figure 3). Nonetheless, it is clear that the relative abundance of birds across a suite of locations can be accurately estimated using point counts, and that this is true for both males and females and for both sparrow species.

These results suggest that point count data from a large suite of sites, such as those presented by Benoit and Askins (2002) and Shriver et al. (2004) could be used to rank sites in terms of their sparrow population sizes and to provide an index of population size that could be used to monitor population trends. Implementing such a program would require that one ensure that sampling is conducted throughout all suitable habitat and representative of the area over which trends will be estimated, but if these standard sampling rules are followed point counts should give informative results. Given additional data on sparrow home range sizes and movement behavior, these results also can be used to extrapolate from point counts to estimate the total population size within a given marsh (see next section for an initial attempt to do this for our study marshes).

Although our results suggest that point count data can be used to index population size, they also suggest that population size does not necessarily indicate where the most productive habitat lies. Long-term population persistence depends on the birds' ability to reproduce and, for saltmarsh sharp-tailed sparrows, our data suggest that there is no relationship between sparrow abundance and the number of nests or the number of fledglings produced (Figure 3). The reasons for this mismatch between where most birds spend their time and where females actually nest are not known, although we are embarking on work to identify them. Regardless of the reasons, the mismatch has important consequences for the way in which monitoring data are used. Most importantly, this result suggests that one cannot use data from point count surveys to identify or evaluate local habitat quality for saltmarsh sharp-tailed sparrows. For instance, it would be unwise to use this technique to prioritize areas of marsh for protection, or to evaluate the success of restoration efforts. As our understanding of the mechanisms underlying the discrepancy improve, better methods for making such assessments may emerge, but for now, it appears that reproductive success will have to be measured directly by searching for nests, or by using behavioral cues that indicate the presence of nesting birds. Determining the reasons for the discrepancy between the number of birds and the number of nests is especially important because it suggests that saltmarsh sharp-tailed sparrows have complex habitat needs, whereby different suites of habitat characteristics are used for different activities. Thus, evaluating the needs of nesting birds, as we have done in this study (see section *Nest site selection*) addresses only one aspect of the species' requirements.

In contrast to our results for saltmarsh sharp-tailed sparrows, we did find that the number of seaside sparrow nests and the number of fledglings were positively correlated with the number of birds detected using both point counts and mist netting (Figure 3). For this species, therefore, the abundance of birds on point counts can be expected to provide an adequate proxy for identifying good quality nesting habitat.

Figure 3. Regression analyses of the total number of birds captured, total number of females captured, number of nests, and number of fledglings produced in relation to the average number of birds detected on point count for saltmarsh sharp-tailed sparrow (a-d) and seaside sparrow (e-f). Solid line represents the regression equation; dotted lines show the 95% prediction interval (i.e., the region within which 95% of individual points are predicted to lie).



Estimating total population size at study marshes

All of our measures of total population size suggest that there were considerable differences in the abundance of both saltmarsh sharp-tailed and seaside sparrows among our study sites (Tables 3 and 4). Densities of saltmarsh sharp-tailed sparrows peaked at Great Island where a mean of about 32 birds used each one-hectare plot, and where nesting densities approached an average of 3.1 nests per hectare. Banding data suggest similarly high mean densities at Hammock River, although the nest density at this site was considerably lower – indeed quite a lot lower than at any other site. In contrast, Black Hall River had a high nest density, but lower numbers of birds caught on each plot. The lowest numbers of birds captured were at McKinney NWR and Barn Island WMA where an average of only 15 birds were caught per plot. McKinney NWR, however, also had a relatively high mean nesting density. These average abundance data for marshes reinforce the notion that the abundance of birds in an area does not relate directly to the number of nests. Moreover, they suggests that the mismatch may extend beyond the scale of individual one-hectare plots and also apply at the larger scale of entire marshes.

Seaside sparrows were far less numerous than were saltmarsh sharp-tailed sparrows across our study marshes (Table 4). Densities of seaside sparrows peaked at Hammock River, where a mean of 10 birds were caught per hectare. Nesting densities reached 4 nests per hectare at this site, an 8-fold increase over the next highest nesting densities, which were found at Hammonasset State Park. At our three smallest marshes seaside sparrow abundance was very low. No nests were found within our one-hectare plots at Black Hall River, Barn Island WMA or McKinney NWR, although we did see evidence of seaside sparrow nesting activity outside our plots at both Black Hall River and Barn Island WMA. In contrast, we saw no seaside sparrow nesting activity at McKinney NWR, where only one individual was captured during the breeding season.

For our first estimate of population size, we used our banding data to extrapolate from the numbers of birds captured in our study plots to the entire marsh. This estimate incorporates a correction factor that approximates the amount of time each sparrow spent in the plot in which it was caught. Saltmarsh sharp-tailed sparrow females were recaptured at a significantly higher rate than were males (proportion of capture periods in which each female was caught: 0.29 ± 0.14%, $n = 223$; males: 0.26 ± 0.10%, $n = 555$; Mann-Whitney $U = 56791$, $P = 0.02$), suggesting that females do not move around as much as males. For seaside sparrows, we found no significant difference in the frequency with which we recaught males and females (females: 0.30 ± 0.15%, $n = 47$; males: 0.28 ± 0.11%, $n = 75$; Mann-Whitney $U = 1659$, $P = 0.42$). The different result for the two species is likely a due to differences in their social systems. Saltmarsh sharp-tailed sparrows are polygamous and non-territorial, which allows them more freedom of movement throughout the marsh, especially for males which are not tied to a nesting site because they provide no parental care. In contrast, seaside sparrows are seasonally monogamous, non-territorial, and both the male and female raise the offspring, requiring them to remain near the nest site for the duration of the nesting period.

To estimate population size from our banding data, we calculated the average recapture rate for males and females separately for each marsh site, and multiplied each value by the respective number of captures (males or females) during the breeding season and by marsh area. Thus, we made separate calculations for each sex, and then summed the two estimates to get the total population size for each marsh.

We obtained a second estimate of the size of the breeding population by extrapolation from our estimates of nest density in each marsh. Because we found evidence for renesting in saltmarsh sharp-tailed sparrows, we corrected for the incidence of renesting using data from 2004, when almost all nests were linked to an attending female providing us with accurate information on renesting rates. Of the 64 saltmarsh sharp-tailed sparrows found, 7 (11%) were confirmed to be the result of renesting. No correction was used for the extrapolation of seaside sparrow nest densities because we found no evidence that breeding pairs nested more than once during the breeding season.

Estimates of the population sizes present in each of our study marshes varied depending on the method used to extrapolate from our plot data (Tables 3 and 4). For saltmarsh sharp-tailed sparrows, extrapolations from our corrected capture and nest density data are highly correlated ($r = 0.97$, $P = 0.0003$), but the relationship was not one-to-one (i.e., the slope of the regression line between the two variables was significantly less than one: $t = -4.06$, df = 5, $P = 0.01$; Figure 4). Estimates based on nest density ranged from 52% lower to 68% higher than those based on the number of captures, however, they were generally more conservative than the capture-based estimates. For seaside sparrows, estimates based on nest density were much lower than those based on banding data for all sites except Hammock River, where average nest densities peaked but the relative area of the marsh was small. *A priori* we expected nest densities, which require considerably more work to obtain, to give better information than banding data, because they directly measure reproductive effort and because fewer assumptions need to be made when extrapolating from these data. Both estimates, however, are prone to error, and better information on renesting rates and the amount that individual birds move around would allow one to calculate more refined population estimates.

Population sizes calculated using the Chao2 estimator were consistently much lower than those obtained using the other two methods (Tables 3 and 4). One possible reason for this is that our sampling intensity (i.e., the number of plots per marsh, number of recaptures obtained, etc.) may not have been sufficiently large for population estimates to stabilize on the true value. Alternatively, both of our other population estimates rely on an estimate of the total area of saltmarsh habitat present at each site. Some portions of the areas delineated as salt marsh on existing maps are undoubtedly unsuitable for nesting sparrows (e.g., because of flooding frequency) leading to overestimates of the total population sizes. Determining the magnitude of the overestimates, however, will depend on much better information on the area of suitable habitat present at each site. Improved maps are currently being created using remote sensing data by Dr. Daniel Civco and colleagues (funded by the LISS). Once these data are available, we hope to use the new maps in combination with our information on sparrow habitat selection (see section *Modelling the relationship between habitat and abundance*) to better delineate the extent of saltmarsh sparrow habitat at each study site. For now, however, the Chao2 estimates and our estimates derived from the banding and nest survey work, respectively, provide useful lower and upper bounds for the size of the sparrow populations at each site.

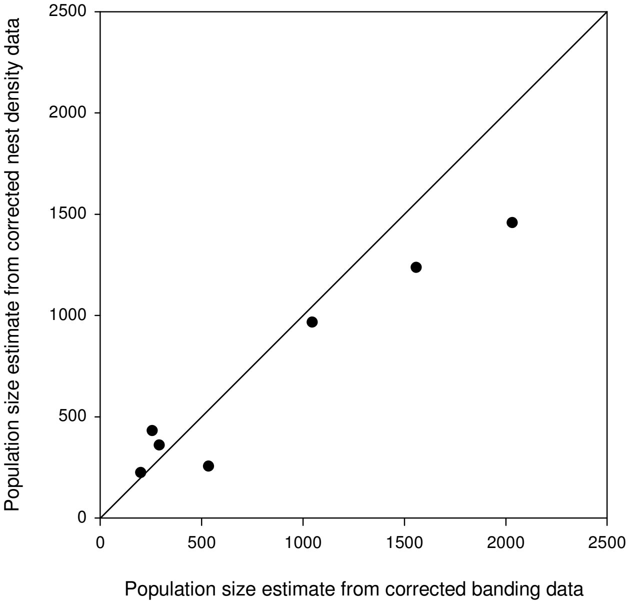


Figure 4. The relationship between saltmarsh sharp-tailed sparrow population size estimates from banding data corrected for rates of recapture and from nest density data corrected for incidence of renesting.

Regardless of the method used to calculate population sizes, it is clear that large numbers of saltmarsh sharp-tailed sparrows nest in the marshes that we studied. Even the most conservative estimates (from the Chao2 calculations) suggest that the number of saltmarsh sharp-tailed sparrows at our study sites ranged from 83 at the Black Hall River marsh to more than 400 at Great Island. The more liberal estimates suggest that the populations at Great Island, East River, and Hammonasset may each exceed a thousand birds. Although considerably fewer seaside sparrows breed in Connecticut, our data suggest that East River, Great Island, Hammock River, and Hammonasset State Park, our four largest sites, are also important breeding sites for this species.

These results also demonstrate that all seven of our study sites support sufficiently large populations of saltmarsh sharp-tailed sparrows to be considered globally important bird areas under current criteria (National Audubon Society, 2005). Given this finding, it is likely that a comprehensive survey of other sites throughout the region would identify additional globally important sites for this species.

Table 3. Average densities (SD) and population size estimates for saltmarsh sharp-tailed sparrows breeding at seven marsh sites in Connecticut. All estimates have potential biases, however the Chao2 estimates provide a lower bound for the size of the sparrow population at each site, and our estimates derived from the banding and nest survey work provide an upper bound (see text for details).

		Marsh Site						
		Black Hall River	Barn Island WMA	East River	Great Island	Hammock River	Hammonasset State Park	McKinney NWR
	Area (ha)	42	78	302	262	95	197	71
	Number of sampling plots	2	5	10	8	2	8	5
Mean number per hectare	Total captured	20.0 (0)	15.4 (10.7)	20.6 (11.4)	32.0 (7.9)	24.0 (5.7)	21.4 (7.2)	15.4 (5.3)
	Females captured	7.5 (2.1)	4.6 (4.2)	4.4 (3.3)	7.1 (1.6)	9.5 (2.1)	6.6 (3.4)	4.2 (2.9)
	Point count detections	3.4 (0.5)	1.1 (0.9)	2.9 (1.8)	3.3 (0.6)	4.0 (1.1)	2.8 (1.0)	1.2 (0.7)
	Nests	3.0 (0.7)	2.6 (3.0)	2.3 (2.7)	3.1 (1.9)	1.5 (0.7)	2.8 (2.3)	3.4 (2.1)
Extrapolated estimate of total population size	Corrected banding data	201	291	1558	2033	534	1045	256
	Corrected banding data (females only)	88	84	405	508	219	375	86
	Corrected nest density * 2	223	359	1236	1456	255	965	431
Chao2 Estimator (SD)		83 (28)	134 (31)	364 (44)	418 (41)	134 (48)	324 (46)	87 (13)

Table 4. Average densities (SD) and population size estimates for saltmarsh sharp-tailed sparrows breeding at seven marsh sites in Connecticut. All estimates have potential biases, however the Chao2 estimates provide a lower bound for the size of the sparrow population at each site, and our estimates derived from the banding and nest survey work provide an upper bound (see text for details).

		Marsh Site						
		Black Hall River	Barn Island WMA	East River	Great Island	Hammock River	Hammonasset State Park	McKinney NWR
	Area (ha)	42	78	302	262	95	197	71
	Number of sampling plots	2	5	10	8	2	8	5
Mean number per hectare	Total captured	2.5 (3.5)	2.2 (1.1)	2.0 (1.8)	5.1 (1.6)	10.0 (2.8)	3.8 (2.3)	0.2 (0.4)
	Point count detections	0.5 (0.7)	0.3 (0.3)	0.4 (0.4)	0.8 (0.4)	3.1 (0.2)	1.5 (0.9)	0.04 (0.09)
	Nests	0	0	0.1 (0.3)	0.4 (0.7)	4.0 (1.4)	0.5 (0.8)	0
Extrapolated estimate of total population size	Corrected banding data	24	48	168	390	222	202	0
	Nest density * 2	0	0	60	196	763	197	0
Chao2 Estimator (SD)		--[a]	14 (5)	30 (9)	61 (12)	55 (37)	42 (9)	--[a]

[a] insufficient number of recaptures to use Chao2 estimator.

2. PREDICTING THE CONSEQUENCES OF HABITAT CHANGE

Modeling the relationship between habitat and abundance

A detailed knowledge of a species' habitat needs is required for the maintenance of viable populations, and is especially important for the conservation and management of populations that live in areas vulnerable to human exploitation and alteration. It has been estimated that 30% of Connecticut's salt marshes have been lost over the last 90 years (Rozsa, 1995) as a direct result of human development, invasive species, and sea level rise. In order to understand the consequences of changing habitat conditions and alternative management options, we developed and tested a series of statistical models, which relate sparrow numbers to marsh characteristics, to determine whether it would be possible to predict changes in population size using habitat information.

Saltmarsh sharp-tailed sparrow-habitat models.—We found substantial variation among plots in saltmarsh sharp-tailed sparrow abundance (Figure 3, Tables 3 and 5), some of which could be explained by variation in their habitat. Our best model describing the number of saltmarsh sharp-tailed sparrows captured in a plot included both the mean and standard deviation of vegetation height, and the proportion of the vegetation that was *J. gerardi* (Table 5a). This model was highly significant ($F_{3,26} = 9.90$, $P = 0.0002$) and explained 48% of the variation. No other models were considered to be equivalent as they all produced $\Delta_i > 2$.

We used the same procedure to find a model that best described the number of female saltmarsh sharp-tailed sparrows captured. Our best model included the same three variables as that for the total number of saltmarsh sharp-tailed sparrows captured: mean vegetation height, standard deviation of vegetation height, and percent *J. gerardi* (Table 5b). This model was significant ($F_{3,26} = 7.30$, $P = 0.001$) and explained 39% of the variation in female saltmarsh sharp-tailed sparrow abundance. No other models were considered equivalent.

Our best model describing the number of saltmarsh sharp-tailed sparrow nests ($F_{2,27} = 4.21$, $P = 0.03$, $R^2 = 0.18$) again included the proportion of the vegetation that was *J. gerardi* (Table 5c), this time in combination with the mean vegetation density. This model, however, could not be distinguished from four alternative models ($0.18 < \Delta_i < 1.19$). Percent *J. gerardi* remained in four of the five models, mean vegetation density in two, and the distance to the marsh edge and the standard deviation of vegetation density were each in one of the alternate models.

Although we were able to develop significant models for three of our measures of sparrow abundance (Table 5a-c), none of the habitat variables that we measured could account for the variation in the number of fledglings produced (Table 5d). Our best model included just the proportion of the vegetation that was tall form *S. alterniflora*, but the model was not significant ($F_{1,28} = 2.02$, $P = 0.17$) and explained only 7% of the variation in the number of fledglings produced.

Overall, our data indicate that more saltmarsh sharp-tailed sparrows were captured where the vegetation was homogenously tall and where the relative proportion of *J. gerardi* was high. The relative abundance of *J. gerardi* was also an important predictor of the number of saltmarsh sharp-tailed sparrow nests, as was vegetation density.

Vegetation that is taller and denser than average is preferred for nesting (Gjerdrum *et al.* submitted MS; see section *Nest-site selection*), and may provide increased cover from predators or a refuge from the flooding tides that inundate the salt marsh twice a day. *J. gerardi* has a low tolerance for high soil salinity, which means that this species grows only in high marsh habitat with minimum exposure to high tides (Niering and Warren, 1980). The relative abundance of *J. gerardi*, therefore, is probably a good indicator of the highest areas of the marsh, where the risk of nest flooding is lowest. Other studies have demonstrated a positive association between saltmarsh sharp-tailed sparrow abundance and the presence of *S. patens* (Reinert and Mello, 1995; Brawley et al., 1998), another high marsh species. In our study, *S. patens* was present, and common, on all of our plots (see Table 9 in section *Nest site selection*) and there may have been insufficient variation among plots to detect this relationship. Since *S. patens* is ubiquitous in high marsh, we propose that the less common *J. gerardi* may be a better indicator of the very best sparrow habitat in that it provides the resolution to distinguish among areas of high marsh that differ in quality. In general, the presence of native vegetation, which includes *J. gerardi* and *S. patens*, has been shown to have a positive effect on saltmarsh sharp-tailed sparrow abundance elsewhere in their range (Burger et al., 1982; Shriver et al., 2004).

Table 5. Results of multivariate linear regression analyses of habitat characteristics on four measures of saltmarsh sharp-tailed sparrow abundance.

Habitat Variable	Std. Coefficient ± SE	*t*	*P*	AIC$_c$ *w*
a) Total captured				0.24
Vegetation height	0.48 ± 0.21	3.32	0.003	
SD Vegetation height	-0.33 ± 0.26	-2.41	0.02	
% *Juncus gerardi*	0.30 ± 0.12	2.06	0.05	
$F_{3,26} = 9.90$, $P = 0.0002$, $R^2\text{adj} = 0.48$				
b) Females captured				0.42
Vegetation height	0.30 ± 0.07	1.96	0.06	
SD Vegetation height	-0.28 ± 0.09	-1.90	0.07	
% *Juncus gerardi*	0.42 ± 0.04	2.67	0.01	
$F_{3,26} = 7.30$, $P = 0.001$, $R^2\text{adj} = 0.39$				
c) (square root) Nests				0.11
Vegetation density	0.29 ± 0.01	1.64	0.11	
% *Juncus gerardi*	0.31 ± 0.01	1.77	0.09	
$F_{2,27} = 4.21$, $P = 0.03$, $R^2\text{adj} = 0.18$				
d) (square root) Fledglings				0.74
(log) % *Spartina alterniflora* (tall)	-0.31 ± 0.53	-1.42	0.17	
$F_{1,28} = 2.02$, $P = 0.17$, $R^2\text{adj} = 0.07$				

Seaside sparrow-habitat models.—Variation in seaside sparrow abundance could best be accounted for by either plot location or vegetation height, or by using both variables together. Our best-fit model included only plot location ($F_{4,25} = 9.80$, $P < 0.0001$), which explained 55% of the variation in the number of birds captured (Table 6). This model could not be distinguished from a model that included both plot location and mean vegetation height ($\Delta_i = 1.18$), or just mean vegetation height ($\Delta_i = 1.80$).

Our best-fit logistic regression model used to describe the presence of seaside sparrow nests included only the relative abundance of short form *S. alterniflora* (Table 6), but adding the standard deviation of vegetation density did not significantly worsen the model ($\Delta_i = 1.18$). Short form *S. alterniflora* was significantly ($t_{28} = 2.44$, $P = 0.02$) less abundant in plots where seaside sparrow nests were present (mean ± SD: 7.3 ± 10.1%) compared to those where they were absent (25.0 ± 15.4%).

Previous studies have shown that seaside sparrows and other saltmarsh birds are vulnerable to habitat fragmentation and are absent from small marshes (Benoit and Askins, 2002; Shriver et al., 2004). The size of the marsh in which a plot lies, therefore, may explain why location is such an important predictor of seaside sparrow abundance. If this is the case, then our results would suggest that marsh size, and perhaps associated landscape features, overwhelm habitat features in their effect on sparrow abundance. The situation at Hammock Marsh – a relatively small marsh, that has the highest densities of nesting seaside sparrows – suggests that the relationship between marsh size and abundance might not be as simple as earlier studies have suggested. The alternative models also suggest another explanation for our data, indicating that the presence of tall vegetation might be the best indicator of seaside sparrow abundance. Very tall vegetation is preferred for nesting and nests are most successful when placed in tall vegetation (Gjerdrum *et al.* submitted MS; see section *Linking habitat to reproductive success*). Vegetation height was not correlated with marsh size ($r = 0.09$, $P = 0.84$) so we can eliminate the possibility that the vegetation in large marshes averages taller (i.e., more suitable) than in small marshes. It is possible, however, that the total area of tall vegetation within a marsh is more important than the marsh size per se, which might account for discrepancies in the area-abundance relationship. Short *S. alterniflora* is presumably avoided by nesting seaside sparrows because it occurs at relatively low elevations in the marsh, and yet is not tall enough for sparrows to build nests that can escape tidal flooding.

Table 6. Results of a) multivariate linear regression analysis of habitat characteristics on seaside sparrow abundance, and b) logistic regression on presence/absence of seaside sparrow nests.

Habitat Variable		R^2_{adj}	$F_{4,25}$	P	AIC$_c$ *w*
Total captured					
Location		0.55	9.80	< 0.0001	0.42
	Coefficient ± SE	Log-likelihood	LRS$_a$	P	AIC$_c$ *w*
Presence of nests					
% *S. alterniflora* (short)	0.11 ± 0.05	-10.30	6.43	0.01	0.26
Hosmer-Lemeshow statistic = 3.65, df = 3, P = 0.30					

Testing model predictions

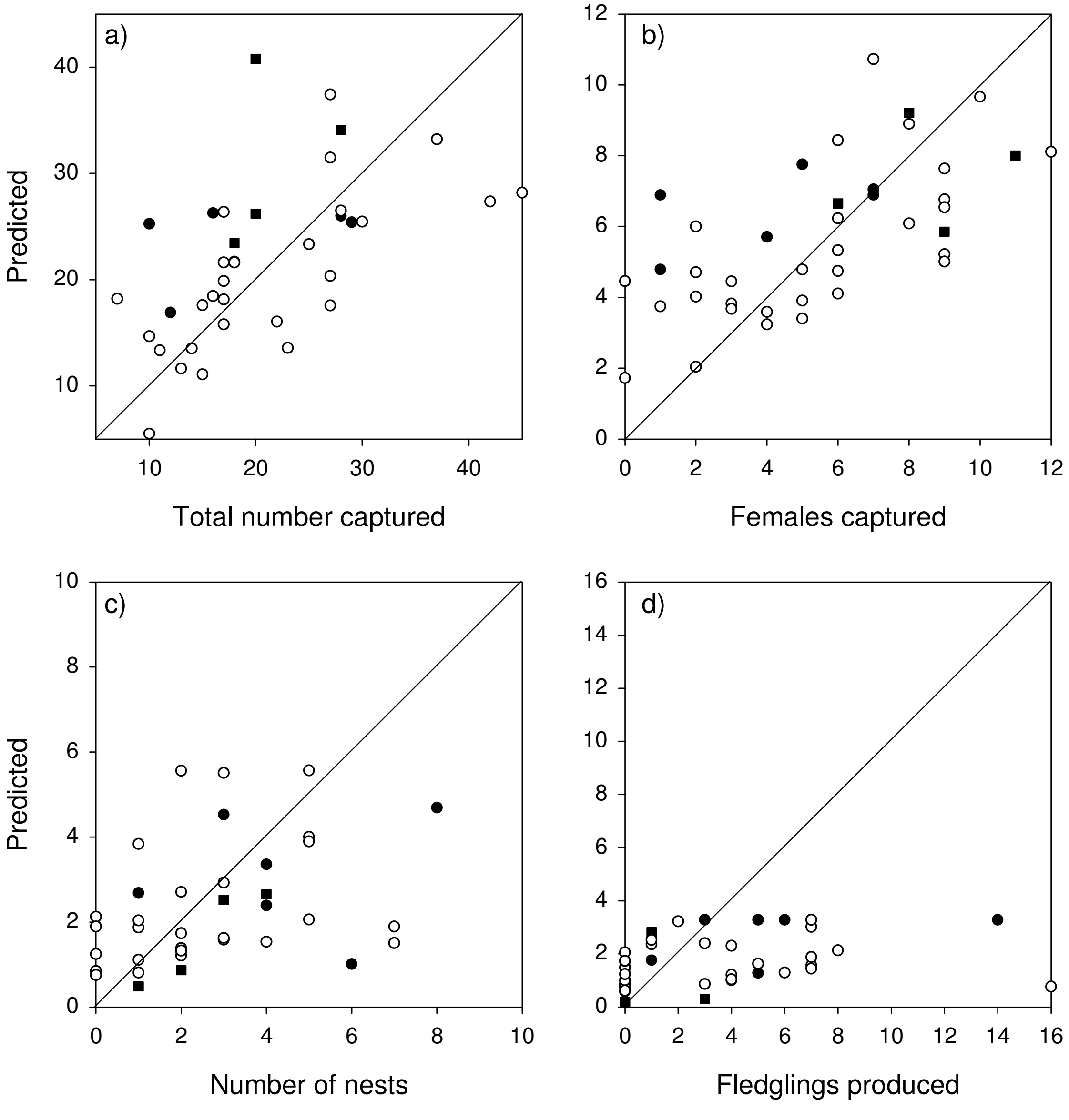
Before quantitative habitat models can be applied, their predictive success should be evaluated to avoid detrimental or misdirected management decisions based on inadequate models. When using a single data set to develop and evaluate a model, jackknife or bootstrap techniques are commonly used for model verification, but these approaches only test the model's internal consistency (Guisan and Zimmermann, 2000). Obtaining new data from the population of interest is a less common approach to model validation, but can tell us how well the model will perform under circumstances different from those used to develop the model (Guisan and Zimmermann, 2000). We used both procedures to validate the performance of our sparrow-habitat models.

Saltmarsh sharp-tailed sparrow.— Despite the highly significant habitat models developed to describe saltmarsh sharp-tailed sparrow abundance, tests of these models revealed very mixed prediction capabilities. First, we used a jackknife approach to evaluate the performance of the model that included mean vegetation height, standard deviation in vegetation height, and the relative proportion of *J. gerardi* as a predictor of the total number of birds captured. We found no significant difference between the observed and predicted number of birds captured (paired *t*-test: $t_{29} = 0.02$, $P = 0.99$), and the predicted number of birds captured was significantly related to the observed number (correlation: $r = 0.63$, $P = 0.0002$; Figure 5a). Using a cross-validation procedure on 10 plots not used for developing the original models, however, we found a significant difference between the observed and predicted number (paired *t*-test: $t_9 = -7.70$, $P = 0.02$) and no significant linear relationship between observations and predictions (correlation: $r = 0.25$, $P = 0.48$; Figure 5a).

For the number of females captured, neither approach revealed a significant difference between the observed and predicted number (jackknife paired *t*-test: $t_{29} = -0.04$, $P = 0.95$; cross-validation paired *t*-test: $t_9 = -1.41$, $P = 0.14$; Figure 5b). A significant correlation between the observed and predicted number of females captured, however, was found only when using data generated from the jackknifing technique (jackknife correlation: $r = 0.55$, $P = 0.002$; cross validation correlation: $r = 0.53$, $P = 0.11$).

We found no significant differences between the observed and predicted number of nests (jackknife paired *t*-test: $t_{29} = -0.01$, $P = 0.93$; cross validation paired *t*-test: $t_9 = 0.30$, $P = 0.13$; Figure 5c), but the fit of the correlations between the predicted and observed numbers were poor (jackknife correlation: $r = 0.32$, $P = 0.09$; cross validation correlation: $r = 0.45$, $P = 0.19$). Similarly, no significant differences were found between the observed and predicted number of fledglings (jackknife paired *t*-test: $t_{29} = -0.01$, $P = 0.98$; cross validation paired *t*-test: $t_9 = 0.26$, $P = 0.43$), and the relationships between the observed and predicted numbers were very weak (jackknife correlation: $r = 0.03$, $P = 0.86$; cross validation correlation: $r = 0.55$, $P = 0.10$; Figure 5d).

Figure 5. Comparison of observed and predicted Saltmarsh Sharp-tailed Sparrow abundance indices based on cross-validation procedure. Solid line indicates line of best fit where all predictions are equal to their associated observations. Open symbols indicate the 30 plots used in the model-building data set and solid symbols indicate the 10 validation plots. Squares distinguish the four plots that were located at marsh locations not used for model building.



For each of our two validation procedures, no difference between observed and predicted values in paired t-tests and a strong relationship between observed and predicted values in a correlation analysis would be signs that a model is performing well. Overall, we found that there was relatively good internal consistency, especially for models that estimate the numbers of birds, but that the models were poor at predicting conditions at new sites (Table 7). All four jackknife tests produced predicted values that did not differ consistently from the observed values, and for both the total number of birds and the total number of females there was a significant relationship between the predicted and observed numbers. In our cross-validation tests we found no support for our predictions of the total number of birds. For the remaining three variables there was no difference between observed and predicted values in paired t-test, but there was also no correlation between these numbers.

Table 7. Summary of results for saltmarsh sharp-tailed sparrow model validation using jackknife and cross-validation approaches. No difference between observed and predicted values in paired t-tests and a significant correlation between observed and predicted values indicate that the model is performing well. Good model performance is indicated here in bold.

	Jackknife (internal consistency)		Cross-validation (external validity)	
	Paired t test	Correlation	Paired t test	Correlation
# bird	**No difference**	**Significant**	Different	Not significant
# females	**No difference**	**Significant**	**No difference**	Not significant
# nests	**No difference**	Not significant	**No difference**	Not significant
# fledglings	**No difference**	Not significant	**No difference**	Not significant

Seaside sparrow.—We did not test the performance of the model describing variation in the number of seaside sparrows captured in a plot because our best model contained no habitat variables (Table 6). Using data from the model-building data set to test the internal consistency of our model for the occurrence of seaside sparrow nests, we found that the model correctly predicted 87% of sites where nests were not found but only 35% of sites with nests (Table 8). The overall correct classification rate was 78%, but the model produced only minimal gains over the random expectation (Table 8). When applied to the validation data set, the model correctly predicted 73% of the sites where nests were not found and 37% of the nesting sites for an overall correct prediction rate of 62% (Table 8). Again, however, the model made only minimal gains over the random model (Table 8).

Table 8. The classification of sites with and without Seaside Sparrow nests from the overall best logistic model (lowest AIC$_c$) applied to the model-building data set (N = 30 plots) and the validation set (N = 10 plots). A probability threshold cut-off of 0.5 was used to classify sites. Model diagnostics are tabulated to evaluate the performance of the model when applied to both datasets.

		Observed	
Predicted		Present	Absent
Original data set	Present	1.7	3.3
	Absent	3.3	21.7
Validation data set	Present	1.1	1.9
	Absent	1.9	5.1

Model diagnostics	Original	Validaton
% Correctly predicted absent	87	73
% Correctly predicted present	35	37
% Overall correctly predicted	78	62
Success index for model predicting absences[a]	0.04	0.18
Success index for model predicting presences[a]	0.02	0.07

[a] Success index measures the gain the model shows over a purely random model.

Summary.—In summary, we found substantial variation among plots in the abundance of both saltmarsh sharp-tailed and seaside sparrows, some of which could be explained by variation in their habitat. Habitat models developed for the total number of saltmarsh sharp-tailed sparrows captured and the total number of females caught appeared robust when applied to the original data set, but their performance was greatly reduced when applied to new sites. The habitat model used to describe the number of saltmarsh sharp-tailed sparrow nests, although significant, did not perform well when applied to either the original or validation data sets. Habitat variables could not account for the variation in the number of fledglings produced, and the model failed to predict more than four fledglings on any plot (Figure 5d). This bias is likely the result of extrapolation, as the variation in the relative proportion of short *S. alterniflora* at the 10 validation plots is out of the range of values at the 30 model-building plots. For seaside sparrows, marsh location accounted for more than half of the variation in number captured. The habitat model developed to describe the presence of seaside sparrow nests, however, did not perform much better than a null model in which sparrow occurrences and absences were assigned to sites randomly.

Overall these results suggest that although habitat conditions are related to certain aspects of the distribution and breeding performance of these sparrows, they tell only part of the story. The apparently strong influence of plot location for seaside sparrow suggests that landscape characteristics of marshes supercede any influence of local habitat features. Landscape characteristics may also play a role in determining the distribution and abundance of saltmarsh sharp-tailed sparrows, although this species is clearly tolerant of a wider range of marshes than are seaside sparrows (Benoit and Askins, 2002; Shriver et al., 2004). Another important set of variables that might influence distribution and abundance are behavioral characteristics of the species. We suspect that behavior may be especially important for saltmarsh sharp-tailed sparrows, because of their atypical social system. Finally, it is possible that there are additional habitat variables that are important to these species, and which we did not measure. Our current analysis has focused primarily on structural characteristics of the environment, but clearly there are other things that could influence where birds spend their time. In particular the distribution of food might be important, and we have initiated field work to test this idea.

Habitat models, such as those developed here, have proven useful for understanding and describing the distribution of many different species (Scott et al., 2002). The ability of such models to make clear predictions, however, is often not tested (Scott et al., 2002). Although perhaps counterintuitive, it is clear from our results that even highly significant models with good internal consistency may not provide good predictions when applied more broadly. Overcoming this problem and producing better models, however, is not an insurmountable problem, although it will probably require the combination of different types of data in a manner that is not typically used to model species distributions. In particular, we suggest that the combination of information on habitat selection, such as that presented here, with information about landscape conditions and an understanding of the behavioral decisions that birds make, into a hierarchical model could prove to be a powerful technique. Future work by our research group will include building such models.

Predicting the consequences of habitat change

One of our initial goals in this project was to use habitat models derived for saltmarsh sharp-tailed and seaside sparrows to predict the consequences of future habitat change. Our analysis, however, suggests that models based on habitat characteristics alone are not adequate to make accurate predictions about the occurrence and abundance of these species (see section *Validating model predictions*). Even those models with strong statistical support have low precision and proved relatively inaccurate when applied to independently collected data. As described above, we have begun collecting the additional data needed to make more sophisticated models, but it is clear that it would be premature and potentially misleading to make predictions about future habitat change until we have completed and tested a second generation of predictive models.

3. NEST-SITE SELECTION AND DEMOGRAPHIC PARAMETERS

Effective species management requires that we understand basic behavioral and demographic characteristics of a species, such as nest site selection, reproductive success, survival, and dispersal. By intensively nest searching and mist-netting birds at several different Connecticut marshes, we provide the first estimates of nest success for this region, examine the relationship between habitat and nest location and success, and lay the groundwork for future analyses of survival and dispersal.

Nest-site selection

Previous studies have shown that saltmarsh sharp-tailed sparrows selectively nest in areas of cordgrass and salt-meadow vegetation communities, and that they typically select relatively drier portions of the marsh (DeRagon, 1988; Greenlaw and Rising, 1994). Seaside sparrows select short-grass meadow habitats similar to those chosen by saltmarsh sharp-tailed sparrows in Connecticut (Benoit and Askins, 1999), although the factors determining nest site placement in seaside sparrows seem to vary regionally and are not well known for northern sites (Post and Greenlaw, 1994 and references therein). In this portion of the study we quantified site selection in Long Island Sound salt marshes in terms of parameters that may influence both nest placement and reproductive success.

We compared habitat characteristics at 160 saltmarsh sharp-tailed sparrow nest sites and 23 seaside sparrow nest sites to 719 non-nest sites (Table 9). Both species placed their nests non-randomly in the marsh with respect to the habitat variables we measured. Saltmarsh sharp-tailed sparrows chose sites where the vegetation was taller and denser than at random locations, where there was a deep layer of thatch, and where the habitat was dominated by *S. patens* (Table 9). They also showed a preference for sites that were slightly higher in elevation than average. Seaside sparrow nests were placed where the vegetation was very tall, relatively sparse, and dominated by the tall form of *S. alterniflora*, largely to the exclusion of *S. patens* (Table 9).

Nest site selection differed between sparrow species in several ways. Seaside sparrows used sites with significantly taller and sparser vegetation than did sharp-tailed sparrows. *S. patens* and short form *S. alterniflora* were less common in the immediate vicinity of 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 9).

Table 9. Univariate comparisons (mean ± SD, range) of habitat variables at nest sites and non-nest sites for saltmarsh sharp-tailed sparrows and seaside sparrows breeding in Connecticut.

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	Saltmarsh sharp-tailed sparrow nest sites compared to seaside sparrow nest sites
Vegetation height (cm)[a]	39.9 ± 16.4	44.9 ± 10.2	64.3 ± 16.1	$t_{367.0} = 4.90, P < 0.001$	$t_{23.5} = 7.15, P < 0.001$	$t_{24.6} = 5.62, P < 0.001$
	(0 - 112)	(21 - 81)	(38 - 97)			
Vegetation density (#stems/100cm^2)[a]	37.1 ± 26.3	52.7 ± 26.2	26.1 ± 20.8	$t_{235.8} = 6.88, P < 0.001$	$t_{23.3} = -2.48, P = 0.02$	$t_{31.8} = 5.62, P < 0.001$
	(0 - 108)	(7 - 128)	(5 - 71)			
Thatch height (cm)[a]	5.5 ± 0.2	8.8 ± 0.4	9.3 ± 7.8	$t_{248.3} = 7.79, P < 0.001$	$t_{22.6} = 2.30, P = 0.03$	$t_{24.3} = 0.31, P = 0.76$
	(0 - 34)	(0 - 22)	(0 - 31)			
% *Spartina patens*[b]	38.9 ± 40.4	54.2 ± 35.2	21.2 ± 32.1	$U = 69097.0, P < 0.001$	$U = 5967.5, P = 0.02$	$U = 911.0, P < 0.001$
	(0 - 100)	(0 - 100)	(0 - 85)			
% *S. alterniflora* (short)[b]	20.6 ± 35.1	10.4 ± 20.6	0.0	$U = 53890.5, P = 0.14$	$U = 5485.5, P < 0.01$	$U = 1242.0, P < 0.01$
	(0 - 100)	(0 - 100)	(0)			
% *S. alterniflora* (tall)[b]	10.9 ± 26.6	14.6 ± 26.3	47.0 ± 44.7	$U = 64716.0, P < 0.01$	$U = 12845.5, P < 0.001$	$U = 2691.5, P < 0.001$
	(0 - 100)	(0 - 100)	(0 - 100)			
% *Distichlis spicata*[b]	10.0 ± 22.0	5.9 ± 14.4	7.4 ± 15.7	$U = 52224.0, P < 0.001$	$U = 7383.0, P = 0.30$	$U = 1796.0, P = 0.81$
	(0 - 100)	(0 - 80)	(0 - 50)			
% *Juncus gerardi*[b]	8.8 ± 23.8	12.2 ± 25.8	14.3 ± 24.7	$U = 62161.5, P = 0.02$	$U = 9407.0, P = 0.08$	$U = 1948.0, P = 0.55$
	(0 - 100)	(0 - 100)	(0 - 85)			
Mean difference in elevation (cm)[c]				2.46 ± 4.96	0.32 ± 6.35	3.11 ± 5.76
				$t_{34} = -2.93, P < 0.01$	$t_{10} = 0.16, P = 0.87$	$t_{9} = -0.10, P = 0.12$

[a] *t*-test comparisons with separate variance; [b] Mann Whitney *U* comparisons; [c] The mean difference in elevation between nest sites and non-nest sites, and SESP and SSTS nest sites were calculated for each plot and compared using a paired *t*-test

Reproductive success

During the two years of our study we found a total of 167 saltmarsh sharp-tailed sparrow nests. Overall, the rate of nest survival for saltmarsh sharp-tailed sparrows was 30% in 2002 and 26% in 2003 (Table 10). Of the 136 nests with known outcomes, 80 (59%) failed to produced fledglings. Flooding was the major cause of nest failure, accounting for 60% of all failed nests. Another 31% of failed nests were depredated. We also found evidence for partial nest failure; 17 (13%) of the 136 nests 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.

The length of the breeding season (i.e., the time span between the date of the first recorded egg to be laid and the last chick to fledge) for saltmarsh sharp-tailed sparrows was 75 days (30 May - 13 August) in 2002, and 78 days (29 May – 15 August) in 2003. For the two years combined, the mean date of clutch completion was estimated to be 27 June (SD = 16 days, *n* = 134). A total of 20 nests had no eggs laid in them. Females laid between 2 and 5 eggs per nesting attempt (mean ± SD: 4.0 ± 0.7, *n* = 121). In addition, we found one nest that contained 8 eggs and was being attended by a single saltmarsh sharp-tailed sparrow female. All but one of these eggs hatched but then immediately failed due to flooding. We obtained blood samples that are currently being analyzed to determine if all 8 eggs were laid by a single female or, if more than one female, by the same species. The average hatching date during our study was 11 July (SD = 16 days, *n* = 88), and the average fledging date was 21 July (SD = 14 days, *n* = 55). We confirmed 7 renesting attempts - six by females whose first nesting attempt had failed, and one by a female whose first attempt produced one fledgling; her second attempt produced an additional 4 fledglings.

Seaside sparrows were far less common at our study sites than saltmarsh sharp-tailed sparrows and we found only 24 nests during the study. Seaside sparrow nest survival was somewhat higher than for their congener with 44% and 38% of nests surviving to fledge at least one chick in 2002 and 2003, respectively (Table 10). Four nests were depredated, three were flooded during incubation, and the fate of one failed nest could not be determined. Seaside sparrow nest survival was higher than that of saltmarsh sharp-tailed sparrows during the chick stage ($z = 2.95$, $P = 0.003$), but not during the egg stage ($z = 0.38$, $P = 0.70$) or over the nesting period as a whole ($z = 0.93$, $P = 0.36$). No seaside sparrow nests were found partially flooded, but one egg went missing in two of the 14 successful nests suggesting partial nest depredation.

The length of the breeding season for seaside sparrows was estimated to be 55 days (22 May – 16 July) in 2002, and 64 days in 2003 (8 June – 11 August). For the two years combined, mean date of clutch completion was 27 June (SD = 15 days, *n* = 20), mean hatching date was 7 July (SD = 16 days, *n* = 13), and the average date that chicks fledged from the nest was 16 July (SD = 15 days, *n* = 12). We found no evidence of nests that were not laid in, and no evidence of renesting. Females laid an average of 3.7 eggs (SD = 0.8, *n* = 19) and fledged an average of 1.8 chicks (SD = 1.9, *n* = 24) per nest.

Table 10. Mayfield estimates of daily nest survival during incubation and chick-rearing periods, overall percent survival, and nest fates for saltmarsh sharp-tailed and seaside sparrows.

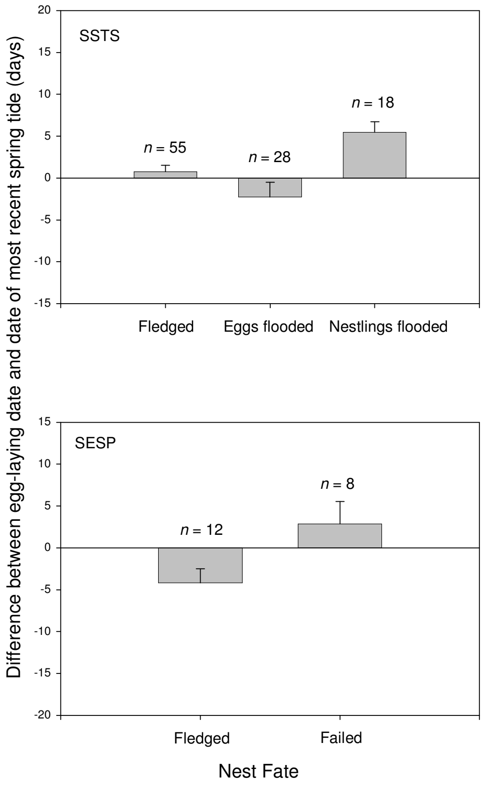
Year	Incubation			Chick-rearing			Overall % survival[b]	Number of failed nests			Total number of nests	
	Daily nest survival ± SE	Number of nests[a]	Observer days	Daily nest survival ± SE	Number of nests[a]	Observer days		Flooding	Predation	Cause of failure unknown	with known outcome	found
Saltmarsh sharp-tailed sparrows												
2002	0.920 ± 0.0004	41	212	0.971 ± 0.0001	31	242	30	13	10	3	51	64
2003	0.949 ± 0.0001	65	491	0.927 ± 0.0002	56	343	26	35	15	4	85	96
Seaside sparrows												
2002	0.900 ± 0.009	2	10	1	4	17	44	0	1	0	6	6
2003	0.933 ± 0.0007	13	90	0.986 ± 0.0002	8	71	38	3	3	1	16	17

[a] Number of nests with at least one observation day and known outcome (fail or succeed); [b] Overall survival = (daily survival during incubation and chick-rearing combined)^{22}

Linking habitat to reproductive success

Although we found that saltmarsh sharp-tailed sparrows selected certain habitat characteristics over others for nesting locations, there was little evidence that vegetation characteristics influenced nest success. 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). 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 high spring tides. We found that the number of days between egg-laying and the nearest spring tide differed considerably among those nests that were successful, those that were flooded during incubation, and those that flooded during chick-rearing ($F_{2,98} = 7.21$, $P = 0.001$; Figure 6). Nests that failed due to flooding during incubation were initiated an average of 2.3 (SD = 9.3) days prior to the spring tide, compared to 0.8 days (SD = 9.3 days) after the spring tide for nests that successfully raised at least one fledgling. Nests that were flooded during chick-rearing were initiated 5.4 (SD = 5.4) days after the spring tide.

Figure 6. The mean ± SE number of days after the last spring tide that female saltmarsh sharp-tailed sparrows (top) and seaside sparrows (bottom) 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 bars.



We found evidence that seaside sparrow nests were more successful when placed in taller, less dense vegetation where there was more *S. alterniflora* and less *S. patens*. In strictly chronological terms, egg-laying date did not affect the fate of seaside sparrow nests ($t_{18} = 1.29$, $P = 0.21$), however, successful nests were initiated significantly earlier in relation to the spring tide than nests that failed ($F_{1,18} = 5.59$, $P = 0.03$; Fig. 4) – a pattern that was quite different to that for saltmarsh sharp-tailed sparrows.

These results suggest that saltmarsh sharp-tailed and seaside sparrows have evolved two very different strategies for reproducing successfully in tidal marshes. Saltmarsh sharp-tailed sparrows cope with the challenge of living in an environment that floods regularly by adjusting their reproductive behavior temporally, such that most nesting does not coincide 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.

Survival, dispersal, and short-term movements

Good estimates of survival and dispersal are necessary for understanding the long-term dynamics of any population, but require multiple years of data. Although beyond the scope of this study, we have laid the groundwork for generating such information by creating a marked population of saltmarsh sharp-tailed and seaside sparrows at several different marshes in Connecticut.

In 2002 and 2003, we banded a total of 784 adult, 81 juvenile, and 177 nestling saltmarsh sharp-tailed sparrows and 128 adult, 18 juvenile, and 37 nestling seaside sparrows. Of the 1042 saltmarsh sharp-tailed sparrows banded, we recaptured 316 (30%). Sixty-seven (37%) of the 183 banded seaside sparrows were also recaptured. All but 6 seaside sparrows were recaptured on the same one-hectare plot on which they were originally captured. In contrast, 88 adult saltmarsh sharp-tailed sparrows were captured on at least two plots, 76 (86%) of which were males. All but four of these movements were of distances under 500 m. The farthest within-marsh movement that we recorded was at Great Island, where a male moved between plots located 700 m apart.

A total of eight juvenile saltmarsh sharp-tailed sparrows were recaptured, two of these in plots other than the one in which they were originally banded. An additional four birds that were banded as nestlings were subsequently recaptured as juveniles, two on different plots from which they were produced. Data from three of these recaptures are worth highlighting as examples of inter-marsh movement and inter-year dispersal of juvenile birds. On 15 July 2002 we banded a saltmarsh sharp-tailed sparrow nestling at the McKinney NWR in Westbrook. On 19 August the same bird was recaptured more than 6 km west at Hammonasset State Park. At East River marsh in Guilford, we banded a juvenile saltmarsh sharp-tailed sparrow on 5 September and recaptured the same individual on 15 October at Barn Island WMA, almost 70 km east of its original location. In the fall of 2002, a juvenile saltmarsh sharp-tailed sparrow was captured and banded at Milford Point, Milford. The following year, on 20 June 2003, we recaptured this individual as a breeding adult male, approximately 65 km farther east, on Great Island in Old Lyme. These data highlight the value of a marked population for elucidating the extent to which different populations are interconnected.

4. INDICATORS OF AVIAN COMMUNITY HEALTH

Monitoring the health of bird communities in Long Island Sound salt marshes may require the development of indicators that can be relied upon to accurately represent the state of the breeding bird community. During point count surveys designed to estimate the size of sparrow populations, we also collected data for the entire avian community at each of our study plots and used two methods to identify appropriate indicator species. First, we used a nested subset analysis, which determines the degree to which the collection of species found at species-poor sites is a nested subset of those found at increasingly species-rich sites. Second, we used data on the abundance, and patterns of occurrence, of both saltmarsh sharp-tailed sparrow and seaside sparrow to determine whether sparrow abundance can be used to determine patterns of species richness, or to identify sites where state listed species are abundant.

Nested subset analysis

The *Nestedness Calculator* calculated a temperature of 18.73° for our species matrix (Table 11). The average temperature for a completely random matrix with the same species richness was 55.25° (SD = 5.75°), and the probability of obtaining a matrix with a more nested structure than the one we observed was 1.12×10^{-10}. Our data, therefore, show a significantly nested pattern, such that species-poor plots contain a subset of the birds found in species-rich plots. Appropriate indicators of high diversity would be those species that are present in the species-rich plots only, limited as to where they occur, but common enough to be detected. The pattern here (Table 11) suggests that saltmarsh sharp-tailed sparrows and seaside sparrows, two of the region's highest priority species for conservation (U.S. Fish and Wildlife Service, 2002), are the most ubiquitous species across our study plots. This paradoxical result probably arises because we focused our attention on the largest marsh sites in Connecticut, where these two species are most likely to be detected (Lori Benoit, unpublished data).

Although the ubiquity of the two sparrows is not surprising, the lack of other species in many of our plots perhaps is. Most of the "rare" species detected on our point counts are not at all rare in the region as a whole. Thus, it seems that the high level of specialization of the two sparrow species makes them better able to cope with salt marsh conditions than other, regionally much more abundant, species.

Expanding the range of sites sampled to include smaller marshes that lack area-sensitive species (as we began to do for other purposes in 2004), might reveal a more complex pattern of community structure than described here. For now, however, it does not appear that information on the nestedness of the saltmarsh bird communities provides any information that is more useful for assessing marsh quality than simply monitoring the species of conservation concern.

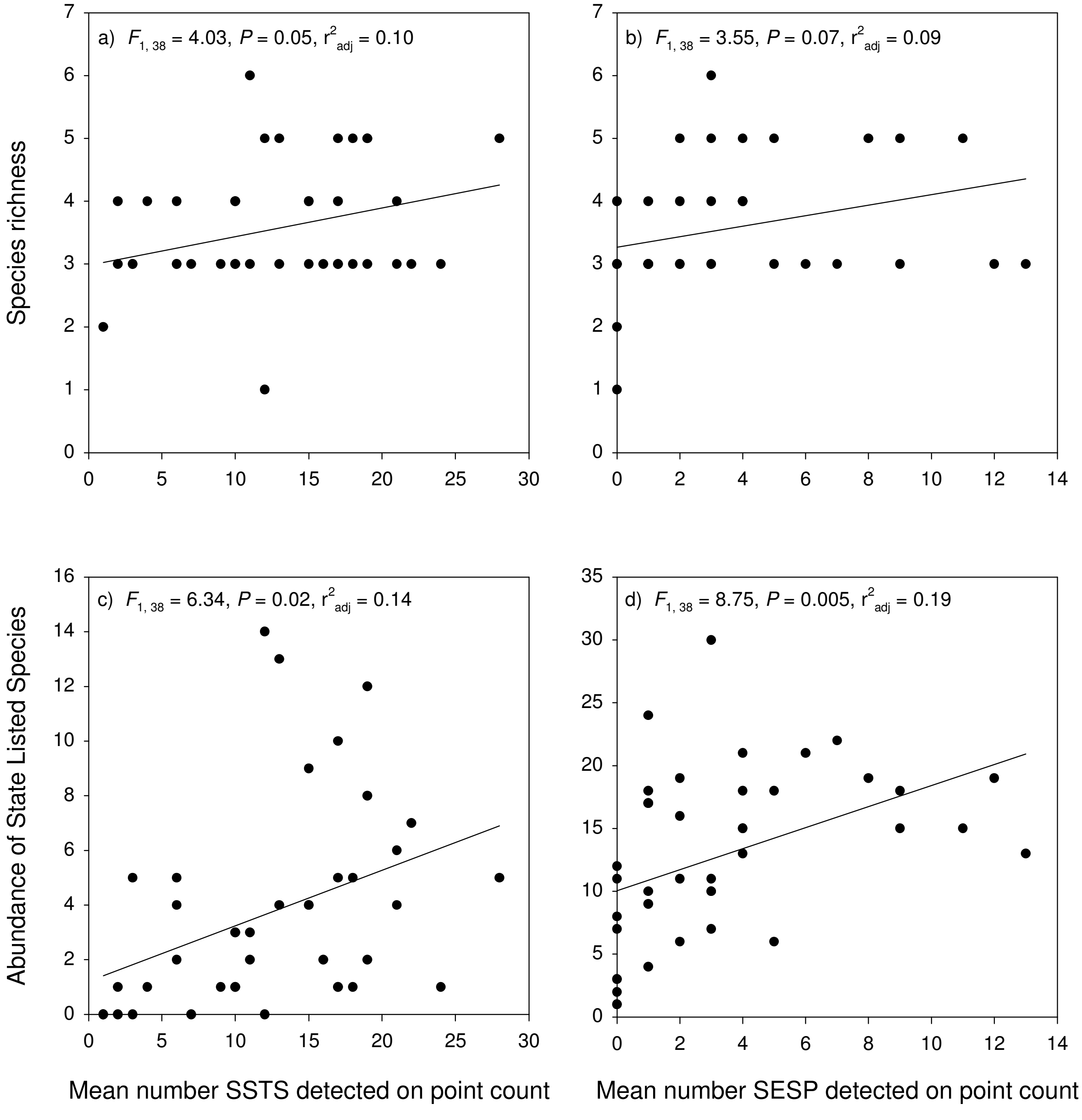
Regression analyses

We used the average number of saltmarsh sharp-tailed sparrows and seaside sparrows detected on point counts to determine whether their abundance could be used to indicate either species richness or the pooled abundance of Connecticut state listed species. We found positive relationships between saltmarsh sparrow abundance and both measures of species richness (Figure 7). This result suggests that, on average, the 'best' marshes are those where the greatest numbers of sparrows are present, and that point count abundance data collected for sparrows can be used to help identify sites that support a diverse salt marsh avifauna or high numbers of state listed species. The fit of the regression models, however, was poor ($r^2 < 0.2$) in all cases, suggesting that although sparrow abundance indicates abundance and richness of saltmarsh bird communities in a general sense, these measures will provide only a weak indicator of the importance of specific sites. Given that it is not difficult to conduct multi-species surveys and that systematic protocols are in development (Conway and Droege, 2004), it does not seem as though the use of indicators is warranted to gauge the status of saltmarsh bird communities. Where saltmarsh sparrow data are being collected without data on other species, however, they will provide a useful, if imprecise, measure of the overall saltmarsh bird community.

Table 11. Species distribution matrix for saltmarsh birds of Connecticut from point count data collected at 40 plots. Species abbreviations are as follows: SSTS, saltmarsh sharp-tailed sparrow; SESP, seaside sparrow; WILL, willet; RWBL, red-winged blackbird; MAWR, marsh wren; OSPR, osprey; SNEG, snowy egret; CLRA, clapper rail; GREG, great egret; GLIB, glossy ibis; MALL, mallard.

Site	Plot	SSTS	SESP	WILL	RWBL	MAWR	OSPR	SNEG	CLRA	GREG	GLIB	MALL
Great Island	8	x	x	x	x	x	x					
Great Island	2	x	x	x	x	x						
Great Island	4	x	x	x	x	x						
Great Island	7	x	x		x	x	x					
Hammonasset SP	4	x	x	x	x		x					
Hammonasset SP	16	x	x	x			x				x	
Hammonasset SP	2	x	x	x					x	x		
East River Marsh	G	x	x	x				x		x		
Black Hall River	19	x	x		x	x						
Barn Island WMA	9	x	x	x	x							
East River Marsh	15	x	x	x	x							
Great Island	6	x	x	x		x						
Hammonasset SP	1	x	x	x	x							
Hammonasset SP	17	x	x	x	x							
Great Island	5	x	x			x				x		
McKinney NWR	3	x		x	x						x	
McKinney NWR	7	x		x				x				x
Barn Island WMA	10	x	x	x								
East River Marsh	14	x		x					x			
East River Marsh	A	x	x	x								
East River Marsh	B	x	x	x								
East River Marsh	C	x		x			x					
East River Marsh	D	x	x	x								
East River Marsh	E	x	x	x								
East River Marsh	F	x	x	x								
East River Marsh	H	x	x	x								
Great Island	1	x	x	x								
Great Island	3	x	x		x							
Hammock River	20	x	x			x						
Hammock River	21	x	x			x						
Hammonasset SP	3	x	x	x								
Hammonasset SP	5	x	x	x								
Hammonasset SP	6	x	x	x								
McKinney NWR	2	x		x	x							
McKinney NWR	5	x	x		x							
Barn Island WMA	2	x	x					x				
McKinney NWR	8	x			x			x				
Barn Island WMA	11	x		x								
Barn Island WMA	13	x			x							
Black Hall River	18	x										

Figure 7. Regression analyses to test for a relationship between mean saltmarsh sparrow numbers detected on point counts and (a-b) plot species richness, and (c-d) the number of CT State listed species present.



AFFILIATED RESEARCH

Ongoing saltmarsh sparrow research

Funding for this project has resulted in the development of a much wider program of research on saltmarsh birds in Long Island Sound. Various aspects of our ongoing research are discussed previously in this report. Current foci include (a) testing alternative mechanisms for area-sensitive marsh occurrence patterns, (b) describing movement behavior and determining how it influences attempts to effectively monitor and predict distributions of saltmarsh sparrows, and (c) determining how saltmarsh sparrows respond to different restoration activities and assessing whether sparrows can be used as an indicator of restoration success.

Student training

Several students have received research experience working on this project. Most notably, two undergraduate students have received funding under the University of Connecticut's Summer Undergraduate Research Fellowship program to conduct research affiliated with our saltmarsh sparrow study. These projects are only indirectly linked to our LISS project, but both provide a better understanding of the basic reproductive biology of saltmarsh sharp-tailed sparrows and thus improve our ability to manage them effectively. The two projects are:

What determines nest construction variability in saltmarsh-sharp-tailed sparrows? (Selena Humphreys)
Nest attendance and brood provisioning in female saltmarsh-sharp-tailed sparrows. (Kira Sullivan-Wiley)

Collaborations

In addition to the work that we have been doing ourselves, we have expanded our overall saltmarsh sparrow project in several directions though collaborations with other researchers. These collaborations include:

1. Using blood samples collected at our study sites, Dr. Chris Hill of Coastal Carolina University has begun genetic analyses to determine the actual mating systems of saltmarsh sharp-tailed and seaside sparrows. Although much of the completed work involves the development of genetic markers, an initial examination of three saltmarsh sharp-tailed sparrow families at only two genetic loci has already shown multiple paternity in at least one nest. The final analysis will include information from about 50 saltmarsh sharp-tailed sparrow families.

2. We also collected blood samples in association with Shannon Kearney of the Department of Pathobiology at the University of Connecticut in order to screen birds for West Nile Virus (WNV). West Nile Virus emerged in the United States in the late summer and early autumn of 1999 affecting thousands of wild birds, as well as causing human deaths. Although individuals of most species that have been sampled have tested positive to the WNV antibody, none of the saltmarsh sharp-tailed or seaside sparrows ($N = 32$) that we have sampled to date were positive for antibody to WNV. Sampling for this project is ongoing.

3. Most recently, we have helped researchers from the Center for Integrated and Applied Environmental Toxicology at the University of Southern Maine with their work to screen sparrows from Long Island Sound salt marshes for mercury exposure. Sampling for this project is ongoing.

Research presentations emanating from our saltmarsh sparrow project

Elphick, C.S., C. Gjerdrum, P. Comins, and M. Rubega. 2003. Point counts accurately reflect sparrow abundance, but not breeding success. (Poster) *Annual meeting, American Ornithologists' Union, Champaign, Illinois, USA.*

Gjerdrum, C., C.S. Elphick, and M. Rubega. 2003. Molt in *Ammodramus* sparrows: differences among species, sexes and sites. (Poster) *Annual meeting, American Ornithologists' Union, Champaign, Illinois, USA.*

Elphick, C.S., C. Gjerdrum, P. Comins, and M. Rubega. 2002. What do point counts tell us about the size of breeding saltmarsh sparrow populations? Preliminary results. (Poster) Animals of tidal marshes symposium, Laurel, Maryland, USA.

Gjerdrum, C., C.S. Elphick, P. Comins, and M. Rubega. 2002. Conservation of saltmarsh sparrows in Long Island Sound marshes. (Poster) Animals of tidal marshes symposium, Laurel, Maryland, USA.

(At least two other presentations are planned for this summer's meeting of the American Ornithologist's Union.)

Research papers emanating from our saltmarsh sparrow project

Greenberg, R., C.S. Elphick, C. Gjerdrum, et al. In press. Between the devil and the deep blue sea: nesting ecology of tidal marsh sparrows. *In* R. Greenberg, S. Droege, J. Maldonado, and M.V. McDonald (eds.) Vertebrates of Tidal Marshes: Ecology, Evolution and Conservation. Studies in Avian Biology, Allen Press, Lawrence, KS, USA.

Gjerdrum, C., C.S. Elphick, and M. Rubega. What determines nest site selection and nesting success in saltmarsh breeding sparrows? Submitted to *Condor* (see APPENDIX 2).

Gjerdrum, C., C.S. Elphick, and M. Rubega. Validating predictive habitat models for the abundance and productivity of saltmarsh-breeding sparrows. Intended for *Biological Conservation* (see APPENDIX 3).

Elphick, C., C. Gjerdrum, P. Comins, M. Rubega. Point counts accurately reflect sparrow abundance, but not breeding success. In preparation; intended for *Auk*.

Humphries, S., C. Elphick, C. Gjerdrum, M. Rubega. The influence of flooding risk on nest structure in Saltmarsh Sharp-tailed Sparrows. Manuscript available; intended for *Journal of Avian Biology.*

Gjerdrum, C., C.S. Elphick, and M. Rubega. Molt in saltmarsh *Ammodramus* sparrows: differences among species, sexes and sites. Manuscript available; intended for *Journal of Field Ornithology*.

King, E., K. Sullivan-Wiley, Gjerdrum, C., C.S. Elphick, and M. Rubega. Female nest attendance during incubation and chick-rearing in saltmarsh sharp-tailed sparrows. In preparation; intended for *Auk*.

ACKNOWLEDGMENTS

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APPENDIX 1

Data Quality Assessments

The data collected in this study were limited to field counts of bird numbers, counts of plant abundance, identifications of both birds and plants, and measurements of marsh elevation. Data quality assessments specific to each category of data are discussed below.

Sparrow enumeration. In the overall project, we used a combination of intensive banding, mark-recapture analysis, and nest searches to determine the size of breeding populations at key sites. All saltmarsh sharp-tailed and seaside sparrows trapped were banded with a uniquely coded leg band to allow for individual identification. During each visit to a study plot, at least three observers conducted systematic nest searches, involving walking throughout the plot to look for birds flushing from the vegetation, and observations of feeding birds to determine the total number of nests in each study plot.

In order to minimize failed detections of birds, three to four people flushed birds into drainage ditches and then into nets which were strategically placed at the edges of plots. Nets were moved between each visit to a study plot to ensure total coverage of each plot. All observers were trained in bird capture and handling techniques by Dr. Elphick, and supervised throughout by both Dr. Elphick and Carina Gjerdrum (Quality Assurance Officer). Nest searching was conducted whenever plots were visited, and the location from which a bird flushed was always examined for nesting activity.

Avian point counts. Five-minute point counts were conducted in each plot on every visit before trapping began. Two observers were present at every point count. The primary observer called out each observation to a secondary observer who recorded these observations. The secondary observer also recorded any birds that the primary observer missed. This double-observer method increased our ability to detect birds present, and provides us with an estimate of the bias associated with different observers. During each point count, we recorded the total number of birds detected and categorized the distance from the point to each bird (within 25m, between 25 and 50m, and beyond 50m). We also noted the behaviour of each bird detected.

All observers were trained prior to the breeding season to ensure that all were familiar with the vocalizations of both seaside and saltmarsh sharp-tailed sparrows. Although all birds detected within the plot were noted, we concentrated our efforts on the two species of sparrows. On no occasion was the bird activity high enough to warrant prioritising the detection of one species over another. The double-observer method, the pre-season training, the open marsh habitat, and the relatively low species diversity ensured the collection of high quality point count data.

Vegetation sampling. Within each plot, we sampled the habitat at nine grid points, at nine randomly selected points, and at the site of each nest. A one-meter quadrat was placed around each sampling point. We measured the height of the vegetation at the corners of the quadrat, and 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 10 x 10 cm sub-quadrats within each main quadrat to estimate vegetation structure.

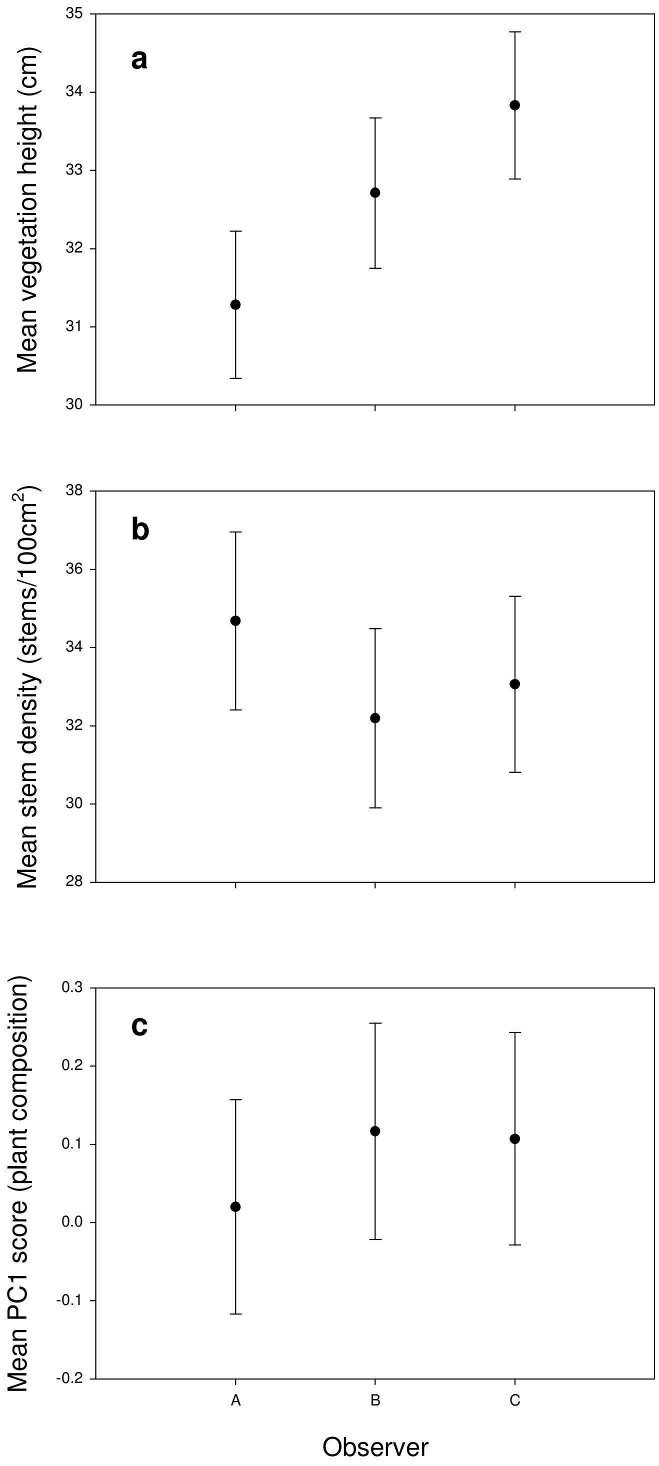
Because salt marsh systems contain relatively few taxa, it was easy to learn to identify the plant species within our study plots. Botanical specialists at the McKinney NWR and University of Connecticut were consulted when we encountered any specimens for which identification was uncertain. To control for errors in measurements of height, stem density, and proportionate abundance of different species, two of three observers sampled the habitat at the center point of each plot on every sampling date throughout the season. This procedure also allowed us to quantify any seasonal changes in vegetation structure because the same points were measured on multiple occasions across time. We constructed three multiple regression models with Plot, Date, and Observer as our independent variables. The dependent variable in the first model was mean vegetation height, and in the second model was mean stem density. A principle components analysis was use to reduce plant community composition data into one dependent variable that could be used in the third model.

Our results indicated that the average height measured differed significantly among observers ($F_{2,119} = 7. 13$, $P = 0.001$), but that the magnitude of the differences were relatively small (Figure 1a). Not unexpectedly, average vegetation height increased through the study period ($F_{1,119} = 25.78$, $P < 0.0001$). We found no significant observer effect on average stem density ($F_{2,120} = 1.18$, $P = 0.31$; Figure 1b), and a marginally nonsignificant decrease in stem density over time ($F_{1,120} = 3.27$, $P = 0.07$). With respect to plant species composition, our data do not indicate a significant observer effect ($F_{2,120}=0.58$, $P=0.58$; Figure 1c).

Marsh elevation sampling. Within each plot, at all nine grid points, random points and nest sites, we determined the height of the ground relative to mean high tide level with a surveying level. Marsh elevation was sampled by only two observers, and measurement errors were estimated for all elevations. Precision varied between 0 and 0.91cm. This precision is high compared to the variation we see among elevations of seaside sparrow nests (3.0 cm), saltmarsh sharp-tailed sparrow nests (8.5 cm), or nonnest sites (25.9 cm).

Additional data quality assessments. All equipment was calibrated throughout the field season to ensure accuracy of measurements. We used GPS to locate the position of each plot, and multiple readings were taken at the same points between June and August in order to calculate the error associated with those measurements. All field data was collated onto standardized data sheets, photocopied once a week, and stored at multiple locations during the field season. All data have now been entered into an electronic database, and have been proofed for errors.

Figure 1. Differences between observers on measurements of (a) plant height, (b) stem density, and (c) plant species composition (indexed here by Principle Component 1).



APPENDIX 2

Nest site selection and breeding success in saltmarsh sparrows

WHAT DETERMINES NEST SITE SELECTION AND NESTING SUCCESS IN SALTMARSH BREEDING SPARROWS?

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Abstract: We examined nest site selection and nesting success in the Saltmarsh Sharp-tailed and Seaside sparrows, at seven sites in Connecticut. We found 160 Saltmarsh Sharp-tailed Sparrows 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 denser than at random locations, where there was a deep layer of thatch, and where *Spartina patens* dominated the vegetation. There was little evidence that habitat characteristics influenced the success of nesting birds. The timing of nest initiation relative to spring tides, however, was important, and flooding was the primary cause of nest failure. Seaside Sparrow nests occurred in even taller vegetation, that was sparser than average and dominated by tall form *S. alterniflora*. Both habitat and nest timing influenced the success of Seaside Sparrow nests: on average, successful nests occurred in taller vegetation, and were initiated immediately prior to the full moon. Overall our results indicate that nest flooding is the primary threat to successful reproduction in both species, but that they have evolved different strategies for avoiding flooding. Saltmarsh Sharp-tailed Sparrows avoid flooding by timing reproduction to avoid especially high tides, while Seaside Sparrows avoid flooding spatially by placing nests in tall vegetation.

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

INTRODUCTION

Birds should be 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 territory (Marshall and Cooper, 2004) should be preferred over more exposed or poorer 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 on differing constraints on successful nesting among regions. Understanding the determinants of nest site selection, and their subsequent consequences for nesting success, is therefore not straightforward. Nonetheless, when considering vulnerable populations, or species that breed in vulnerable habitats, this information can be critically important since it can guide management activities.

Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*) is the world's only bird species that is found only in salt marshes, and the closely related Seaside Sparrow (*A. maritimus*) is also largely restricted to this habitat (R. Greenberg pers. comm.). Saltmarsh Sharp-tailed Sparrow has been ranked as globally Vulnerable using IUCN Red List criteria (Birdlife International 2004). Partners in Flight (PIF) – an international consortium of organizations that determines avian conservation needs, and facilitates corrective actions, in North America – has estimated that half of the world population breeds in the coastal marshes of southern New England (Dettmers and Rosenberg, 2000) and identified the species 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 found only in large marshes (Benoit and Askins 2002, Shriver et al. 2004) and populations in several regions have been identified as species of conservation concern (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 Society 2002) and are ranked by the US Fish and Wildlife Service as priorities both nationally and regionally (U.S. Fish and Wildlife Service 2002).

Much of the concern about these species centers on the limited extent and perceived vulnerability of saltmarsh habitat. Since salt marshes are located along the coast and at the mouths of large rivers, often in industrial areas, their inhabitants are especially vulnerable to pollution, habitat change due to development, and sea level rise. The small overall area of salt marsh habitat, restricted to a very narrow strip along the coast, exacerbates these problems.

Several studies have shown that both Saltmarsh Sharp-tailed Sparrow and Seaside Sparrow are most likely to be found in habitats dominated by native vegetation, such as *Spartina patens*, *S. alterniflora* and *Juncus gerardi* (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 Sparrow and indicated a preference for deeper thatch (i.e. the depth of the accumulated dead plant material) (Maine: Shriver, 2002), higher elevations (Maine: Shriver 2002; Rhode Island: DiQuinzio et al. 2002), and sites with taller vegetation (Rhode Island: DiQuinzio et al., 2002). Shriver (2002) also has looked for a relationship between habitat (specifically, elevation) and nest success, but found none. 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 site in New York (Post et al., 1983), but tall *S. alterniflora* was chosen preferentially for nesting sites in Massachusetts (Marshall and Reinert, 1990). In contrast, the vegetation surrounding Seaside Sparrow nests in Florida was shorter and less dense than at random points (Post et al., 1983).

Since prior studies have been limited to single marshes, it is unclear whether patterns seen, and especially differences among sites, are representative of the species or due to idiosyncratic differences among studies. Working at multiple sites along the Connecticut coast, we examined nest-site selection in sympatric populations of Saltmarsh Sharp-tailed Sparrow and Seaside Sparrow, and determined whether the variables associated with nest-habitat influenced nesting success.

METHODS

STUDY AREA

The study was conducted at seven sites along the Connecticut coast during the summers of 2002 and 2003. We set up a total of 40 one-hectare square study plots across all sites in which we focused our research activities. 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 USGS topographic maps. If a large, deep channel (> 5 m across) 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, to band birds as part of a larger study of sparrow breeding biology. 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 refind 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 the nest's fate. Nests that were found incidentally outside of plots were also marked and monitored. Nests were considered to have failed due 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. Failure due to flooding always coincided with especially high tides. 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 disappeared from the nest. A nest was considered successful if at least one nestling fledged from it.

HABITAT SAMPLING

Within each plot, we sampled the habitat at nine grid points (the center, the four corners, and the mid-points of each side) and at the site of each nest. We also sampled at nine randomly selected points within each plot to determine whether our grid points produced biased estimates of available habitat. A one-meter quadrat was placed around each sampling point. We measured the height of the vegetation at the corners of the quadrat, and 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 10 x 10 cm sub-quadrats 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

We began our analysis by testing whether there were habitat differences between our two types of non-nest data. We performed analyses of variance (ANOVA), in which plot was treated as a blocking factor, to compare habitat characteristics between quadrats placed at grid points and those placed at random points.

To determine whether birds were selecting nest sites on the basis of habitat characteristics, we used logistic regression to compare habitat between nest and non-nest locations for both sparrow species. 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*. Within each plot, we also compared the elevation between nest sites and non-nest sites using paired *t*-tests. Using the results of our univariate tests, we built an initial multivariate model for each species using only those variables that were significant at $P < 0.25$ (after Hosmer and Lemenshow 2000).

To determine whether there were other, more parsimonious, models that provided an equivalent or better fit to the data, we used a stepwise process of variable elimination. From our initial model, we systematically removed each variable one at a time. If the removal of a variable resulted in a substantially worse fit then we put it back into the model; if it did not worsen the model's fit, then we considered the removed variable to be unnecessary and discarded it. Models were compared by calculating Akaike's Information Criterion (AIC) for each model and determining the difference in AIC values

(Δ_i) compared to the model with the lowest AIC in the set of candidate models (Burnham and Anderson, 2002). All models with $\Delta_i < 2$ were considered to be equally as good as the best model (the one with the lowest AIC) and were retained as plausible models.

After completing this process we took the new set of models and repeated the process of systematically eliminating each variable one at a time from each of them, and then comparing the resulting models using Δ_i as described above. This process continued until we had a set of models from which it was not possible to reduce the number of variables without producing $\Delta_i > 2$ in all reduced models.

In almost 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). In the data set used to compare nest success and failure, vegetation density and the amount of tall *S. alterniflora* were highly correlated ($r = -0.81$) and were entered separately into the models.

For each analysis, we present the likelihood ratio statistic (LRS) and associated P-value for the model with the lowest AIC. Goodness-of-fit for these best-fit models was evaluated using the Hosmer-Lemeshow test (Hosmer and Lemeshow, 2000), where a non-significant 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 the Mayfield method (Mayfield, 1975) to determine daily nest survival rates with variance calculated according to Johnson (1979). We assumed a 22-day nesting period for both species (Greenlaw and Rising, 1994; Post and Greenlaw, 1994). To estimate the date incubation began for nests found with an incomplete clutch, we assumed that females lay one egg a day and determined the number of additional days until the clutch was complete. For nests where hatch date was known, we assumed a 12 day incubation period (Greenlaw and Rising, 1994; Post and Greenlaw, 1994) and counted backwards in time to determine when incubation began. For the remaining 42 cases, when a nest that was found during incubation failed before hatching, we estimated the first date of incubation using the following formula (Martin et al., 1997):

$$\text{First day of incubation} = \text{date found} - \left(\left(\text{incubation period} - \text{number of days observed} \right) \div 2 \right)$$

This equation assumes that, on average, nests are found exactly in the middle of the incubation period. To test this assumption, we used 54 nests for which the first day of incubation was known and determined whether nest discovery dates were biased towards either early or late in the incubation period. The mean discovery date was 5.4 days (SD 3.6) after incubation started, and there was no significant skew to the distribution (skewness = 0.13, $z = 0.35$, $P = 0.73$). Thus we concluded that the assumption of the Martin et al. (1977) equation was reasonable. We compared nest survival estimates between years using a Z-test (Johnson, 1979).

To predict nest fates we used logistic regression following the same procedure described above. Because prior research has shown that flooding is a major source of nest failure in saltmarsh sparrows (Shriver 2002), we conducted two tests for each species. First, we compared habitat variables for successful versus failed nests; second, we determined whether there were differences between successful nests and those that failed due to flooding. For each nest, we also calculated the number of days between the egg-laying date and the nearest full moon tide (when the height of the high tide reaches its maximum) and used analysis of variance to test whether nest fate was related to the timing of the full moon tide. All analyses were performed using SYSTAT 8.0 (SPSS Inc., 1998).

RESULTS

HABITAT CHARACTERISTICS

We measured habitat characteristics in 359 one-meter square quadrats located at grid points and in 360 quadrats located randomly within our 40 study plots. There were no significant differences in relative elevation, vegetation height, thatch depth, or in species composition between random and grid 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; after Cohen, 1988: 290). Random points had higher stem density counts on average (mean difference = 4.3 stems; $P = 0.02$), however, the difference was not statistically significant after adjusting the significance level to control Type I error rates for multiple tests (Bonferroni adjustment: $P_{\text{adj}} = 0.05/9$ comparisons = 0.006). Perhaps, more importantly, a difference of four stems is quite small (12%) relative to the average stem density in plots, and two and a half to six times smaller than the differences in stem density between nest sites and non-nest sites (see Table 1). Thus, it seems unlikely that this difference is large enough to be biologically significant and we pooled the habitat data taken at the grid and random locations.

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

NEST SITE SELECTION

We compared habitat characteristics at 160 Saltmarsh Sharp-tailed Sparrow nest sites to 719 non-nest sites. Univariate analyses indicated taller, denser vegetation, a deeper layer of thatch, and higher elevations at nest sites compared to non-nest sites (Table 1). In addition, *S. patens*, tall *S. alterniflora*, and *J. gerardi* were significantly more common at nest sites compared to non-nest sites, and *Distichlis spicata* was less common. We found no high intervariable correlations ($r > 0.7$) and therefore all potentially important variables (defined as $P < 0.25$) were entered into the initial multivariate model.

Systematically reducing the initial model demonstrated that the removal of vegetation height or percent *Distichlis spicata*, either separately or together, resulted in models that were just as good as the initial model ($\Delta_i < 0.27$ in all cases); removal of any other variable worsened the model (Δ_i ranged from 2.76 with the removal of the percent of *S. patens* to 31.37 with the removal of thatch depth). Similarly, the systematic removal of each remaining variable after vegetation height and percent *Distichlis spicata* had been removed worsened the model (Δ_i ranged from 3.06 to 38.45). Thus, our analysis suggests that the preferred model includes vegetation density, thatch depth, and the relative amounts of *S. patens, S. alterniflora* (both forms), and *J. gerardi* (Table 2).

Habitat measurements at the same 719 non-nest sites were also compared to those at 23 Seaside Sparrow nest sites. Univariate test suggest that these nest sites had taller, less dense, vegetation with a deeper layer of thatch than non-nest 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 proportion of tall *S. alterniflora* than non-nest sites, but less short *S. alterniflora* and *S. patens*. Our best model for the difference between nest sites and non-nest sites included vegetation height, density, and the amount of both forms of *S. alterniflora* (Table 2). Dropping the tall *S. alterniflora* variable resulted in an equally good model ($\Delta_i = 0.71$).

Nest site selection differed between Saltmarsh Sharp-tailed and Seaside Sparrows in several ways. Seaside Sparrows used sites with significantly taller and sparser vegetation. *S. patens* and short form *S. alterniflora* were less common near Seaside Sparrow nests, than at 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).

LINKING HABITAT TO NEST SUCCESS

Of the 167 Saltmarsh Sharp-tailed Sparrow nests found in the two years of this study, 106 were observed for at least one day during incubation and had known outcomes, and thus could be used for Mayfield calculations of survival during the incubation period (Table 3). A total of 87 nests were used for Mayfield calculations during the chick-rearing period (Table 3). Daily nest survival rates for the egg and chick stages combined did not differ significantly between years ($z = 0.53$, $P = 0.60$). Of the 136 nests with known outcomes, 80 (59%) failed to produced fledglings (Table 3). Flooding was the major cause of nest failure, accounting for 60% of all failed nests. Another 31% of failed nests were depredated (Table 3). We also found evidence for partial nest failure; 17 (13%) of the 136 nests 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 (Table 4; $P > 0.19$ in all comparisons). Although successful nests were initiated 4.8 days later in the season on average than failed nests, there was not strong statistical support for a difference between groups (*t*-test: $t_{130} = -1.70$, $P = 0.09$). The number of days between egg-laying and the nearest spring tide, however, differed considerably among nests that were successful, those that were flooded during incubation, and those that flooded during chick-rearing ($F_{2,98} = 7.21$, $P = 0.001$; Fig. 1a). Nests that failed due to flooding during incubation were initiated an average of 2.3 (SD = 9.3) days prior to the spring tide, compared to 0.8 days (SD = 9.3 days) after the spring tide for nests that successfully raised at least one fledgling. Nests that were flooded during chick-rearing were initiated 5.4 (SD = 5.4) days after the spring tide.

Only 15 and 12 Seaside Sparrow nests could be used for Mayfield calculations of nest survival during incubation and chick-rearing respectively (Table 3). Four nests were depredated and three were flooded during incubation, and the fate of one failed nest could not be determined (Table 3). Daily nest survival rates for egg and chick stages combined were not significantly different between years ($z = 0.16$, $P = 0.87$). Seaside Sparrow nest survival was higher than that of Saltmarsh Sharp-tailed Sparrows during the chick stage ($z = 2.95$, $P = 0.003$), but not during the egg stage ($z = 0.38$, $P = 0.70$) or over the nesting period as a whole ($z = 0.93$, $P = 0.36$). No Seaside Sparrow nests were found partially flooded, but one egg went missing in two of the 14 successful nests.

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). The model that best explained nest success included only vegetation height and density, but several other models were only marginally different (Table 6).

In strictly chronological terms, egg-laying date did not affect the fate of Seaside Sparrow nests ($t_{18} = 1.29$, $P = 0.21$), however, successful nests were initiated significantly earlier in relation to the spring tide than nests that failed ($F_{1,18} = 5.59$, $P = 0.03$; Fig. 1b).

DISCUSSION

Both Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows placed their nests non-randomly in the marsh with respect to the habitat variables we measured. Saltmarsh Sharp-tailed Sparrows chose sites where the vegetation was taller and denser than at random locations, where there was a deep layer of thatch, and where the habitat was dominated by *S. patens.* They also showed a preference for sites that were slightly higher in elevation than average.

Studies at two other marshes have also examined nest site selection in Saltmarsh Sharp-tailed Sparrows in detail (DiQuinzio et al. 2002, Shriver 2002). In both cases, nest sites were found at higher elevations than random locations. At Scarborough Marsh in Maine the difference was much larger (~15 cm) than at Galilee, Rhode Island, or at our Connecticut sites (~ 2 cm in both cases), perhaps reflecting the much smaller tidal range in Long Island Sound, compared to the Gulf of Maine. Both studies also provided evidence for the selection of *S. patens*, albeit weaker evidence than that found in our study, and neither study found any relationships between site selection and the abundance of other plant species. In Maine, a relationship with *S. patens* was found when vegetation was sampled at a 10 m scale, but not at a 1 m scale similar to that used in our study (Shriver 2002). In Rhode Island, statistical support for the relationship with *S. patens* was much weaker than in our study (DiQuinzio et al. 2002). These differences could arise through some combination of different sampling techniques, larger sample sizes in our study, or different behavior when sparrows are faced with subtle differences in marsh habitats across the species range. In Maine, vegetation height and density were not sampled, but thatch depth was greater at nest sites than at random locations (Shriver 2002), as in Connecticut. In Rhode Island, nests were found at sites with taller vegetation than at random locations. Moreover, sparrows were found to select sites with significantly taller vegetation and deeper thatch following marsh restoration that resulted in deeper tidal flooding (DiQuinzio et al. 2002), suggesting a facultative response to flooding risk.

Seaside Sparrow nests were placed where the vegetation was very tall, relatively sparse, and dominated by the tall form of *S. alterniflora*, largely to the exclusion of *S. patens*, similar to the findings of studies in Massachusetts (Marshall and Reinert, 1990; Reinert and Mello, 1995). Although both species selected vegetation that was taller than average, Seaside Sparrows used much taller vegetation than Saltmarsh Sharp-tailed Sparrows. The opposite responses to vegetation density found in the two species apparently relates to their respective selection of sites with the less dense, tall form *S. alterniflora* and the more dense *S. patens*.

Although we found that Saltmarsh Sharp-tailed Sparrows selected certain habitat characteristics over others for nesting locations, there was little evidence that vegetation characteristics influenced nest success. This result matched similar analyses from studies elsewhere (DeRagon 1988, Shriver 2002). One explanation for this pattern is that birds chose only to nest in the best possible areas, and that there was insufficient variation among nest sites to find differences. The amount of variation in each habitat characteristic, however, was similar at nest sites and random sites, and the range of situations used for nesting broadly overlapped with what was available (compare SD and ranges in Table 1). Other explanations are that characteristics of the nest itself (e.g., height of the nest, nest concealment) may influence success more than the habitat in which the nest is placed, or that nest construction is modified to compensate for placement in an otherwise vulnerable location.

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 the especially high spring tides, that coincide with the full moon. Saltmarsh Sharp-tailed Sparrows apparently time their breeding so that their nesting period fits within the 28 days between extreme tides (Shriver 2002). Since 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 to date, causing approximately 60% of nest failures in this study, and others (DeRagon, 1988), (Shriver, 2002). One study found that predation was the primary source of nest loss, but the restoration of natural tidal flows at the study site resulted in a shift to match the pattern of the other studies (DiQuinzio et al. 2002).

We found evidence that Seaside Sparrow nests were more successful when placed in taller, less dense vegetation where there was more *S. alterniflora* and less *S. patens* (Table 6). Our multivariate analysis suggests that vegetation height is especially important, since it occurs in 4 of the 6 models that were considered equally good after comparing AIC values. Indeed, the model that included only vegetation height was barely different from the best model, which also included vegetation density. Timing of reproduction was again important to success, but not in the manner we would have predicted given the relationship observed for Saltmarsh Sharp-tailed Sparrows. Although Seaside Sparrows take roughly the same amount of time to raise offspring to fledging age as do Saltmarsh Sharp-tailed Sparrows, the most successful nests were initiated prior to the full moon tide, suggesting that these birds are not timing their nesting cycle to fit between spring tides. Nelson's Sharp-tailed Sparrows also do not synchronize their breeding to match the tidal cycles closely, resulting in significantly reduced nesting success compared to Saltmarsh Sharp-tailed Sparrows (Shriver 2002). Our data suggest that Seaside Sparrows have higher nest survival during the nestling stage than do Saltmarsh Sharp-tailed Sparrows, but overall survival did not differ between the species.

These results suggest that Saltmarsh Sharp-tailed and Seaside Sparrows have evolved two very different strategies for reproducing successfully in salt marshes. Saltmarsh Sharp-tailed Sparrows cope with the challenge of living in an environment that floods regularly by adjusting their reproductive behavior temporally, such that most nesting does not coincide 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, increasing 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 tidal wetlands 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 Sparrow and Seaside Sparrow have 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 mesh with the 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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Figure Legends

Figure 1 The mean ± SE number of days after the last spring tide that female Saltmarsh Sharp-tailed Sparrows (top) and Seaside Sparrows (bottom) 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.

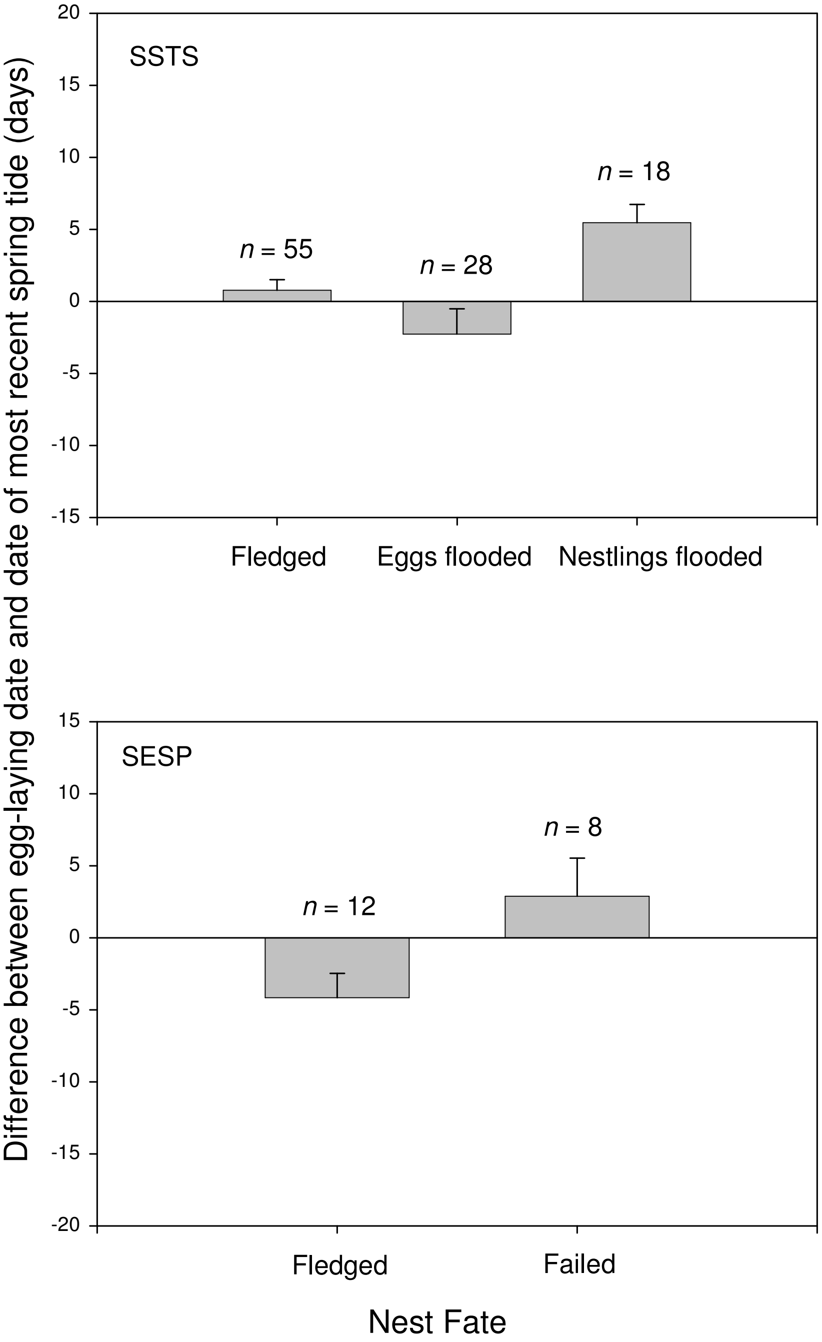
Difference between egg-laying date and date of most recent spring tide (days)
SSTS
20
15
10
5
0
-5
-10
-15
n = 55
n = 28
n = 18
Fledged
Eggs flooded
Nestlings flooded
SESP
15
10
5
0
-5
-10
-15
-20
n = 12
n = 8
Fledged
Failed
Nest Fate

Table 1. Univariate comparisons (mean ± SD, range) of habitat variables at nest sites and non-nest sites for Saltmarsh Sharp-tailed Sparrows and Seaside Sparrows breeding in Connecticut.

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	Saltmarsh Sharp-tailed Sparrow nest sites compared to Seaside Sparrow nest sites
Vegetation height (cm)[a]	39.9 ± 16.4 (0 - 112)	44.9 ± 10.2 (21 - 81)	64.3 ± 16.1 (38 - 97)	$t_{367.0} = 4.90$, $P < 0.001$	$t_{23.5} = 7.15$, $P < 0.001$	$t_{24.6} = 5.62$, $P < 0.001$
Vegetation density (#stems/100cm^2)[a]	37.1 ± 26.3 (0 - 108)	52.7 ± 26.2 (7 - 128)	26.1 ± 20.8 (5 - 71)	$t_{235.8} = 6.88$, $P < 0.001$	$t_{23.3} = -2.48$, $P = 0.02$	$t_{31.8} = 5.62$, $P < 0.001$
Thatch height (cm)[a]	5.5 ± 0.2 (0 - 34)	8.8 ± 0.4 (0 - 22)	9.3 ± 7.8 (0 - 31)	$t_{248.3} = 7.79$, $P < 0.001$	$t_{22.6} = 2.30$, $P = 0.03$	$t_{24.3} = 0.31$, $P = 0.76$
% *Spartina patens*[b]	38.9 ± 40.4 (0 - 100)	54.2 ± 35.2 (0 - 100)	21.2 ± 32.1 (0 - 85)	$U = 69097.0$, $P < 0.001$	$U = 5967.5$, $P = 0.02$	$U = 911.0$, $P < 0.001$
% *S. alterniflora* (short)[b]	20.6 ± 35.1 (0 - 100)	10.4 ± 20.6 (0 - 100)	0.0 (0)	$U = 53890.5$, $P = 0.14$	$U = 5485.5$, $P < 0.01$	$U = 1242.0$, $P < 0.01$
% *S. alterniflora* (tall)[b]	10.9 ± 26.6 (0 - 100)	14.6 ± 26.3 (0 - 100)	47.0 ± 44.7 (0 - 100)	$U = 64716.0$, $P < 0.01$	$U = 12845.5$, $P < 0.001$	$U = 2691.5$, $P < 0.001$
% *Distichlis spicata*[b]	10.0 ± 22.0 (0 - 100)	5.9 ± 14.4 (0 - 80)	7.4 ± 15.7 (0 - 50)	$U = 52224.0$, $P < 0.001$	$U = 7383.0$, $P = 0.30$	$U = 1796.0$, $P = 0.81$
% *Juncus gerardi*[b]	8.8 ± 23.8 (0 - 100)	12.2 ± 25.8 (0 - 100)	14.3 ± 24.7 (0 - 85)	$U = 62161.5$, $P = 0.02$	$U = 9407.0$, $P = 0.08$	$U = 1948.0$, $P = 0.55$
Mean difference in elevation (cm)[c]				2.46 ± 4.96 $t_{34} = -2.93$, $P < 0.01$	0.32 ± 6.35 $t_{10} = 0.16$, $P = 0.87$	3.11 ± 5.76 $t_{9} = -0.10$, $P = 0.12$

[a] *t*-test comparisons with separate variance; [b] Mann Whitney *U* comparisons; [c] The mean difference in elevation between nest sites and non-nest sites, and SESP and SSTS nest sites were calculated for each plot and compared using a paired *t*-test

Table 2. Results of multivariate logistic regression of Saltmarsh Sharp-tailed Sparrow (SSTS) and Seaside Sparrow (SESP) nest occurrence on vegetation structure and composition.

Habitat variable	Coefficient ± SE	Log-likelihood	LRS[a]	*P*
SSTS nest site selection best-fit model		-361.48	104.29	< 0.001
Vegetation density	0.023 ± 0.005		21.86	< 0.001
Thatch depth	0.114 ± 0.020		40.44	< 0.001
% Spartina patens	0.012 ± 0.006		5.06	0.02
% Spartina alterniflora (short form)	0.023 ± 0.006		8.17	< 0.01
% Spartina alterniflora (tall form)	0.018 ± 0.006		18.02	< 0.001
% Juncus gerardi	0.02 ± 0.007		7.89	< 0.01
Hosmer-Lemeshow statistic = 10.58, df = 6, *P* = 0.10				
SESP nest site selection best-fit model		-75.92	46.26	< 0.001
Vegetation height	0.048 ± 0.014		12.34	< 0.001
Vegetation density	0.004 ± 0.013		7.06	< 0.01
Presence of *Spartina alterniflora* (short form)	-11.798 ± 126.819		4.63	0.03
% Spartina alterniflora (tall form)	0.011 ± 0.007		2.71	0.10
Hosmer-Lemeshow statistic = 3.71, df = 3, *P* = 0.30				

[a] Likelihood Ratio Statistic

Table 3. Mayfield estimates of daily nest survival during incubation and chick-rearing periods, overall percent survival, and nest fates for Saltmarsh Sharp-tailed and Seaside Sparrows.

Year	Incubation			Chick-rearing			Overall % survival[b]	Number of failed nests			Total number of nests	
	Daily nest survival ± SE	Number of nests[a]	Observer days	Daily nest survival ± SE	Number of nests[a]	Observer days		Flooding	Predation	Cause of failure unknown	with known outcome	found
Saltmarsh Sharp-tailed Sparrows												
2002	0.920 ± 0.0004	41	212	0.971 ± 0.0001	31	242	30	13	10	3	51	64
2003	0.949 ± 0.0001	65	491	0.927 ± 0.0002	56	343	26	35	15	4	85	96
Seaside Sparrows												
2002	0.900 ± 0.009	2	10	1	4	17	44	0	1	0	6	6
2003	0.933 ± 0.0007	13	90	0.986 ± 0.0002	8	71	38	3	3	1	16	17

[a] Number of nests with at least one observation day and known outcome (fail or succeed); [b] Overall survival = (daily survival during incubation and chick-rearing combined)^{22}

Table 4. Habitat characteristics (mean ± SD) at successful, failed (includes flooded, depredated, and nests where the cause of failure was unknown), and flooded Saltmarsh Sharp-tailed Sparrow nests only. Statistical comparisons between successful and failed nests and flooded versus failed nests are included.

Habitat variable	Successful (n = 54)[a]	Failed (n = 76)[a]	Flooded (n = 45)[a]	Successful vs. Failed	Successful vs. Flooded
Vegetation ht. (cm)[b]	44.2 ± 11.2	45.4 ± 9.8	44.7 ± 9.0	$t_{128} = 0.61$, $P = 0.54$	$t_{97} = 0.24$, $P = 0.81$
Vegetation density (#stems/100cm^2)[b]	53.8 ± 27.6	56.9 ± 26.2	61.2 ± 27.6	$t_{128} = 0.65$, $P = 0.51$	$t_{97} = 1.32$, $P = 0.19$
Thatch ht. (cm)[b]	9.5 ± 5.2	9.2 ± 4.0	9.3 ± 4.1	$t_{128} = -0.28$, $P = 0.78$	$t_{97} = -0.21$, $P = 0.84$
% *Spartina patens*[c]	59.1 ± 4.5	54.0 ± 3.7	56.8 ± 5.1	$U = 1995.0$, $P = 0.70$	$U = 1190.0$, $P = 0.86$
% *Distichlis spicata*[c]	6.5 ± 2.1	5.5 ± 1.4	7.2 ± 2.3	$U = 2118.0$, $P = 0.70$	$U = 1318.0$, $P = 0.37$
% *S. alterniflora* (short)[c]	9.2 ± 2.4	11.0 ± 2.2	7.7 ± 2.2	$U = 2000.5$, $P = 0.76$	$U = 1219.0$, $P = 0.97$
% *S. alterniflora* (tall)[c]	13.9 ± 3.7	13.3 ± 2.6	11.2 ± 3.5	$U = 2031.5$, $P = 0.91$	$U = 1185.0$, $P = 0.80$
% *Juncus gerardi*[c]	8.0 ± 2.7	13.8 ± 2.8	15.2 ± 4.5	$U = 2229.5$, $P = 0.26$	$U = 1329.0$, $P = 0.27$

[a] Vegetation characteristics were not measured at two of the successful nests and four of the failed nests, two of which were flooded; [b] *t*-test comparisons with pooled variance; [c] Mann Whitney *U* comparisons

Table 5. A comparison between the habitat characteristics (mean ± SD) at successful and failed Seaside Sparrow nests.

Habitat variable	Successful (n = 14)	Failed (n = 8)	Successful vs. Failed
Vegetation ht. (cm)[a]	70.3 ± 13.2	53.5 ± 16.8	t_{20} = -2.60, P = 0.02
Vegetation density (#stems/100cm^2)[b]	20.1 ± 17.3	38.2 ± 20.2	U = 78.0, P = 0.06
Thatch ht. (cm)[b]	9.5 ± 9.1	9.1 ± 6.2	U = 55.5, P = 0.97
% *Spartina patens*[b]	10.7 ± 25.9	42.3 ± 34.6	U = 86.0, P = 0.02
% *Distichlis spicata*[b]	5.7 ± 15.0	5.0 ± 9.3	U = 60.0, P = 0.69
% *S. alterniflora* (short)[c]	--	--	--
% *S. alterniflora* (tall)[b]	61.8 ± 44.3	23.8 ± 38.9	U = 24.5, P = 0.03
% *Juncus gerardi*[b]	14.6 ± 26.9	12.5 ± 27.8	U = 54.0, P = 0.86

[a] *t*-test comparisons with pooled variance; [b] Mann Whitney *U* comparisons; [c] No nests sites contained any short *S. alterniflora*

Table 6. Results of multivariate logistic regression of Seaside Sparrow nest success on vegetation structure and composition. We present the best-fit model with the lowest Akaike Information Criterion (AIC) and five alternative models that were only marginally different.

Habitat variable	Coefficient ± SE	Log-likelihood	LRSa	*P*	AIC
Best-fit model		-10.09	7.73	0.02	28.18
Vegetation height	-0.072 ± 0.045		3.34	0.07	
Vegetation density	-0.027 ± 0.034		2.47	0.12	
Hosmer-Lemeshow statistic = 4.04, df = 7, *P* = 0.78					
Alternate model I		-10.37	8.09	0.02	28.75
Vegetation height	-0.061 ± 0.039				
% *Spartina patens*	-0.025 ± 0.019				
Alternate model II		-10.76	7.32	0.03	29.52
Vegetation height	-0.063 ± 0.039				
% *Spartina alterniflora* (tall form)	-0.014 ± 0.014				
Alternate model III		-11.33	6.19	0.01	28.65
Vegetation height	-0.081 ± 0.038				
Alternate model IV		-11.90	5.04	0.03	29.80
% *Spartina patens*	-0.033 ± 0.016				
Alternate model IV		-11.76	4.39	0.04	29.52
Vegetation density	-0.053 ± 0.028				

[a] Likelihood Ratio Statistic

APPENDIX 3

Predictive habitat models for saltmarsh sparrows

VALIDATING PREDICTIVE HABITAT MODELS FOR THE ABUNDANCE AND PRODUCTIVITY OF SALTMARSH-BREEDING SPARROWS

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ABSTRACT

Statistical models used to describe the occurrence and abundance of species need to be tested in order to evaluate their predictive performance. A single data set is commonly used to develop and evaluate a model. Obtaining new data from the population of interest is the less common approach to model validation, but can tell us how well the model will perform under circumstances different from those used to develop the model. We used an information-theoretic approach to develop multiple and logistic regression models that explain variation in abundance of both saltmarsh sharp-tailed and seaside sparrows. The performance of these models was tested both using the original data set, and with data collected from plots that were not used during the model-building procedure. More saltmarsh sharp-tailed sparrows used areas where the vegetation was homogenously tall and where the relative proportion of *Juncus gerardi* was high. The relative abundance of *J. gerardi* was also an important predictor of the number of saltmarsh sharp-tailed sparrow nests, as was vegetation density. Habitat variables, however, could not account for the variation in the number of fledglings produced. Marsh location accounted for more than half of the variation in the number of seaside sparrows, suggesting that landscape characteristics of marshes may be more important than habitat features. Areas of short form *Spartina alterniflora* were avoided by nesting seaside sparrows. The habitat models developed here provide detailed information on the specific habitat features that are selected by sparrows but, despite their statistical significance, do not provide good predictions when applied to novel data.

Keywords: Statistical models; Habitat use; Productivity; Model validation; *Ammodramus*

1. Introduction

A detailed knowledge of a species' habitat needs is often required for the management of viable populations. Statistical models are commonly used to examine species-habitat relationships where the presence or absence of a species (Franco et al., 2000; Karl et al., 2000; Luck, 2002), or its abundance (Maurer, 1986; Latham et al., 1997; Franco et al., 2000), is correlated with particular habitat features. Models that attempt to predict a species' productivity are less common (Heglund, 2002), but are especially important because the best habitat does not necessarily support the greatest number of individuals (Fretwell, 1972; Van Horne, 1983; Vickery et al., 1992; Sutherland, 1996). Ultimately, the identification of species-habitat associations can be used to detect new areas that will support individuals, identify which areas will produce the most offspring, predict the consequences of environmental change, or evaluate the effects of various land-use actions (Scott et al., 2002). Statistically and biologically robust species-habitat models are especially useful for the conservation and management of populations that live in areas vulnerable to human exploitation and alteration.

Before quantitative habitat models can be applied, however, the predictive success of a model must be evaluated to avoid detrimental or misdirected management decisions based on inadequate models. When using a single data set to develop and evaluate a model, jackknife or bootstrap techniques are commonly used for model verification, but these approaches only test the model's internal consistency (Guisan and Zimmermann, 2000). Obtaining new data to compare to model predictions is less common, but can tell us how well the model will perform under circumstances different from those used during its development (Fielding and Haworth, 1995; Guisan and Zimmermann, 2000). Given the number of habitat models that have been found to have poor predictive performance when tested (Maurer, 1986; Morrison et al., 1987; Karl et al., 2000; Dettmers et al., 2002; Luck, 2002), the importance of model validation cannot be overestimated.

The purpose of our study was to determine how saltmarsh birds respond to habitat variation and to use this information to develop predictive models that could provide practical information for salt marsh bird conservation. Saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*) is the world's only salt marsh obligate bird species (R. Greenberg, personal communication). The breeding range extends along the U.S. Atlantic coast from Maine to Virginia (Greenlaw and Rising, 1994), and it has been estimated that half of the world population breeds in the coastal marshes of southern New England (Dettmers and Rosenberg, 2000). Throughout its range, this sparrow is nonterritorial and promiscuous; males occupy large, overlapping home ranges in which they search for receptive females for copulations (Greenlaw and Rising, 1994). There are no documented pair bonds and the female provides all parental care. The closely related seaside sparrow (*A. maritimus*) is also largely restricted to salt marsh habitat and breeds from New Hampshire to northeastern Florida, as well as along the north coast of the Gulf of Mexico (Post and Greenlaw, 1994). This sparrow is monogamous across its range, defends nesting territories, and both the male and female feed the young (Post and Greenlaw, 1994).

Both species are on the National Audubon Society's WatchList of high conservation concern species (National Audubon Society, 2002) and are ranked by the US Fish and Wildlife Service as priorities both nationally and regionally (U.S. Fish and Wildlife

Service, 2002). Saltmarsh sharp-tailed sparrow is considered globally vulnerable using IUCN Red List criteria (BirdLife International, 2004), and although more widespread than saltmarsh sharp-tailed sparrows, seaside sparrows are found only in large marshes (Benoit and Askins, 2002; Shriver et al., 2004) and populations in several regions have been identified as species of conservation concern (Post and Greenlaw, 1994; Rich et al., 2004).

The abundance of both sparrow species varies considerably both within and among marshes (Benoit and Askins, 2002; Shriver et al., 2004). Past studies of Connecticut's coastal marsh birds have provided information on broad species distributions and correlative information about the general habitat needs of these species (Marshall and Reinert, 1990; Reinert and Mello, 1995; Brawley et al., 1998; Benoit and Askins, 1999; DiQuinzio et al., 2002; Shriver, 2002; Shriver et al., 2004), but currently we lack the detailed information on population densities and within-marsh habitat selection that are needed to prioritize and manage sites for the protection of marsh birds. Evaluating the productivity of populations in key marshes is essential to determining the health of these populations, and understanding the underlying environmental factors that influence reproductive success, breeding density, and species occurrence is fundamental to effective management.

Our objectives with this study were to determine (1) whether sparrow abundance, probability of occurrence, and productivity vary as a function of habitat, and (2) whether sparrow abundance and productivity can be predicted based on habitat associations, especially when extrapolating beyond the main study area. To do this we used an information-theoretic approach to identify bird-habitat relations for both the saltmarsh sharp-tailed and seaside sparrow at 30 locations in Connecticut, and tested the generality of the resulting models at 10 additional locations.

2. Methods

2.1. Study area

The study was conducted at seven marshes along the coast of Connecticut ranging in size from 42 to 302 ha (Figure 1). We set up a total of 40 one-hectare study plots across all sites in which we focused our research activities. Plot locations at each site were chosen by randomly selecting grid points placed within the marsh boundaries on USGS topographic maps. Areas totally dominated by common reed (*Phragmites australis*), an introduced plant in which our study species do not nest (Benoit and Askins, 1999), were excluded from the area in which our plots were placed. If a large, deep channel (> 5 m across) 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.

2.2. Bird sampling

Each plot was visited five times at approximately two-week intervals in order to estimate sparrow population sizes. On each visit we set up an array of six mist nets across the plot in order to capture birds present within the plot's boundaries. The location of nets was changed each visit to maximize coverage within each plot. We flushed birds into the nets by waking along channel edges and through the vegetation towards the nets. Mist-netting occurred in the mornings and each visit lasted approximately four hours. All birds captured were fitted with a standard USFWS metal leg band and up to three plastic color bands, to allow for individual recognition. We determined sex of adult birds by the presence of a brood patch (females) or an enlarged cloacal protuberance (males), and we distinguished juvenile birds from adults by plumage features and by the extent of skull ossification.

2.3. Nest monitoring

On each date that banding occurred in a plot, we also conducted a thorough search of the plot to look for nests. In addition to these intensive searches, we looked for nests every three to five days when checking 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 refind the nest easily, but reduced the risk of identifying the location to predators. Nests were monitored every three to five days in order to determine nest fate and, if the nest was successful, the number of fledglings produced.

2.4. Habitat sampling

Within each plot, we sampled the habitat at nine grid points (the center, the four corners, and the mid-points of each side), and at nine randomly selected points. 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 depth of the accumulated dead plant material, the "thatch depth", in 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 10 x 10 cm sub-quadrats within each quadrat to estimate vegetation density. Habitat sampling occurred between mid-July and mid-August in both years. Habitat variables were not significantly different between grid and random points (Gjerdrum et al., submitted manuscript) and we therefore combined the sampling points for all analyses. We used a GPS to locate the center of each plot, and determined the distance from the center of each plot to the nearest marsh edge using Arcview GIS 3.2 (Environmental Systems Research Institute, Inc.) and scanned USGS Topographic Quadrangle Map Images (CT State Plane 1927).

2.5. Statistical analyses

2.5.1. Model building

Data collected from 30 plots across five marsh sites (East River Marsh, Guilford; Hammonasset State Park, Madison; McKinney National Wildlife Refuge, Westbrook; Great Island Wildlife Management Area, Old Lyme; and Barn Island Wildlife Management Area, Stonington; Figure 1) were used to develop the habitat models. We chose these sites as they were known to have high densities of saltmarsh sparrows during the breeding season (Lori Benoit, unpublished data). To validate the models, we collected new data from an additional 10 plots, six from sites used for model building (two plots each in East River Marsh, Hammonasset State Park, and Great Island Wildlife

Management Area) and four from new marsh sites (Hammock River Marsh, Clinton and Black Hall River Marsh, Old Lyme; Figure 1).

We used four measures of sparrow abundance in a plot as dependent variables in our analyses for saltmarsh sharp-tailed sparrows: (1) the total number of birds captured over the course of a breeding season, (2) the number of females captured, (3) the number of nests found, and (4) the number of young birds fledged from those nests. We included a separate analysis of the number of females because males are nonterritorial, polygynous, and provide little parental care (Greenlaw and Rising, 1994), meaning that their abundance in an area may bear little relationship to the amount of reproductive activity in the area. The number of females on a particular plot, therefore, may better reflect the productivity of the site than the total number of birds, since females occupy small home ranges within which they nest and provide all parental care (Greenlaw and Rising, 1994). The number of nests and the number of fledglings produced provide direct measures of where females choose to nest and where they are most successful.

The predictor variables of interest included the distance from the center of the plot to the nearest point on the edge of the marsh, vegetation height, vegetation density, thatch depth, and percent cover for the five most common vegetation types; *Spartina patens*, short form *S. alterniflora* (< 50 cm), tall form *S. alterniflora* (> 50 cm), *Distichlis spicata*, and *Juncus gerardi*. For each plot, we used the mean value for each habitat variable across the 18 sampling points. The standard deviations of vegetation height and vegetation density were also included to test whether the structural heterogeneity of the habitat was important.

We first made univariate comparisons (Pearson or Spearman rank correlation coefficients, as appropriate) of predictor variables and sparrow abundance, and included all variables with $P > 0.25$ in an initial multivariate model (Hosmer and Lemeshow, 2000). To account for any site effects on sparrow abundance, or seasonal variation in the structure or composition of the habitat, we evaluated the effects of plot location (i.e., the marsh in which the plot lay) and habitat sampling date on each of the predictor variables. Plot location had a strong significant effect on the habitat variables measured ($P < 0.0001$ in all comparisons), but the date on which we measured the vegetation did not ($P > 0.05$ in all comparisons). Therefore, we included plot location, but not habitat sampling date, in the initial multivariate model for each measure of sparrow abundance.

From our initial model, we systematically removed each variable one at a time. The set of reduced models were compared by calculating Akaike's Information Criterion for small sample sizes (AIC_c) for each model and determining the difference in AIC_c values (Δ_i) compared to the model with the lowest AIC_c in the set of candidate models (Burnham and Anderson, 2002). All models with $\Delta_i < 2$ were considered to be equally as good as the best model (the one with the lowest AIC_c) and were retained as plausible models. We then took the reduced set of models and repeated the process of systematically eliminating each variable one at a time from each of them to create a new set of candidate models, which were then compared to each other using Δ_i as described above. This process continued until we had a set of models from which it was not possible to reduce the number of variables without producing $\Delta_i > 2$ in all reduced models (i.e. all reduced models were significantly worse than the current set).

For seaside sparrows, we defined our first dependent variable as the total number of birds that used a plot over the course of a breeding season. We did not separately analyze the number of females banded because we had no *a priori* reason to expect that this measure would provide information different from the total number of birds in this territorial and socially monogamous species. All variables with $P > 0.25$ in univariate comparisons between predictor variables and the number of sparrows were included in an initial multivariate model. We used the same procedure described for saltmarsh sharp-tailed sparrows to determine which predictor variables to include in the final multivariate model describing the variation in the number of sparrows captured.

Due to the small number of plots in which seaside sparrow nests were found, we transformed data on the number of seaside sparrow nests in a plot to reflect presence/absence and used logistic regression to evaluate nest-habitat associations. Wherever nests were found, fledglings were produced, so we did not separately analyze the relationship between habitat and the presence of fledglings as this analysis would have been identical to that for the presence of nests. For the logistic regressions we used the same model-building strategy that we used for our linear regression models. To determine the significance of the best-fit model (i.e. the model with the lowest $\mathrm{AIC_c}$), we calculated the likelihood ratio statistic (LRS) and associated *P*-value. Goodness-of-fit was evaluated using the Hosmer-Lemeshow test, where a non-significant 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 and report its associated statistic, the LRS. We also report the Akaike weights (w) for all selected models as a measure of the relative likelihood of the selected model given the data and the set of models evaluated (Burnham and Anderson, 2002).

We used SYSTAT 8.0 (SPSS Inc. 1999) to develop all abundance and presence/absence models (GLM, multiple and logistic regressions). To meet the assumptions of multiple regression, we first transformed several variables to reduce skewness, reduce the number of outliers, and improve the normality, linearity, and homoscedasticity of residuals (Tabachnick and Fidell, 2001). Logarithmic transformations ($\log_{10}(y + 1)$) were used for the distance to the marsh edge, percent cover of *Distichlis spicata*, percent cover of tall form *Spartina alterniflora*, and total number of seaside sparrows captured. We used square-root transformations for the number of saltmarsh sharp-tailed sparrow nests and fledglings produced. No transformation improved the distribution for percent cover of *Juncus gerardi* (skewness: 1.51 ± 0.43; kurtosis: 0.98 ± 0.83) and so these data were not transformed. We did not transform any of the predictor variables for the logistic regression as this procedure makes no assumptions about their distributions (Hosmer and Lemeshow, 2000).

2.5.2. Testing model predictions

We estimated the validity of the four final model equations resulting from the model-building procedure for saltmarsh sharp-tailed sparrows in two ways. First, we used a jackknife approach in which we sequentially, one plot at a time, removed one of the 30 plots from the data set, estimated the model coefficients with the remaining data, and then obtained a predicted value for the plot that had been dropped. This process was repeated for each plot, and the predicted values were compared to observed values. Second, we used our final models to predict sparrow abundance at 10 validation plots that were not used during the model-building procedure, and again compared the predicted sparrow abundance to the observed values obtained from those plots. For both the jackknife and cross-validation approaches, we examined the fit between the observed and predicted values with paired *t*-tests for which a significant value indicates a bad fit (i.e., rejection of the null hypothesis that the two groups are equal). We also measured the strength of the association between the observed and predicted values using simple correlation coefficients. We used the same two approaches to test model performance for the number of seaside sparrows captured.

To assess the prediction performance of the best-fit logistic regression model describing the presence/absence of seaside sparrow nests, we compared the distribution of predicted outcomes to actual observations to determine the proportion of cases that were classified correctly. We also examined the 'success index', which measures the gain the model shows over a purely random model (SPSS Inc., 1999). We then applied the best-fit regression model to our validation data set to determine its prediction success when applied to the new data.

3. Results

3.1. Sparrow abundance

In 2002 and 2003 combined, we captured a total of 584 adult saltmarsh sharp-tailed sparrows of which 161 (28%) were females, and 79 seaside sparrows of which 27 (34%) were females. In addition, we monitored 89 saltmarsh sharp-tailed sparrow nests, which produced 90 fledglings, and 6 seaside sparrow nests, which produced 13 fledglings. Mean numbers of birds captured across plots are summarized in Table 1.

3.2. Habitat characteristics

Study plots were located between 40 m and 940 m from the edge of the marsh (Table 1). We measured habitat characteristics in 540 one-meter square quadrats at our 30 study plots and found that the vegetation was dominated by *Spartina patens*, followed by short form *S. alterniflora*, *Distichlis spicata*, *Juncus gerardi*, and tall form *S. alterniflora* (Table 1). Interspersed were small amounts of the herbaceous *Limonium carolinianum*, *Salicornia europaea* and *Gerardia maritima*. The only high ($r > 0.7$) intervariable correlation was found between vegetation density and percent cover of *S. patens* (Pearson's correlation, $r = 0.71$, $n = 30$).

3.3. Linking habitat to sparrow abundance

3.3.1. Saltmarsh sharp-tailed sparrow

Univariate analyses suggested that more saltmarsh sharp-tailed sparrows were captured in plots with taller vegetation, a deeper layer of thatch, a greater proportion of *J. gerardi*, but with less short form *S. alterniflora* (Table 2). We found no high intervariable correlations ($r > 0.7$) and therefore all potentially important variables (defined as $P < 0.25$; Table 2) were entered into the initial multivariate model in addition to plot location.

Our best model describing the number of saltmarsh sharp-tailed sparrows captured in a plot included both the mean and standard deviation of vegetation height, and the proportion of the vegetation that was *J. gerardi* (Table 3a). This model was highly significant and explained 48% of the variation. No other models were considered to be equivalent as they all produced $\Delta_i > 2$.

We used the same procedure to find a model that best described the number of female saltmarsh sharp-tailed sparrows captured. Our best model included the same three variables as that for the total number of saltmarsh sharp-tailed sparrows captured: mean vegetation height, standard deviation of vegetation height, and percent *J. gerardi* (Table 3b). This model was significant and explained 39% of the variation in female saltmarsh sharp-tailed sparrow abundance. No other models were considered equivalent.

Our best model describing the (square root) number of saltmarsh sharp-tailed sparrow nests again included the proportion of the vegetation that was *J. gerardi*, this time in combination with the mean vegetation density (Table 3c). This model, however, could not be distinguished from four alternative models ($0.18 < \Delta_i < 1.19$). Percent *J. gerardi* remained in four of the five models, mean vegetation density in two, and the (log) distance to the marsh edge and the standard deviation of vegetation density were each in one of the alternate models (Table 4).

Although we were able to develop significant models for three of our measures of sparrow abundance (Table 3a-c), none of the habitat variables that we measured could account for the variation in the (square root) number of fledglings produced (Table 3d). Our best model included just the proportion of the vegetation that was (log) tall form *S. alterniflora*, but the model was not significant and explained only 7% of the variation in the number of fledglings produced.

3.3.2. Seaside sparrow

Variation in seaside sparrow abundance could best be accounted for by either plot location or vegetation height, or by using both variables together (Table 4). Our best-fit model included only plot location ($F_{4,25} = 9.80$, $P < 0.0001$, AIC $w = 0.42$), which explained 55% of the variation in the number of birds captured. This model could not be distinguished from a model that included both plot location and mean vegetation height ($\Delta_i = 1.18$), or just mean vegetation height ($\Delta_i = 1.80$). Our best-fit logistic regression model used to describe the presence of seaside sparrow nests included only the relative abundance of short form *S. alterniflora* (LRS = 6.43, $P = 0.01$, AIC $w = 0.26$; Hosmer-Lemenshow statistic = 3.65, df = 3, $P = 0.30$), but adding the standard deviation of vegetation density did not significantly worsen the model ($\Delta_i = 1.18$; Table 4). Short form *S. alterniflora* was significantly ($t_{28} = 2.44$, $P = 0.02$) less abundant in plots where seaside sparrow nests were present (mean ± SD: 7.3 ± 10.1%) compared to those where they were absent (25.0 ± 15.4%).

3.4. Testing model predictions

3.4.1. Saltmarsh sharp-tailed sparrow

Despite the highly significant habitat models developed to describe saltmarsh sharp-tailed sparrow abundance, tests of these models revealed very mixed prediction capabilities. Overall, we found that there was relatively good internal consistency, especially for models that estimate the numbers of birds, but that the models were poor at predicting conditions at new sites (Table 5). All four paired *t*-tests on jackknifed data produced predicted values that did not differ consistently from the observed values, and for both the total number of birds and the total number of females there was a significant correlation between the predicted and observed numbers (Table 5). In our cross-validation tests we found no support for our predictions of the total number of birds. For the remaining three abundance variables there was no difference between observed and predicted values in paired *t*-tests, but there was also no significant correlation between these numbers (Table 5).

3.4.2. Seaside sparrow

We did not test the performance of the model describing variation in the number of seaside sparrows captured in a plot because our best model contained no habitat variables. Using data from the model-building data set to test the internal consistency of our model for the occurrence of seaside sparrow nests, we found that the model correctly predicted 87% of sites where nests were not found but only 35% of sites with nests (Table 6). The overall correct classification rate was 78%, but the model produced only minimal gains over the random expectation (Table 6). When applied to the validation data set, the model correctly predicted 73% of the sites where nests were not found and 37% of the nesting sites for an overall correct prediction rate of 62% (Table 6). Again, however, the model made only minimal gains over the random model (Table 6).

4. Discussion

Habitat modeling serves two general purposes of relevance to conservation biologists. First, the development of statistical models that relate habitat features to abundance, or to demographic measures, can provide important information about a species' needs and thereby act as a guide to management and habitat protection. Second, if models are good enough to make accurate predictions about habitat use, they can be used to provide short cuts to the identification of good habitat and to forecast the consequences of future habitat changes.

Overall, our data indicate that more saltmarsh sharp-tailed sparrows occur where the vegetation was homogenously tall and where the relative proportion of *J. gerardi* was high. The amount of *J. gerardi* was also an important predictor of the number of saltmarsh sharp-tailed sparrow nests, as was vegetation density. These patterns make sense because vegetation that is taller and denser than average is selected for nesting (Gjerdrum et al. submitted manuscript), and may provide increased cover from predators or a refuge from the flooding tides that inundate the salt marsh twice a day. *J. gerardi* has a low tolerance for high soil salinity and grows in high marsh habitat with minimum exposure to tidal water (Niering and Warren, 1980). The relative abundance of *J. gerardi*, therefore, is probably a good indicator of the areas of marsh where the risk of nest flooding is lowest.

Other studies have demonstrated a positive association between saltmarsh sharp-tailed sparrow abundance and the presence of *S. patens* (Reinert and Mello, 1995; Brawley et al., 1998), another high marsh species. In our study, *S. patens* was present, and common, on all of our plots (see Table 1) and there may have been insufficient variation among plots to detect this relationship. Since *S. patens* is ubiquitous in high marsh, we propose that the less common *J. gerardi* may be a better indicator of the very best sparrow habitat in that it provides the resolution to distinguish among areas of high marsh that differ in their propensity for flooding. In general, the presence of native vegetation, which includes *J. gerardi* and *S. patens*, has been shown to be favored by saltmarsh sharp-tailed sparrows elsewhere in their range (Burger et al., 1982; Shriver et al., 2004).

Previous studies have shown that seaside sparrows and other saltmarsh birds are vulnerable to habitat fragmentation and are absent from small marshes (Benoit and Askins, 2002; Shriver et al., 2004). The size of the marsh in which a plot lies, therefore, may explain why location is such an important predictor of seaside sparrow abundance in our study. If this is the case, then our results would suggest that marsh size, and perhaps associated landscape features, overwhelm habitat features in their effect on seaside sparrow abundance. The highest densities of nesting seaside sparrows, however, were found at a relatively small marsh (Hammock River, Figure 1), suggesting that the relationship between marsh size and abundance might not be as simple as it may seem. The alternative models produced by our analysis also suggest another explanation for the species' occurrence pattern, indicating that the presence of tall vegetation might be an equally good indicator of seaside sparrow abundance. Very tall vegetation is preferred for nesting and nests are most successful when placed in tall vegetation (Gjerdrum et al. submitted manuscript). It is possible, therefore, that the area of tall vegetation within a marsh is more important than the marsh size *per se*, and that this relationship accounts for discrepancies in the area-abundance pattern. Short *S. alterniflora* was presumably avoided by nesting seaside sparrows because it occurs at relatively low elevations in the marsh, and is not tall enough for sparrows to build nests that can escape tidal flooding.

Although our results show clear relationships between habitat features and several of our sparrow abundance measures, with highly significant relationships and up to 55% of the variance explained, the predictive performance of the models was generally not very good. The habitat models developed for the total number of saltmarsh sharp-tailed sparrows captured and the total number of females caught appeared robust when applied to the original data set, but abundance was overestimated when applied to data from new sites (Figure 2). Similarly, the model used to describe the number of saltmarsh sharp-tailed sparrow nests, although significant, did not perform well when applied to either the original or validation data sets, underestimating the number of nests that occurred on each plot.

Poor predictions might mean that we simply did not identify and measure important habitat variables, or it could mean that habitat selection is inherently far from perfect in these sparrows. A third possibility, however, is that habitat selection alone is not sufficient to explain species distributions. That behavior and social interactions can influence settlement patterns is well established (e.g., Fretwell, 1972). Territoriality can depress abundance below expected levels in high quality habitat. High site fidelity, such as is found in both our study species (Greenlaw and Rising, 1994; DiQuinzio et al., 2002) can result in birds continuing to use sites even after habitat quality has declined (Weins et al., 1986). Conspecific attraction also could be important as it can both cause absences from apparently suitable habitat, and higher than expected numbers in areas where birds do choose to settle. We suspect that behavior may be especially important for saltmarsh sharp-tailed sparrows, because of their atypical social system. Saltmarsh sharp-tailed sparrow spacing behavior has not been studied in detail, however, nests are often clustered (species have been described as "colonial": Murray, 1969) in ways that are not apparently related to habitat conditions (personal observations).

Social behavior is not the only thing that might be missing from our distribution models. Landscape characteristics have been identified as important influences on the distribution of many species (Freemark et al., 1995), and we know that marsh size can have a significant effect on saltmarsh sparrow occurrence and abundance (Benoit and Askins, 2002; Shriver et al., 2004). Our current analysis has focused primarily on structural characteristics of the environment, but clearly there are other things that could influence where birds spend their time. In particular the distribution of food might be important, and we have initiated field work to test this idea.

Combining data collected at the scales of individual birds, study plots, and entire marshes, is difficult using standard regression methods because the level of replication differs among scales. This problem could be overcome through the use of hierarchical models that account for the nested structure of the data collection and the spatial behavior of individuals (e.g., Cushman and McGarigal, 2004; Gelfand et al., in press; Latimer et al., in press), and thereby accounting better for the complex manner in which birds make decisions about where to settle. For field workers, the challenge with implementing such models will be ensuring adequate replication at the highest hierarchical level.

Habitat models, such as those developed here, have proven useful for understanding and describing the distribution of many different species (Scott et al., 2002). For instance, our study provides detailed information on the specific habitat features found in areas of high saltmarsh that are selected by sparrows and thus identifies likely indicators of good quality high marsh. For applied questions, the utility of habitat models will be greatest when they can be used predicatively (Rushton et al., 2004), and thus their ability to make clear predictions must be tested. The use of two independent data sets, one for developing and the other for validating the model, is the best method to evaluate the model's generality (Fielding and Haworth, 1995; Guisan and Zimmermann, 2000; Luck, 2002; Vaughan and Ormerod, 2003), but is not frequently used. Although perhaps counterintuitive, it is clear from our results, and those of others (e.g., Weins, 2002), that even highly significant models with good internal consistency may not provide good predictions when applied to a broader set of situations than were used to collect the initial data. Overcoming this problem and producing better models is not an insurmountable problem, although it will likely require combining different types of data and integrating habitat selection behaviors that occur at different scales.

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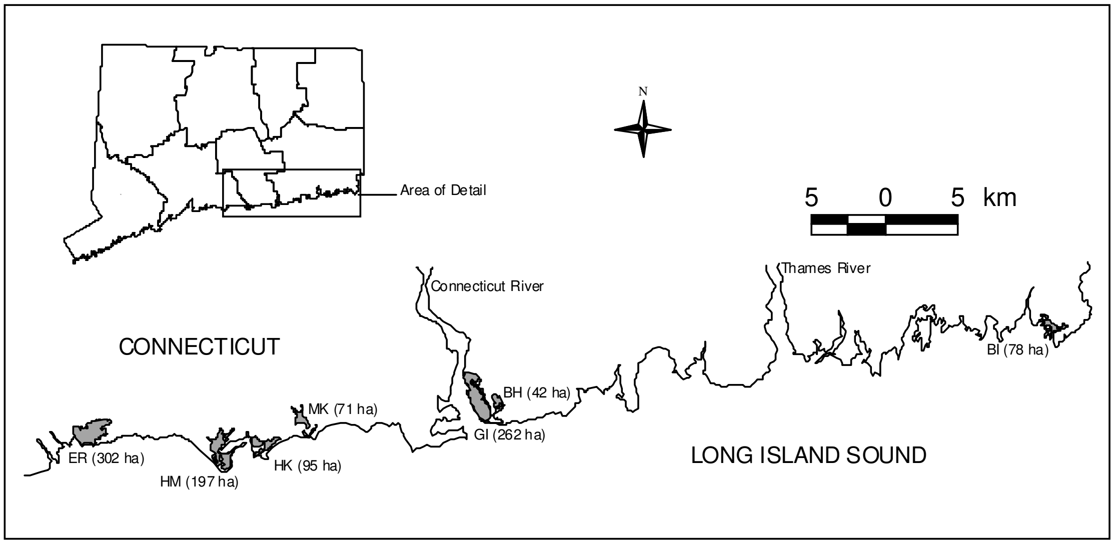
Figure legends

Figure 1. Location of saltmarsh study sites in Connecticut during 2002 and 2003. ER = East River Marsh, Guilford (10 plots); HM = Hammonasset State Park, Madison (8 plots); HK = Hammock River Marsh, Clinton (2 plots); MK = McKinney National Wildlife Refuge, Westbrook (5 plots); GI = Great Island Wildlife Management Area, Old Lyme (8 plots); BH = Black Hall River Marsh, Old Lyme (2 plots); BI = Barn Island Wildlife Management Area, Stonington (5 plots).

Figure 2. Comparison of observed and predicted Saltmarsh Sharp-tailed Sparrow abundance indices based on jackknife and cross-validation procedures. Solid line indicates line of best fit where all predictions are equal to their associated observations. Open symbols indicate the 30 plots used in the model-building data set and solid symbols indicate the 10 validation plots. Squares distinguish the four plots that were located at marsh locations not used for model building.


Area of Detail
N
5 0 5 km
Connecticut River
Thames River
CONNECTICUT
BH (42 ha)
MK (71 ha)
GI (262 ha)
BI (78 ha)
ER (302 ha)
HM (197 ha)
HK (95 ha)
LONG ISLAND SOUND

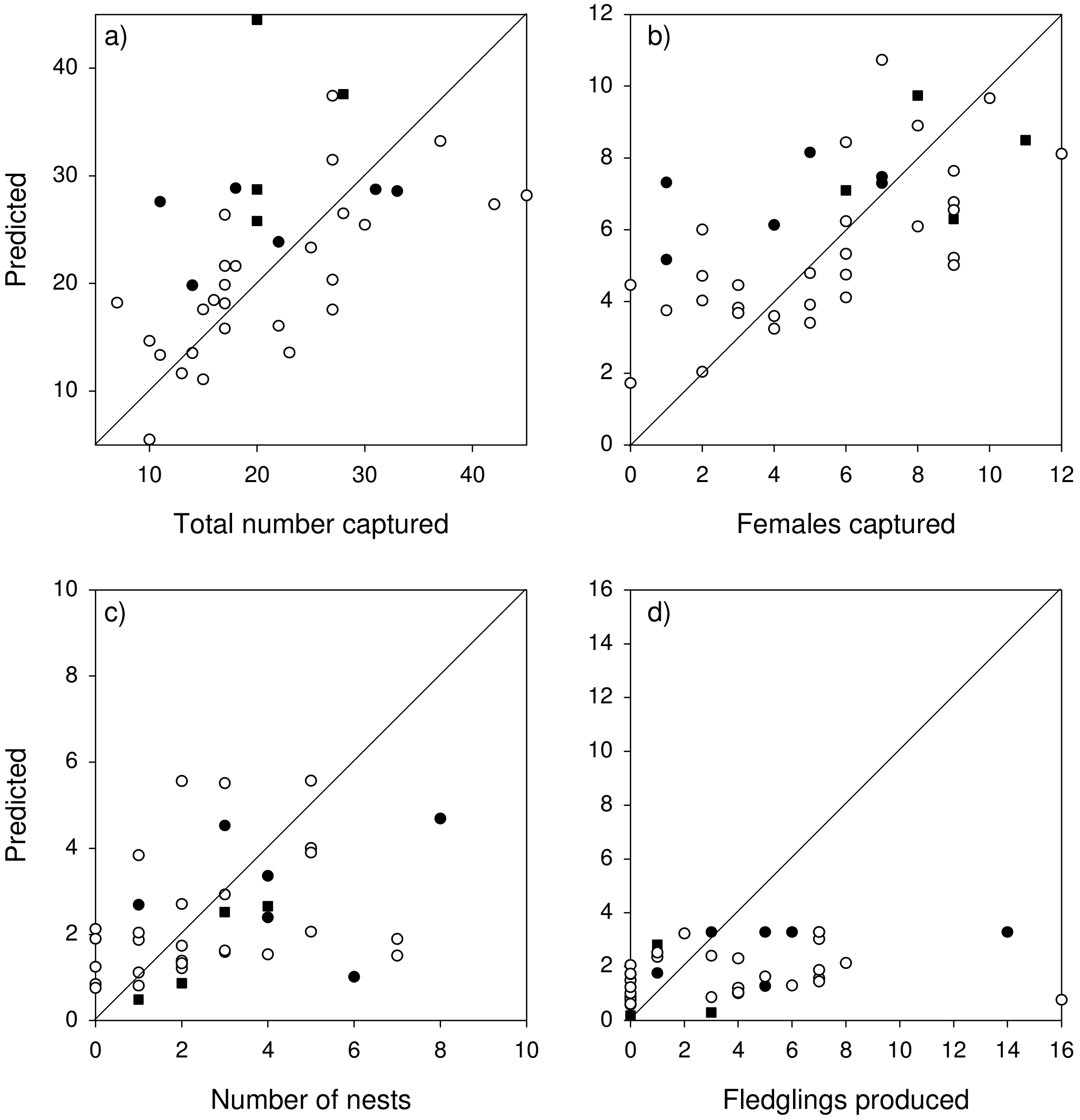

a)
b)
c)
d)
Predicted
Predicted
Total number captured
Females captured
Number of nests
Fledglings produced
10
20
30
40
0
2
4
6
8
10
12
14
16

Table 1. Mean, standard deviation and range of sparrow abundance measures and habitat variables across 30 one-hectare plots in Connecticut.

Variable	Mean (SD)	Range
Saltmarsh Sharp-tailed Sparrow		
Number captured	21.9 (10.8)	4 - 47
Females captured	5.8 (3.3)	0 - 12
Nests	3.0 (2.8)	0 - 11
Fledglings produced	3.0 (3.9)	0 - 19
Seaside Sparrow		
Total captured	2.6 (2.1)	0 - 7
Nests monitored	0.2 (0.5)	0 - 2
Distance to marsh edge (m)	265.3 (212.7)	40 – 940
Vegetation height (cm)	37.8 (7.4)	22.5 - 53.3
Vegetation density (# stems/100 cm^2)	36.7 (11.4)	15.8 - 61.2
Thatch height (cm)	5.0 (2.1)	1.1 - 8.8
Frequency of cover types (%)		
Spartina patens	37.6 (17.8)	5.8 - 69.8
short *S. alterniflora*	22.0 (16.0)	0 - 55.6
Distichlis spicata	10.4 (12.6)	0 - 52.5
Juncus gerardi	8.7 (13.3)	0 - 41.3
tall *S. alterniflora*	8.5 (8.7)	0 - 31.1

Table 2. Correlations between habitat variables and measures of saltmarsh sharp-tailed sparrow abundance. Only those correlations with $P < 0.25$ are listed.

Habitat variable	Correlation coefficient	*P*
a) Total captured		
(log) Distance to marsh edge[a]	0.32	0.09
Vegetation height[a]	0.56	0.001
SD Vegetation height[a]	-0.35	0.06
Vegetation density	0.22	0.24
Thatch depth[a]	0.49	0.006
% *Spartina alterniflora* (short)[a]	-0.49	0.006
% *Juncus gerardi*[b]	0.54	0.002
b) Females captured		
Vegetation height[a]	0.43	0.02
SD Vegetation height[a]	-0.32	0.08
Vegetation density	0.24	0.21
Thatch depth[a]	0.29	0.12
% *Spartina alterniflora* (short)[a]	-0.35	0.06
% *Juncus gerardi*[b]	0.49	0.006
c) (square root) Nests		
(log) Distance to marsh edge[a]	0.31	0.09
Vegetation density[a]	0.39	0.04
SD Vegetation density[a]	0.28	0.14
% *Spartina alterniflora* (short)[a]	-0.25	0.18
% *Juncus gerardi*[b]	0.47	0.01
d) (square root) Fledglings		
(log) % *Spartina alterniflora* (tall)[a]	-0.26	0.16

[a] Pearson's correlation coefficient; [b] Spearman's Rank correlation coefficient.

Table 3. Results of multivariate linear regression analyses of habitat characteristics on four measures of saltmarsh sharp-tailed sparrow abundance.

Habitat Variable	Std. Coefficient ± SE	t	P	AIC$_c$ w
a) Total captured				0.24
Vegetation height	0.48 ± 0.21	3.32	0.003	
SD Vegetation height	-0.33 ± 0.26	-2.41	0.02	
% *Juncus gerardi*	0.30 ± 0.12	2.06	0.05	
$F_{3,26} = 9.90$, $P = 0.0002$, R^2adj = 0.48				
b) Females captured				0.42
Vegetation height	0.30 ± 0.07	1.96	0.06	
SD Vegetation height	-0.28 ± 0.09	-1.90	0.07	
% *Juncus gerardi*	0.42 ± 0.04	2.67	0.01	
$F_{3,26} = 7.30$, $P = 0.001$, R^2adj = 0.39				
c) (square root) Nests				0.11
Vegetation density	0.29 ± 0.01	1.64	0.11	
% *Juncus gerardi*	0.31 ± 0.01	1.77	0.09	
$F_{2,27} = 4.21$, $P = 0.03$, R^2adj = 0.18				
d) (square root) Fledglings				0.74
(log) % *Spartina alterniflora* (tall)	-0.31 ± 0.53	-1.42	0.17	
$F_{1,28} = 2.02$, $P = 0.17$, R^2adj = 0.07				

Table 4. Summary of important habitat variables describing variation in Saltmarsh Sharp-tailed Sparrow abundance. Stars indicate variables included in the overall best multivariate model (i.e. lowest AIC_c). Habitat variables included in any alternate models ($\Delta_i < 2.00$) are grouped by common letters.

Habitat Variable	Saltmarsh Sharp-tailed Sparrow				Seaside Sparrow	
	Total captured	Females captured	Nests	Fledglings	Total captured	Nests
Plot location					☆ b	
Distance to edge			e			
Vegetation height	☆	☆			b c	
SD vegetation height	☆	☆				
Vegetation density			☆ d			
SD vegetation density			c			b
Thatch depth						
% *S. patens*						
% *D. spicata*						
% *S. alterniflora* (short)						☆ b
% *S. alterniflora* (tall)				☆		
% *J. gerardi*	☆	☆	☆ b c e			

Table 5. Summary of results for saltmarsh sharp-tailed sparrow model validation using jackknife and cross-validation approaches. No difference between observed and predicted values in paried t-tests and a significant correlation between observed and predicted values indicate that the model is performing well. Good model performance is indicated here in bold.

	Jackknife (internal consistency)		Cross-validation (external validity)	
	Paired *t*- test	Correlation	Paired *t*- test	Correlation
Total caputured	**t_{29} = 0.02, P = 0.99**	**r = 0.63, P = 0.0002**	t_{9} = -7.70, P = 0.02	r = 0.25, P = 0.48
Females captured	**t_{29} = -0.04, P = 0.95**	**r = 0.55, P = 0.002**	**t_{9} = -1.41, P = 0.14**	r = 0.53, P = 0.11
(sqrt) Nests	**t_{29} = -0.01, P = 0.93**	r = 0.32, P = 0.09	**t_{9} = -0.30, P = 0.13**	r = 0.45, P = 0.19
(sqrt) Fledglings	**t_{29} = -0.01, P = 0.98**	r = 0.03, P = 0.86	**t_{9} = 0.26, P = 0.43**	r = 0.55, P = 0.10

Table 6. The classification of sites with and without Seaside Sparrow nests from the overall best logistic model (lowest AIC_c) applied to the model-building data set (*N* = 30 plots) and the validation set (*N* = 10 plots). A probability threshold cut-off of 0.5 was used to classify sites. Model diagnostics are tabulated to evaluate the performance of the model when applied to both datasets.

		Observed	
		Present	Absent
Original predicted	Present	1.7	3.3
	Absent	3.3	21.7
Validation predicted	Present	1.1	1.9
	Absent	1.9	5.1
Model diagnostics		Original	Validaton
% Correctly predicted absent		87	73
% Correctly predicted present		35	37
% Overall correctly predicted		78	62
Success index for model predicting absences[a]		0.04	0.18
Success index for model predicting presences[a]		0.02	0.07