# Modeling Saltmarsh Sparrow Distribution in Connecticut

Susan Therese Meiman

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# Modeling Saltmarsh Sparrow Distribution in Connecticut

Presented by

Susan Therese Meiman, B.S.

Major Advisor _____
Chris S. Elphick

Associate Advisor _____
Daniel L. Civco

Associate Advisor _____
Kent E. Holsinger

University of Connecticut
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**THESIS ABSTRACT**

Why saltmarsh sparrows are found in some salt marsh areas of Connecticut but not in others is a question of both ecological and conservation concern. Because the sparrows are restricted to salt marshes for their existence, they are vulnerable to changes in conditions. Therefore, conservation planning would require an assessment of the current extent and condition of habitat for sparrows. Multiple studies have documented various components of salt marshes that show strong associations with the sparrows, but predictive models using remote sensing have not yet been constructed that are specifically calibrated for this species.

To develop a map that would predict where the sparrows live and reproduce in Connecticut, I compared models to test a) whether field data or remote-sensing data most effectively characterized within-marsh conditions that relate to sparrow occurrence, and b) whether including landscape-level variables improved model fit. Models that best fit the data for sparrow presence and sparrow nesting used different variables. The best sparrow presence model used a variable derived from raw spectral reflectance values associated with plots where sparrows did not occur, while the best nest presence model used a combination of vegetation structure descriptions. A second nest model, built using high resolution remote sensing data that organized marsh characteristics into high and low marsh categories, had enough support for state-wide application.

When the models were tested using new data, model performance, assessed by determining the area under a receiver operating curve and the model deviance, was significantly better than expected by chance alone.

I then used model results to build maps of habitat conditions for saltmarsh sparrow presence and nesting across the state. A large proportion of the saltmarsh area in Connecticut was predicted to have a high probability of being occupied by sparrows, yet a much smaller proportion of marsh was predicted to have a high probability of having nests. While detailed delineation of plant communities in the marsh provided good predictions of sparrow nesting, they poorly predicted presence. On the

other hand, because areas of nesting activity are not well-identified by species presence models, a distribution model that describes only species presence would provide misleading information about where the most important areas for reproduction lie. Additional research is needed to establish how sparrow persistence may be influenced by the areas that are likely to have sparrows but not nests.

# Chapter 1.  Comparing saltmarsh sparrow habitat models using ground-based and remote sensing data

**ABSTRACT**

Remote sensing data can represent various habitat characteristics, and can thus replace detailed ground sampling in the construction of habitat models.  Remote sensing data may also distinguish additional variation in conditions that can be useful in discriminating presence and absence of species. To predict saltmarsh sparrow distribution and nesting activity in Connecticut salt marshes, I compared a set of Bayesian hierarchical models in which variables were generated from field or remote sensing data, at a scale of 1-ha plots and at the landscape scale.  Field data consisted of plant structure and plant composition variables.  Data derived from remote sensing included high and low marsh classifications, LiDAR elevation data, and a classification derived from spectral characteristics specifically associated with saltmarsh sparrow presence or absence.  The best sparrow presence model used a variable derived from raw spectral reflectance values associated with plots where sparrows did not occur, indicating that the remote sensing data included additional information about marsh conditions associated with saltmarsh sparrow presence and absence than was detected using plant composition, structure, or community classes.  Nest presence, in contrast, was modeled best using vegetation structure variables that required data collection on the ground.  Saltmarsh sparrow presence, therefore, will not necessarily indicate that an area provides all conditions suitable for reproduction and persistence.

Keywords:  *Ammodramus caudacutus*, Bayesian hierarchical models, habitat use, occupancy modeling, remote sensing, salt marsh, saltmarsh sparrow

## I. INTRODUCTION

Habitat loss and fragmentation contribute to the decline of many species (Andren 1994, Fahrig 1997, Jenkins *et al.* 2003, IUCN 2009). Describing the link between an organism and its environment is therefore necessary to conservation efforts for at least two reasons. First, this information provides the basis for identifying how the population's size and dynamics relate to the amount and type of land cover present (Garrison and Lupo 2002, Underwood *et al.* 2004). Second, understanding this relationship should guide land protection and management to improve a target organism's status (Rotenberry 1981, Scott *et al.* 1993, Rhodes *et al.* 2006).

Habitat models quantify the factors associated with an organism's presence in an attempt to understand better why the organism is found in some areas and not in others. These models can then be used to predict where the organism occurs. When the organism uses different features for different purposes, such as nesting or foraging, habitat modeling should be associated with specific activities. As more information is collected about the organism, the more detailed the model can become (Guisan and Thuiller 2005), ultimately allowing one to identify potentially limiting factors or processes (Van Horne 2002, Kristan 2007, Okes *et al.* 2008).

In addition to conditions within a patch that affect patterns of occupancy, features of the landscape around a patch can affect whether or not it is occupied. Several factors may contribute to this context-dependence. First, processes operating on a scale larger than a patch may alter conditions across a large region (Diez and Pulliam 2007). For example, proximity to urban development may be associated with increased pollution levels. Second, distribution of the organism may be constrained by a spatial factor such as dispersal limitation (Pulliam 2002, Bahn *et al.* 2008). Predictions of patch occupancy may be improved by including variables that describe landscape-level conditions in addition to those that describe local habitat characteristics (Wiegand *et al.* 2003, Diez and Pulliam 2007, McIntire and Fajardo 2009).

Geographic Information Systems (GIS) are often used to quantify the spatial relationships and context associated with patches of habitat.  Increasingly-available high resolution data from satellites and aerial images offer a great deal of detail about land cover features that may be relevant to the organism of interest (Van Horne 2002).  Although regional analyses frequently use aerial images to classify areas into land cover or plant composition categories, this approach assumes that all of the variables of interest are present at the resolution of the aerial image (Seoane *et al.* 2004). Processing remote sensed images involves organizing data into categories, and *a priori* decisions are made that guide how the computer handles the array of information.  These decisions may divide the data into too many categories to detect differences in use patterns, or the resolution of the information may be too coarse to distinguish differences (Gottschalk *et al.* 2005).  Comparing models that use ground-based vegetation data to those using remote sensing data can determine whether important information is missing from either set of data, and identify which approaches most effectively discriminate between suitable and unsuitable areas for the organism under study (Mack *et al.* 1997, Wiegand *et al.* 2000, Gottschalk *et al.* 2007).

In New England, salt marshes have been subjected to considerable development pressure and alterations in tidal flow (Rozsa 1995, Gedan *et al.* 2009).  These landscape changes have reduced the total amount of salt marsh, and in some cases changed their plant composition (Warren *et al.* 2002). In particular, nonnative *Phragmites australis*, a tall reed, has spread into many marshes, greatly altering their vegetation structure (Roman *et al.* 1984, Chambers *et al.* 1999).  Changes in sea level may further modify how much and what type of marshes occur along the New England coast (Warren and Niering 1993, Hoover 2009).  Saltmarsh sparrows (*Ammodramus caudacutus*) are found only in salt marshes along the eastern seaboard of the USA (Greenlaw and Rising 1994).  Female sparrows place their nests close to the ground (Humphreys *et al.* 2007), and flooding is a major cause of nest failure (Greenberg *et al.* 2006, Gjerdrum *et al.* 2008a, Bayard and Elphick 2011).  Consequently, changes in saltmarsh conditions are likely to have a large impact on saltmarsh sparrow populations.

In Connecticut, a relatively large population of saltmarsh sparrows occurs along with a wide range of marsh conditions, offering an opportunity to investigate the relationship between marsh conditions and sparrow presence.  Previous research has identified vegetation composition and structural characteristics within marshes that are associated with saltmarsh sparrow presence and reproductive effort (Benoit and Askins 2002, DiQuinzio *et al.* 2002, Shriver *et al.* 2004, Gjedrum *et al.* 2005, 2008b).  However, areas of marsh with the most sparrows are not always those where the most females nest (Elphick *et al.*, unpublished data), suggesting that different marsh features may be important for different activities.  Additionally, previous studies have indicated that a marsh's size and proximity to other marsh areas may influence whether or not saltmarsh sparrows occur in a given marsh (Benoit and Askins 2002, Shriver *et al.* 2004), suggesting that landscape-scale factors may affect sparrow presence.

My research was designed to test a) whether field data or remote sensing data most effectively characterized within-marsh conditions for saltmarsh sparrows, b) which remote sensing data and data processing approach produced the best predictor of habitat use, and c) whether attributes of the landscape at the marsh-system level improved model fit.

## II. METHODS

### A. Candidate Models

I developed an *a priori* series of alternative models for the presence of saltmarsh sparrows or for saltmarsh sparrow nests, based on information in the literature on saltmarsh sparrows. Models were subdivided into those that used only marsh-level characteristics (*e.g.* isolation), those that used only within-marsh characteristics (*e.g.* elevation), and those that combined both marsh-level attributes and within-marsh information (Table 1).  Within-marsh models were further subdivided into those that used field-based measurements of vegetation composition and structure to characterize conditions, and those in which conditions were characterized by remotely-sensed elevation data or by

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vegetation community classifications derived from digital aerial imagery.  Additional models that

were considered included factors related to location within the marsh and whether restoration efforts

had taken place.  Within-marsh characteristics were described from 1-ha plots, while landscape-level

factors were measured at the scale of the marsh system in which plots were located.

**1.** *Within-marsh characteristics*

Gjerdrum *et al.* (2008b) have previously found that models that included structural

characteristics of the vegetation fit sparrow abundance data better than models based on vegetation

composition alone.  The means of stem density, thatch height, and the maximum vegetation height

were identified as the best predictor variables.  Consequently, for my analysis, I included models that

assessed each of these structural characteristics individually and in combination to determine whether

all components were needed to represent conditions suitable for saltmarsh sparrow presence or

nesting (Models 1-4, Table 1).

Although measurements of structural characteristics produced better model fit than plant

composition variables (Gjerdrum *et al.* 2008b), my study included marshes across a wider salinity

gradient and thus a wider range of vegetation assemblages.  I therefore also included models based on

vegetation composition to assess whether the earlier results persisted across this broader range of

conditions.  I examined single-species composition models using the percent cover of *Spartina*

*patens*, *S. alterniflora,* and *Juncus gerardii* (Models 5-7).  *S. patens* and *S. alterniflora* frequently are

the dominant species in Connecticut salt marshes (Tiner 1987).  *S. patens* is common in high marsh

areas, while the tall form of *S. alterniflora* is frequently found in lower areas of marsh (Fig. 1; Niering

and Warren 1980, Bertness and Ellison 1987).  *J. gerardii* is a species that occurs in the higher zones

of high marsh (Bertness and Ellison 1987), and has been identified as a good indicator of sparrow

nest locations (Gjerdrum *et al.* 2005, 2008b).   Single-species composition models using *S. patens* and

tall *S. alterniflora*, therefore, could be considered to distinguish generally between zones of high and

low marsh, while *J. gerardii* could be considered to identify a subset of the high marsh zone of specific interest to nesting saltmarsh sparrows. I also combined tall *S. alterniflora*, *J. gerardii*, and *P. australis* (Model 8) for a model that provides a more comprehensive description of the plants occurring in a plot by including a low marsh species, a high marsh species, and an introduced species of great management interest. Because the amount of *S. patens* can be negatively correlated with the amount of tall *S. alterniflora* present in salt marshes (Wigand *et al.* 2003), these two species were not included in the same model.

To characterize within-marsh conditions using remote sensing data, I first included models that tested whether marsh community classes defined *a priori* predicted suitable conditions for saltmarsh sparrow presence and nesting. Using a plant community classification that subdivided salt marsh areas into "low" and "high" marsh based on spectral characteristics of plant species and elevation data (Hoover 2009), I included models in which habitat was represented by the proportion of a plot's area that was high marsh (Model 9) or the proportion that was low marsh (Model 10). Multispectral images integrate information from a range of environmental factors, and thus might provide more information than variables based on individual species or structural features (Gottschalk *et al.* 2005). Hence, I created a third remote sensing model using a classification based solely on spectral characteristics of plots associated with known sparrow presence or absence for the sparrow presence model (Model 11), and on spectral characteristics of plots associated with known nest presence or absence for the nest model. Because plant communities in salt marshes are greatly influenced by elevation relative to tidal inundation (Niering and Warren 1980), I also included a model that tested whether elevation data alone could be used to discriminate between areas of saltmarsh sparrow presence and absence (Model 12). For this model, Light Detection and Ranging (LiDAR) data were used to represent the height of the vegetation canopy relative to mean high tide.

Two other within-marsh features were considered in my model set. Previous studies have found that the distance to the edge of the marsh influences where saltmarsh sparrows occur and where

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they place their nests (Gjerdrum *et al.* 2008b, Hill 2008).  Thus, I included a model that estimated

sparrow or nest presence as a function of the distance from the sampled area to the upland edge

(Model 13), as well as models in which this distance was combined with vegetation structure (Model

14) or with vegetation composition (Model 15).

The second additional factor I considered that might affect whether saltmarsh sparrows were

present in an area of marsh was whether there had been any restoration efforts aimed at reducing the

impacts of invasive *P. australis*.  Two types of restoration have been conducted along the Connecticut

coast: a) restoration of tidal flow and b) direct control of *P. australis* through mowing or herbicide

application.  Subsequent changes in saltmarsh vegetation composition have varied depending on the

type of restoration undertaken and the time since the restoration work (Rosza 1995, Warren *et al.*

2001, 2002).  I therefore included models that tested whether restoration affected sparrow presence or

nesting, whether the method of restoration mattered, and whether the time since restoration mattered

(Models 16-18).  Sites with direct control of *P. australis* were all restored 4-10 years before my field

work, while the tidal restorations all took place 13-55 years previously (P. Capotosto and R. Wolfe,

personal communication).  As a result, the temporal effect could only be examined within each

restoration type.


### 2. Marsh-level characteristics

The effects of three marsh-level characteristics were examined in our candidate model set,

both individually and in combination: marsh size, isolation, and the degree of development in the

surrounding uplands.  Size (Model 19) was included because larger marshes are likely to be less

subject to edge effects if upland factors influence sparrows.  Marsh size may also affect the likelihood

that sparrows encounter a marsh during dispersal or migration (Andren 1994).  Most importantly,

marsh size has been previously identified as a predictor of occupancy and density in saltmarsh

sparrows, suggesting that the species is "area-sensitive" (Benoit and Askins 2002, Shriver *et al.*

2004).  Similarly, marsh isolation (Model 20) has previously been found to influence sparrow

presence (Shriver *et al.* 2004).  Finally, the amount of development in the vicinity of a marsh (Model

21) may be important because marshes in highly developed areas are subject to more pollution,

restricted sediment deposition due to water management structures, and increased runoff from

impermeable surfaces of roads and rooftops, with consequences for saltmarsh function and plant

community composition (Wigand *et al.* 2003, Gedan *et al.* 2009).  For example, plant growth and

competition in marshes are affected by increased nitrogen levels (Bertness *et al.* 2002).  The marsh-

level variables were also assessed in combination with each other (Models 22-25), and all marsh-level

models were compared to a model that included only a random effect for each marsh system (Model

26).


### 3. Combined marsh-level and within-marsh characteristics

I created a series of models that combined marsh-level characteristics with within-marsh

variables.  Marsh size and distance from the plot center to upland edge were combined (Model 27) to

test whether relative fit was improved by including factors at both spatial scales.  To explore further

the fit of marsh size models relative to distance-from-edge models, I also compared models that

combined marsh size with vegetation structure (Model 28) or vegetation composition (Model 29) to

those that combined distance-from-edge with vegetation structure (Model 14) or vegetation

composition (Model 15), respectively.  I also tested whether the addition of marsh-level information

improved within-marsh models, by comparing the fit of two other model pairs: a) area of high marsh

with and without marsh size (Models 30 vs. 9), and b) spectral characteristics associated with sparrow

or nest presence, with and without marsh size (Models 31 vs. 11).

To test whether sparrow presence or nesting in a plot that had suitable within-marsh

characteristics was influenced by isolation, I compared the relative fit of models of vegetation

structure with and without isolation (Model 32 vs. 4), and area of high marsh with and without

isolation (Model 33 vs. 9). These combinations were selected as representations of highly detailed ground-based data and high resolution general-classification remote sensing data.

Finally, whether a site had received restoration and the amount of surrounding development were combined (Model 34) to compare to the restoration-only model (Model 18) and test whether development influenced the probability that sparrows were present in marshes that had undergone restoration. Previous studies have linked development with differences in plant structure and composition (Bertness *et al.* 2002, Wigand *et al.* 2003), which may have greater impact at sites where restoration took place, affecting subsequent use by saltmarsh sparrows.

### B. Data Collection

Field data were collected between 2006 and 2008 from 60 1-ha plots that were distributed across 27 marshes from Westport to Stonington, Connecticut (Fig. 2). In 2006, 20 plots were sampled and site selection was designed to broaden sampling to a wider range of sites than had been included in our group's previous research (Gjerdrum *et al.* 2005, 2008b), and specifically to include smaller marshes. Two plots were located in areas that had undergone tidal restoration. In 2007 and 2008, sampling was conducted to examine the effects of restoration efforts, with another 14 plots in marshes that had undergone tidal-flow restoration, and eight plots with direct control of *P. australis*. For the 2007-2008 data, restoration plots were paired with 18 plots in nearby reference areas of marsh that were unaffected by *P. australis* invasion and had no history of tidal restriction. In all years, placement of each plot was randomized within the relevant marsh or marsh section. Minor adjustments in plot locations were sometimes required due to the proximity of osprey (*Pandion haliaetus*) nests (due to state permit constraints), private property boundaries, or inaccessibility due to marsh features such as major channels; in these cases the plot was placed as close to the randomly selected point as possible.

Saltmarsh sparrow presence was determined using 5-minute point counts and 3-hour mist-netting sessions.  Point counts were conducted between sunrise and 09:30 Eastern Daylight Time.  Three surveys per plot were conducted in 2006, and five in 2007 and 2008; different plots were sampled each year.  During each year, surveys were timed to occur at least two weeks apart between late May and mid-August.  Immediately after each point count, mist-netting was conducted in the plot between 06:00 and 13:00 hours, using an array of six 12-m 2-panel mist-nets.  The location of the array in the plot was changed for each session to ensure broad plot coverage.  Captured saltmarsh sparrows were banded and sexed based on the presence of a brood patch or cloacal protuberance.  Nests were detected by walking through the plots and carefully noting origin points of flushing birds, or by watching females flying with food in their bills as they returned to nests.

Vegetation composition and structural characteristics were measured between mid-July and mid-August to standardize measurements into a period when new growth was limited.  Each plot had nine sampling points, at the center, corners, and mid-points of the plot edges.  Previous work found this design to produce similar results to random-placement of points (Gjerdrum *et al.* 2005).  A 1-m quadrat was placed over the center of the sampling point.  Within the quadrat, the percent of bare ground and cover of each plant species were visually estimated.  The height from the ground to the top of the layer of dead rooted vegetation – the thatch height – was measured at the center of the quadrat.  The height of the tallest piece of vegetation in each of the four corners of the quadrat was measured and the mean maximum height calculated.  Stem density was estimated as the mean of the stem counts in five randomly-selected 10 x 10 cm subunits.  For each vegetation variable, the mean across all nine points was used to provide a single measure for each plot.  Distance from the plot to the upland edge was quantified from aerial images by measuring the shortest distance from the center of the plot to the edge of the nearest upland patch greater than 0.5 ha in size.

The first remote sensing GIS data layer was developed for other purposes and used a combination of digital aerial images, elevation data, extensive ground-truthing, and object-oriented

classification to create a high-resolution (1 m) map of Connecticut salt marshes, organized by plant species into high and low marsh communities (Hoover 2009). Using this data layer, I calculated the proportion of high and low marsh for each plot (Fig. 3A).

To create an alternative supervised classification of plot characteristics based on the birds' actual distribution patterns, I used infrared aerial images taken September 20 and 22, 2004, with 0.5-m resolution, along the entire Connecticut coast (National Oceanic and Atmospheric Administration Coastal Services Center and the United States Geological Survey 2004). I created a mosaic from all the images with salt marshes, resampling to a final resolution of 1 m in order to keep the file from becoming unmanageably large. The 60 study plots were used as training areas for the spectral reflectance properties of marsh conditions within Connecticut. After examining the spectral characteristics of each plot, I delineated homogeneous areas within plots to provide spectral signatures. I then used a maximum-likelihood algorithm in ERDAS Imagine to classify each salt marsh pixel in the state according to its resemblance to a signature derived from the original study plots (Fig. 3B). Based on whether at least one sparrow had been detected in the parent training plot during the 2006-2008 surveys, the pixel classes were then coded according to whether one would expect sparrows to be present or absent (Fig. 3C). After subtracting all pixels classified as water, the proportions of pixels classified as having sparrows either present or absent were calculated for each plot. For the nest presence analysis, this recoding step was repeated based on whether or not nests had been observed in the parent training plot (Fig. 3D). Because the presence and absence pixel classes were highly correlated, only the classes that denoted sparrow or nest absence were used in the models.

A third remote sensing data product was used in the elevation model (Model 12). In addition to generating the digital images used to create a supervised classification, the NOAA 2004 flight generated a surface-return elevation model (National Oceanic and Atmospheric Administration Coastal Services Center and the United States Geological Survey 2004). The resulting Digital Surface

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Model (DSM), which indicates the height of the vegetation canopy relative to sea level, had vertical resolution of 0.33 m, and horizontal resolution of 2 m. I calculated the mean elevation for each plot. At this resolution, the data for all emergent land showed a gradient of increasing elevation from east to west associated with the increasing tidal amplitude in Long Island Sound. This likely arises because the elevations at which salt marshes develop are determined by the mean high tide level (Bertness and Ellison 1987) rather than the average sea level, against which DSM is measured. Because sparrows are affected by mean high tides both directly through nest flooding and indirectly through the tide's effects on the vegetation, DSM values needed to be adjusted to give a measure of elevation relative to high tide levels. To do this, I determined the deviation between observed elevation and that predicted for a given longitude based on a different digital elevation model (ground return elevation) (Hoover 2009). I then subtracted the estimated elevation from the mean DSM elevation for an estimate of canopy-return elevation relative to general marsh surface height specific to that longitude (see Appendix A for adjustment analysis).

Marsh-level variables were measured using the Connecticut Coastal Environmental Sensitivity Index Mapping Polygons (NOAA 2004), which delineated salt- and brackish-water marsh along the Connecticut coast in 1999. I defined a marsh unit as the group of all tidal marsh polygons separated by less than 100 m. Size was then calculated by summing the areas of all saltmarsh polygons within a marsh unit. Isolation was measured as the shortest distance from the edge of the marsh unit to the nearest point on the edge of another marsh unit. To determine the amount of development in the vicinity of each marsh unit, I used the Connecticut Changing Landscape GIS 30-m resolution land cover for 2002 (Hurd 2006). I generated a 500 m buffer around each marsh unit, and calculated the proportion of land within the buffer that was classified as developed. I chose 500 m for the buffer because the major rivers in CT are approximately 300 to 750 m wide. As some of the marshes are islands, a buffer zone much less than 500 m would have consisted primarily of water,

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and buffer size much larger than 500 m would have overlapped adjacent marshes, decreasing the independence of the measured variables.

Areas of marsh along the Connecticut coast are not all organized into clearly discrete units. It is not known which arrangements of marsh systems are conducive to sparrows moving between them, although male sparrows have been recorded as siring chicks up to 1.37 km from where the males were banded (Hill *et al.* 2010).  As a result, deciding what constitutes a marsh unit that has biological significance for sparrows is not straightforward and all of the marsh-level variables may be sensitive to user-defined scale decisions.  To investigate whether the marsh-level variables were sensitive to the definition of marsh unit, I repeated the analyses with the marsh unit defined as the group of all marsh polygons separated by less than 500 m and compared the relative ranks of the models from each set of analyses.

### C. Model Specification

I used WinBUGS (Spiegelhalter *et al.* 2000) to fit hierarchical logistic regression models of sparrow presence and nesting.  I used a Bernoulli distribution to model sparrow presence, such that the logit of the probability of detecting sparrows at the sampled plot was a function of the explanatory variables and the regression coefficients. Because I sampled multiple plots within individual marshes, and previous work has shown that the marsh in which a surveyed plot was located influenced sparrow abundance (Gjerdrum *et al.* 2008b), I also included a marsh-specific random effect.  The marsh-associated random effect was assumed to be drawn from a global distribution, with the marsh-specific mean determined by a global intercept and the marsh-level variables (Diez and Pulliam 2007).  The magnitude of variation in marsh systems could then be assessed by comparing the random effect estimates of the top models.

Regression coefficients were given normally-distributed prior distributions with means of 0 and precisions of 0.01, and the random effect estimates and the global intercept estimate were given

normally-distributed prior distributions with means of 0 and precisions of 0.1. More diffuse priors resulted in model instability and lack of convergence. Each model was run using two Monte-Carlo Markov chains, and I examined the time series plots to check that the chains were mixing well. I further examined the Gelman-Rubin statistic graph for evidence of lack of convergence. The first 2000 iterations of the Monte-Carlo Markov chain were discarded as the burn-in phase, and each model subsequently ran for 25,000 iterations. The Deviance Information Criterion (DIC) calculated for each model was used to compare their relative fit. WinBUGS code is included in Appendix B.

Because logistic regression is robust to non-normal data distributions, I did not transform any of the variables. Pearson correlation coefficients for all pair-wise comparisons of variables included in the same models were < 0.50 (n = 60).

## III. RESULTS

Saltmarsh sparrows were detected in 52 of 60 plots and in 26 of 27 marshes. Nests were found in 22 plots and 14 marshes. Marshes in which sampling took place had a mean size of 86 ha, a mean distance of 306 m to the nearest marsh, and an average of 36% developed land within the 500 m buffer around the marsh (Table 2). Of the within-marsh variables measured on the ground, the mean coverage of *S. patens* and *J. gerardii* were higher at plots where sparrows and sparrow nests were present than at plots where sparrows and sparrow nests were not found (Table 3), while tall *S. alterniflora* was more extensive at plots where sparrows and nests were not found. Higher stem density was associated with plots where sparrows and sparrow nests were found, while thatch height and mean maximum vegetation height were similar for sites with and without both sparrows and nests. On average, there were also greater proportions of high marsh and lower proportions of low marsh in plots with sparrow nests.

When pixels in the marshes were classified into sparrow-absent or sparrow-present categories, plots known to contain sparrows were dominated by sparrow-present pixels (mean =

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78%), while those where sparrows were not detected generally had similar proportions of sparrow-present and sparrow-absent pixels (Table 3). An average of 57% of pixels were classed as nest-present in plots known to contain nests, with an average of 35% classed as nest-absent pixels. On average, 58% of pixels in plots where no nests were present were classed as nest-absent pixels, and 38% were classed as nest-present pixels. The elevation adjustment analysis estimated that for every degree of longitude (83.8 km), marsh surfaces were associated, on average, with a 0.38 m (SE 0.05 m) change in elevation. As measured by LiDAR, the mean height of the vegetation canopy relative to mean high tide in each plot was 0.44 m (min – max: -0.92 m – 1.8 m) after adjusting for the longitudinal gradient. Canopy height of plots with sparrows present averaged 0.45 m above mean high tide, while plots without sparrows present measured 0.41 m above mean high tide. Plots that contained nests had canopy heights that averaged 0.37 m above mean high tide, while those without nests averaged 0.49 m above mean high tide. Sites that had undergone tidal restoration had sparrows present in 11 of 16 plots, two of which also had nests. Sparrows were found at all nine *P. australis* control sites, and nests were found in five. Vegetation characteristics at restoration and control sites were directly compared in a separate analysis (Elphick *et al.* unpublished manuscript).

**A. Presence /Absence Models**

Sparrow presence Model P11, in which habitat was represented by the abundance of sparrow-absent pixels derived from the supervised classification, fit substantially better than any other representation of within-marsh conditions, with a lower probability of sparrow presence associated with a greater proportion of the sparrow-absent pixels (Table 4). All other within-marsh models had much less support ($\Delta$DIC > 10). Of the remaining within-marsh models, those describing restoration variables produced the best fit ($\Delta$DIC: 10.9 – 13.1), although these models were not substantially better than others: vegetation structure ($\Delta$DIC: 15.5 – 22.1); vegetation composition ($\Delta$DIC: 11.9 –

19.4); other remote sensing data ($\Delta$DIC: 18.5 – 21.4); and distance to upland edge ($\Delta$DIC: 15.4 – 21.2).

The models that included only marsh-level variables (P19-26) had model fits toward the lower end of the range from within-marsh models ($\Delta$DIC: 17.9 – 21.0). A similar DIC ranking was obtained when the marsh unit was defined by less than 500 m between constituent sections of marsh, with similar variation between the models.

When marsh-level variables were combined with within-marsh variables, models fit at best only marginally better when directly compared to equivalent models that included only the within-marsh variables (compare Models P27-34 with Models P1-13; Table 4). The model with the most support included both marsh size and the proportion of sparrow-absent pixels from the supervised classification, although the fit and parameter estimates were very similar to those for the single-variable sparrow-absent classification model (Table 4). The next closest-competing model, which included size in combination with the full composition model, had notably lower support with a $\Delta$DIC of 9.4, but the parameter estimate for the effect of marsh size was similar to the estimate of the best model (Table 5).

Across models, marsh size was consistently estimated as being positively associated with the probability of sparrow presence (parameter estimates ranged from 0.036 to 0.043), while isolation was consistently estimated as being negatively associated with the probability of sparrow presence (min – max: -0.001 to -0.007). Parameter estimates for the effects of development were both positive and negative, with the standard deviations at least 4 times the coefficient estimates, suggesting there is considerable uncertainty associated with estimating the relationship between sparrow presence and the amount of development at this scale.

Of the model comparisons used to investigate the relative effects of marsh size versus the distance of a plot from the marsh edge, the single-variable model that included distance to upland edge (Model P13) had slightly less support than the single-variable model that included size (Model

16

P19). The model that included both size and distance (Model P27) had similar support to Models P13 and P19. When marsh size and within-marsh characteristics were combined, model fit of within-marsh characteristic models improved but the change in DIC values were consistently less than 2. When combined with composition or structure, size improved the within-marsh model more than distance to the upland edge did.

Models that included restoration as a factor influencing sparrow presence had little support compared to the best fitting models ($\Delta$DIC: 10.9 – 13.1), but had similar support to models of field-measured vegetation composition and structure. Parameter estimates for an overall restoration effect were negative (Model P16), although estimates for Model P17 suggest that this effect was driven largely by the tidal restoration sites (Table 6). When time since restoration was included in the model, credible intervals overlapped zero for the parameter estimates of both restoration types and the associated time effects.

The random effect estimates from the simplest top model (Model P11) suggest little variation between marshes, and all 95% credible intervals overlapped each other (Fig. 4). The very best model (P31) showed more variation in the larger marshes, but all 95% credible intervals overlapped each other as well.

**B. Nest models**

Of all the within-marsh models considered, that based on multiple measures of vegetation structure, Model N4, provided the best fit (Table 7). Model N1, which included only stem density, fit the data almost as well as Model N4 ($\Delta$DIC = 3.5 vs. 0.9). Of the variables included in the vegetation structure model, the measurement of stem density appeared to be responsible for much of the model's fit, because single-variable models that included thatch height and vegetation height fit poorly ($\Delta$DIC: 18.1 and 18.9, respectively). Compared to models that included vegetation structure, models that included vegetation composition had little to no support ($\Delta$DIC: 6.8 – 16.7). There was some support

for the remote sensing model N9, which used the proportion of high marsh to represent habitat conditions (ΔDIC = 4.6), but other remote sensing models (Models N10-12), models that included distance to the marsh's upland edge (Model N13), and restoration models (Models N16-18) were all poorer, but relatively equivalent, fits (ΔDIC: 10.2 – 23.2).

Models using only marsh-level variables (Models N19-26) all had similar fit and little support (ΔDIC > 21). Parameter estimates for these variables also were very low (≤ 0.01), suggesting little effect of these variables. Consistent with this pattern is the observation that when marsh-level variables were combined with within-marsh variables, model fit remains largely the same (compare Models 27-34 with their simpler counterparts in Table 7). Adding marsh size to the vegetation structure model achieved a marginally-better fit (ΔDIC = 0.0 vs. 0.9), but in most cases the more complex landscape model was marginally worse. Estimates of within-marsh variable parameters in models that combined landscape and within-marsh variables were similar to estimates from models that included within-marsh variables only (Table 8). As with the presence models, the nest models had similar DIC rankings when the marsh unit was defined by less than 500 m between constituent sections of marsh.

When random effect estimates from the top models were compared, there was minor variation between marshes in both the vegetation structure model and the high-marsh model, with 95% credible intervals for all estimates overlapping each other (Fig. 5).

## IV. DISCUSSION

A major conclusion of this study is that the marsh characteristics that are best for modeling the presence of saltmarsh sparrows are different from those that best distinguish sites where nesting actually occurs. This finding has important repercussions for management because the presence of saltmarsh sparrows will not necessarily indicate that an area provides all conditions suitable for

reproduction and persistence. Because habitat quality is not necessarily related to abundance or density (Van Horne 1983, Vickery *et al.* 1992, Johnson 2007), modeling saltmarsh sparrow habitat based only on presence could be very misleading if one wanted to identify areas important to species conservation. Because the mating system of this species, in which females are polyandrous and males provide no parental care (Greenlaw and Rising 1994, Hill *et al.* 2010), obscures the links between habitat and reproductive success in areas that are not providing nesting habitat, additional research is needed to determine why birds spend time in those areas.

Plots in which saltmarsh sparrows are found have different spectral characteristics than plots where sparrows are not found, and this distinction provided a better basis for representing sparrow habitat than did the vegetation composition, vegetation structure, or classifications of marsh type. The difference in model fit suggests that there are features of marshes that have not been accounted for in ground-based data collection, but that can be detected using near-infrared aerial images, and that matter to sparrows. What these variables are has yet to be determined, but possibilities include duration of tidal inundation, which could result in more water occurring in the image and thereby affecting the spectral reflectance (Kearney *et al.* 2009), or in salinity differences, or combinations of inundation and salinity, which are associated with different growth responses in both *S. alterniflora* and *S. patens* (Naidoo *et al.* 1992).

Models using saltmarsh restoration history to generate predictions about sparrow presence would be of limited utility for broad-scale predictions, as restoration effort would be a factor in only a limited set of saltmarsh areas in Connecticut not already included in this study. However, the better fit of the restoration models when compared to models that included detailed vegetation composition and structure suggests that the effects of restoration are not minor. Importantly, the negative parameter estimates for these effects in some models indicate that restoration frequently does not result in suitable habitat for saltmarsh sparrows. The parameter estimates further indicate that it is primarily sites with tidal marsh restoration that lack birds.

The best models of actual nesting included characteristics of the vegetation structure that were collected on the ground. Stem density in particular appeared to be responsible for much of the fit, matching the results of previous studies (Gjerdrum *et al.* 2005, 2008b), and reinforcing the idea that females select nest sites based on vegetation density, rather than by any one species of plant.

Although measuring vegetation structure on the ground provides the best fit for saltmarsh sparrows' nesting locations, collecting stem density data over large areas is not practical. Consequently, this model would be difficult to use for predicting where nesting areas lie over large scales. The model based on the relative abundance of high marsh habitat (Model N9), however, is not substantially worse ($\Delta DIC = 4.6$ vs. 0.9) and can be used for prediction, as this data layer has been constructed for all of the marshes along the Connecticut coast (Hoover 2009). Even creating this data layer, however, involved considerable ground-truthing and separate decision rules for each of the more than 30 high-resolution image/elevation data combinations that spanned the area under study (M. Hoover, personal communication). Extending predictions using this classification over larger geographic regions, therefore, is not a trivial matter.

Despite previous indications that the distance from an upland edge could affect sparrow distributions (Gjerdrum *et al.* 2008, Hill 2008), I found little evidence to support this hypothesis. The wider range of environmental conditions, or broader collection of explanatory variables sampled in this study may have overwhelmed an effect that may exist in more homogeneous areas.

The marsh-level models considered in this study generally had little support compared to the best within-marsh models, although adding marsh size marginally improved each of the best within-marsh models. The models that included marsh-level variables had similar rankings when the marsh unit was redefined to include more widely spaced parcels, which suggests these results are not sensitive to the decision rules used to define marsh units in this study.

In conclusion, I found that saltmarsh sparrow presence appears to be modeled most effectively using remote sensing data rather than ground-based data. However, because the best

model used remote sensing data that were not organized into categories of known ground cover types, some of the differences may not be apparent on the visible spectrum and are difficult to relate to specific ecological factors.  As a result, directing effort toward developing a detailed map based only on vegetation composition or vegetation structure maps from remote sensing, or using general landcover data layers developed for other purposes, would fail to incorporate components that appear to be important for sparrows.  In addition, because areas of nesting activity are not well-identified by species presence models, the best species presence models would provide misleading information about where the most important areas for reproduction lie.  Focusing conservation efforts on improving or maintaining the saltmarsh areas suitable for nesting will be critical for saltmarsh sparrow persistence, but because sparrows also occur in areas that are not directly associated with reproductive activity, further investigations are needed to establish what contribution, if any, these other areas make toward sparrow persistence.

Remote sensing data can be rendered into highly detailed representations of environmental features, which can then be used to detect ecologically important variation even in relatively simple systems such as salt marshes (Morris *et al.* 2005, Gilmore *et al.* 2008, Tuxen *et al.* 2011).   However, applying remote sensing data to habitat association models requires more than organizing the data into categories that are familiar from ground-based data collection.  Comparing models that use these different types of data is one way to check assumptions about what features on the ground have strong links to the organism under study, and where additional investigation may be warranted.

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**Table 1** Candidate models used to describe characteristics of salt marshes where saltmarsh sparrows and their nests occur in coastal Connecticut.  Models are grouped according to the type of data used, and whether the models include within-marsh variables, marsh-level variables, or a combination of the two

**I. Within-marsh models**

A. Vegetation structure data
| | |
|---|---|
| 1 | Stem density |
| 2 | Thatch height |
| 3 | Mean maximum vegetation height |
| 4 | Stem density + Mean maximum height + Thatch height (Full structure model) |

B. Vegetation composition data
| | |
|---|---|
| 5 | *S. alterniflora* (tall form) |
| 6 | *J. gerardii* |
| 7 | *S. patens* |
| 8 | Tall *S. alterniflora* + *J. gerardii* + *P. australis* (Full composition model) |

C. Remote sensing data
| | |
|---|---|
| 9 | Community classification: % High marsh |
| 10 | Community classification: % Low marsh |
| 11 | Spectral characteristics (Presence: % Sparrow-absent pixels; Nests: % Nest-absent pixels) |
| 12 | Mean elevation: Digital Surface Model |

D. Location data
| | |
|---|---|
| 13 | Distance to upland edge |
| 14 | Distance + Structure |
| 15 | Distance + Composition |

E. Restoration history
| | |
|---|---|
| 16 | Restoration (absent or present) |
| 17 | Restoration (absent, tidal flow restoration, or direct *P. australis* control) |
| 18 | Restoration (absent, tidal flow x time since restoration, or *P. australis* control x time since restoration) |

**II. Marsh-level models**
| | |
|---|---|
| 19 | Size |
| 20 | Isolation |
| 21 | Development |
| 22 | Size + Development |
| 23 | Size + Isolation |
| 24 | Isolation + Development |
| 25 | Size + Isolation + Development (Full marsh-level model) |
| 26 | Random effects only |

**III. Combined marsh-level and within-marsh models**
| | |
|---|---|
| 27 | Size + Distance |
| 28 | Size + Structure |
| 29 | Size + Composition |
| 30 | Size + Community classification: % High marsh |
| 31 | Size + Spectral signature (Presence: % Sparrow-absent pixels; Nests: % Nest-absent pixels) |
| 32 | Isolation + Structure |
| 33 | Isolation + Community classification: % High marsh |
| 34 | Development + Restoration (absent, tidal flow restoration, or *P. australis* control) |

**Table 2** Marsh-level characteristics of surveyed marshes, when defined as including all areas of marsh that were within 100 m of each other, and when redefined as all areas of marsh within 500 m of each other. Measures given as means ± SD (median, min – max)

| | Total marsh system units | Marsh size (ha) | Marsh isolation (m) | % development within 500 m of marsh |
|---|---|---|---|---|
| **Marsh units defined as < 100 m between components** | 27 | 86 ± 94 (48.8, 13 – 417) | 306 ± 218 (255.4, 101 – 756) | 36.5 ± 13.7 (34, 15 – 62) |
| **Marsh units defined as < 500 m between components** | 22 | 167 ± 163 (87, 13 – 572) | 767 ± 340 (652, 505 – 2005) | 36.2 ± 12.6 (37, 15 – 64) |

**Table 3** Within-marsh characteristics of plots where sparrows were present and absent and where sparrow nests were present and absent

| | | Ground-collected data | | | | | | | | | | Remote sensing data | | | |
| | | Vegetation structure | | | | Vegetation composition | | | Community composition | | Elevation | Spectral characteristics | | | |
| | Distance to upland edge (m) | Mean maximum height (cm) | Stem density | Thatch height (cm) | % cover *S. patens* | % cover tall *S. alterniflora* | % cover *J. gerardii* | % cover *P. australis* | % high marsh | % low marsh | Corrected DSM (m) | % sparrow-present pixels | % sparrow-absent pixels | % nest-present pixels | % nest absent pixels |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sparrows present (n = 52)** | | | | | | | | | | | | | | | |
| mean | 132.6 | 41.3 | 27.7 | 7.4 | 21.9 | 18.1 | 4.6 | 3.9 | 36.2 | 53.0 | 0.45 | 77.5 | 16.7 | - | - |
| SD | 115.4 | 15.7 | 16.1 | 4.2 | 18.0 | 19.7 | 10.7 | 7.3 | 27.4 | 30.4 | 0.35 | 11.1 | 11.5 | - | - |
| median | 83.5 | 39.5 | 27.8 | 7.4 | 19.1 | 11.3 | 0.0 | 0.0 | 31.7 | 56.1 | 0.41 | 79.4 | 13.1 | - | - |
| min | 29.9 | 14.7 | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | -0.09 | 46.7 | 1.1 | - | - |
| max | 487.7 | 95.1 | 63.8 | 16.9 | 68.9 | 90.6 | 46.8 | 37.2 | 89.2 | 100.0 | 1.83 | 94.0 | 52.7 | - | - |
| **Sparrows absent (n = 8)** | | | | | | | | | | | | | | | |
| mean | 60.2 | 42.6 | 15.2 | 7.9 | 12.5 | 34.8 | 1.0 | 5.4 | 26.0 | 63.8 | 0.41 | 47.5 | 47.7 | - | - |
| SD | 17.0 | 23.4 | 13.8 | 5.4 | 14.7 | 24.9 | 2.7 | 9.6 | 35.1 | 29.8 | 0.17 | 25.3 | 26.2 | - | - |
| median | 54.4 | 34.2 | 9.0 | 7.4 | 5.3 | 23.9 | 0.0 | 0.3 | 3.9 | 69.0 | 0.42 | 52.3 | 35.5 | - | - |
| min | 42.7 | 19.8 | 2.8 | 1.3 | 0.0 | 10.6 | 0.0 | 0.0 | 0.0 | 17.6 | 0.14 | 11.9 | 18.5 | - | - |
| max | 93.3 | 85.3 | 37.6 | 19.6 | 32.2 | 81.1 | 7.8 | 27.2 | 82.4 | 93.6 | 0.66 | 80.5 | 87.4 | - | - |
| **Nests present (n = 22)** | | | | | | | | | | | | | | | |
| mean | 134.3 | 37.7 | 37.2 | 8.5 | 29.5 | 11.8 | 7.5 | 3.4 | 53.5 | 38.1 | 0.37 | - | - | 56.7 | 34.7 |
| SD | 131.2 | 11.8 | 13.7 | 3.9 | 19.5 | 14.7 | 13.1 | 6.3 | 26.2 | 25.6 | 0.22 | - | - | 17.9 | 16.8 |
| median | 69.0 | 37.5 | 39.5 | 7.5 | 22.9 | 8.6 | 0.0 | 0.3 | 64.1 | 32.0 | 0.29 | - | - | 58.0 | 33.6 |
| min | 29.9 | 21.9 | 14.1 | 3.1 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | 0.09 | - | - | 25.6 | 6.5 |
| max | 487.7 | 60.6 | 63.8 | 16.9 | 68.9 | 65.0 | 46.8 | 22.2 | 89.2 | 91.0 | 1.09 | - | - | 83.4 | 69.9 |
| **Nests absent (n = 38)** | | | | | | | | | | | | | | | |
| mean | 116.4 | 43.7 | 19.5 | 6.8 | 15.5 | 25.3 | 2.1 | 4.5 | 24.0 | 64.0 | 0.49 | - | - | 38.4 | 54.3 |
| SD | 97.6 | 18.8 | 14.1 | 4.5 | 14.6 | 22.7 | 7.2 | 8.2 | 24.0 | 28.9 | 0.38 | - | - | 20.3 | 19.8 |
| median | 81.2 | 39.6 | 17.5 | 6.6 | 14.2 | 20.6 | 0.0 | 0.0 | 15.4 | 65.8 | 0.47 | - | - | 42.9 | 49.7 |
| min | 31.4 | 14.7 | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | -0.09 | - | - | 3.6 | 12.2 |
| max | 438.9 | 95.1 | 62.0 | 19.6 | 48.9 | 90.6 | 34.7 | 37.2 | 82.4 | 100.0 | 1.83 | - | - | 79.1 | 91.8 |

**Table 4** Model comparison results for models examining the presence or absence of saltmarsh sparrows, organized by the type of data included in the model. All models include a random effect for the marsh system in which a sample plot was located. The Deviance Information Criterion (DIC) is a measure of the fit of the model to the data, with lower numbers indicating better fit; ΔDIC shows the fit of each model compared to the best model of all those considered

| I. Within-marsh models | | DIC | ΔDIC |
|---|---|---|---|
| **A. Vegetation structure data** | | | |
| P1 | Stem density | 42.1 | 16.1 |
| P2 | Thatch height | 48.0 | 22.1 |
| P3 | Mean maximum vegetation height | 46.2 | 20.2 |
| P4 | Stem density + Mean maximum height + Thatch height (Full structure model) | 41.5 | 15.5 |
| **B. Vegetation composition data** | | | |
| P5 | *S. alterniflora* (tall form) | 45.4 | 19.4 |
| P6 | *J. gerardii* | 40.3 | 14.3 |
| P7 | *S. patens* | 43.3 | 17.3 |
| P8 | Tall *S. alterniflora* + *J. gerardii* + *P. australis* (Full composition model) | 37.9 | 11.9 |
| **C. Remote sensing data** | | | |
| P9 | Community classification: % High marsh | 44.4 | 18.5 |
| P10 | Community classification: % Low marsh | 46.4 | 20.5 |
| P11 | Spectral characteristics: % Sparrow-absent pixels | 27.1 | 1.1 |
| P12 | Mean elevation: Digital Surface Model | 47.4 | 21.4 |
| **D. Location data** | | | |
| P13 | Distance to upland edge | 47.2 | 21.2 |
| P14 | Distance + Structure | 41.4 | 15.4 |
| P15 | Distance + Composition | 38.2 | 12.2 |
| **E. Restoration history** | | | |
| P16 | Restoration (absent or present) | 39.1 | 13.1 |
| P17 | Restoration (absent, tidal flow restoration, or direct *P. australis* control) | 39.1 | 13.1 |
| P18 | Restoration (absent, tidal flow restoration x time since restoration, or *P. australis* control x time since restoration) | 35.9 | 10.9 |
| **II. Marsh-level models** | | | |
| P19 | Size | 45.2 | 19.2 |
| P20 | Isolation | 45.8 | 19.8 |
| P21 | Development | 47.0 | 21.0 |
| P22 | Size + Development | 45.5 | 19.5 |
| P23 | Size + Isolation | 43.9 | 17.9 |
| P24 | Isolation + Development | 46.0 | 20.0 |
| P25 | Size + Isolation + Development (Full marsh-level model) | 44.1 | 18.1 |
| P26 | Marsh-system random effects only estimated | 46.9 | 20.9 |

**Table 4 (continued)**

| III. Combined marsh-level and within-marsh models | | DIC | ΔDIC |
|---|---|---|---|
| P27 | Size + Distance | 47.4 | 21.4 |
| P28 | Size + Structure | 40.0 | 14.0 |
| P29 | Size + Composition | 35.3 | 9.4 |
| P30 | Size + Community classification: % High marsh | 42.7 | 16.7 |
| P31 | Size + Spectral characteristics: % Sparrow-absent pixels | 26.0 | 0.0 |
| P32 | Isolation + Structure | 41.8 | 15.8 |
| P33 | Isolation + Community classification: % High marsh | 43.4 | 17.4 |
| P34 | Development + Restoration (absent, tidal flow restoration, or *P. australis* control) | 39.2 | 13.2 |

**Table 5** Parameter estimates, standard deviations, and credible intervals for the top sparrow presence models: P11, P31, and P29

**Presence model P11 (% Sparrow-absent pixels, ΔDIC = 1.1)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 7.31 (1.5) | 4.55 | 10.43 |
| % Sparrow-absent pixels | -0.17 (0.05) | -0.27 | -0.08 |

**Presence model P31 (Marsh size + % Sparrow-absent pixels, ΔDIC = 0.0)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 8.17 (1.72) | 5.04 | 11.80 |
| % Sparrow-absent pixels | -0.16 (0.05) | -0.26 | -0.08 |
| Size of marsh | 0.04 (0.02) | -0.001 | 0.09 |

**Presence model P29 (Marsh size + Vegetation composition, ΔDIC = 9.4)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 6.37 (1.67) | 3.47 | 10.05 |
| Size of marsh | 0.04 (0.02) | 0.006 | 0.09 |
| % tall *S. alterniflora* | -0.07 (0.04) | -0.16 | -0.05 |
| % *J. gerardii* | 0.56 (0.38) | 0.05 | 1.46 |
| % *P. australis* | -0.26 (0.11) | -0.50 | -0.04 |

**Table 6** Parameter estimates, standard deviations, and credible intervals for the presence models that include restoration factors: P16, P17, and P18

**Presence model P16 (Restoration absent or present, ΔDIC = 13.1)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 5.1 (1.2) | 2.9 | 7.4 |
| Restoration | -3.5 (1.3) | -6.4 | -0.9 |

**Presence model P17 (Restoration absent, tidal flow restoration or direct *P. australis* control, ΔDIC = 13.1)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 5.0 (1.2) | 2.8 | 7.3 |
| Tidal flow restoration | -3.9 (1.5) | -7.1 | -1.2 |
| *P. australis* control | -1.1 (2.8) | -6.3 | 4.5 |

**Presence model P18 (Restoration absent, tidal flow restoration x time since restoration, *P. australis* control x time since restoration, ΔDIC = 10.9)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | 2.5% | 97.5% |
| Global intercept | 4.9 (1.2) | 2.8 | 7.3 |
| Tidal flow restoration | 1.5 (3.9) | -5.6 | 9.7 |
| Tidal flow restoration time effect | -0.3 (0.2) | -0.7 | 0.05 |
| *P. australis* control | -7.5 (7.1) | -22.3 | 5.6 |
| *P. australis* control time effect | 1.8 (2.1) | -0.8 | 6.0 |

**Table 7** Model comparison results for presence/absence of saltmarsh sparrow nests, organized by type of data included in the model. All models include a random effect for the marsh system in which a sample plot was located

| I. Within-marsh model | | DIC | ΔDIC |
|---|---|---|---|
| **A. Vegetation structure data** | | | |
| N1 | Stem density | 63.8 | 3.5 |
| N2 | Thatch height | 79.3 | 19.0 |
| N3 | Mean maximum vegetation height | 80.1 | 19.8 |
| N4 | Stem density + Mean maximum height + Thatch height (Full structure model) | 61.2 | 0.9 |
| **B. Vegetation composition data** | | | |
| N5 | *S. alterniflora* (tall form) | 77.0 | 16.7 |
| N6 | *J. gerardii* | 69.1 | 8.8 |
| N7 | *S. patens* | 72.6 | 12.3 |
| N8 | Tall *S. alterniflora* + *J. gerardii* + *P. australis* (Full composition model) | 67.1 | 6.8 |
| **C. Remote sensing data** | | | |
| N9 | Community classification: % High marsh | 64.9 | 4.6 |
| N10 | Community classification: % Low marsh | 70.5 | 10.2 |
| N11 | Spectral characteristics: % Nest-absent pixels | 74.2 | 13.9 |
| N12 | Mean elevation: Digital Surface Model | 81.7 | 21.4 |
| **D. Location data** | | | |
| N13 | Distance to upland edge | 82.3 | 22.0 |
| N14 | Distance + Structure | 62.2 | 1.9 |
| N15 | Distance + Composition | 68.1 | 7.8 |
| **E. Restoration history** | | | |
| N16 | Restoration (absent or present) | 83.5 | 23.2 |
| N17 | Restoration (absent, tidal flow restoration or direct *P. australis* control) | 79.4 | 19.1 |
| N18 | Restoration (absent, tidal flow x time since restoration, or *P. australis* control x time since restoration) | 82.7 | 22.4 |
| **II. Marsh-level models** | | | |
| N19 | Size | 81.9 | 21.6 |
| N20 | Isolation | 82.6 | 22.3 |
| N21 | Development | 82.0 | 21.7 |
| N22 | Size + Development | 81.9 | 21.6 |
| N23 | Size + Isolation | 82.2 | 21.9 |
| N24 | Isolation + Development | 82.5 | 22.2 |
| N25 | Size + Isolation + Development (Full marsh-level model) | 81.8 | 21.5 |
| N26 | Marsh-system random effects only estimated | 82.2 | 21.9 |

Table 7 (continued)

| III. Combined marsh-level and within-marsh models | | DIC | ΔDIC |
|---|---|---|---|
| N27 | Size + Distance | 82.4 | 22.1 |
| N28 | Size + Structure | 60.3 | 0.0 |
| N29 | Size + Composition | 68.1 | 7.8 |
| N30 | Size + Community classification: % High marsh | 64.9 | 4.6 |
| N31 | Size + Spectral characteristics: % Nest-absent pixels | 74.2 | 13.9 |
| N32 | Isolation + Structure | 61.7 | 1.4 |
| N33 | Isolation + Community classification: % High marsh | 65.0 | 4.7 |
| N34 | Development + Restoration (absent, tidal flow restoration, or *P. australis* control) | 79.2 | 18.9 |

**Table 8** Parameter estimates, standard deviations, and credible intervals for the top presence models N4, N29, N9, and N30

**Nest model N4 (Vegetation structure, ΔDIC = 0.9)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | *2.5%* | *97.5%* |
| Global intercept | -2.94 (1.19) | -6.71 | 0.69 |
| Stem density | 0.15 (0.04) | 0.08 | 0.24 |
| Thatch height | 0.25 (0.15) | -0.04 | 0.056 |
| Mean maximum vegetation height | -0.12 (0.05) | -0.22 | -0.02 |

**Nest model N29 (Marsh size + Vegetation structure, ΔDIC = 0.0)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | *2.5%* | *97.5%* |
| Global intercept | -2.99 (1.9) | -6.76 | 0.68 |
| Marsh size | 0.01 (0.008) | -0.005 | 0.03 |
| Stem density | 0.16 (0.04) | 0.08 | 0.26 |
| Thatch height | 0.25 (0.15) | -0.05 | 0.56 |
| Mean maximum vegetation height | -0.12 (0.05) | -0.24 | -0.03 |

**Nest model N9 (% High marsh, ΔDIC = 4.6)**

| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | *2.5%* | *97.5%* |
| Global intercept | -3.86 (1.06) | -6.00 | -1.81 |
| % High marsh | 7.88 (2.11) | 3.95 | 12.19 |

**Nest model N30 (Marsh size + % High marsh, ΔDIC = 4.6)**

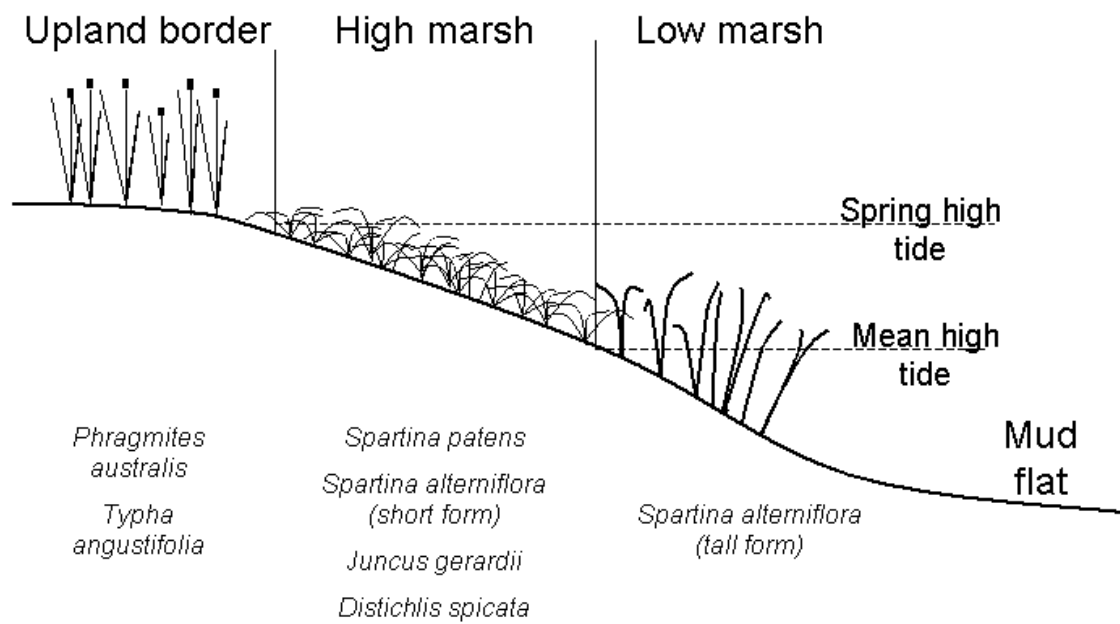| Variable | Parameter estimate (SD) | Credible interval | |
|---|---|---|---|
| | | *2.5%* | *97.5%* |
| Global intercept | -3.93 (1.08) | -3.91 | -1.88 |
| Marsh size | 0.007 (0.007) | -0.008 | 0.02 |
| % High marsh | 7.98 (2.13) | 4.04 | 12.37 |

**Fig. 1** Plant community zones within a salt marsh relative to tidal inundation (after Warren and Niering 1990)
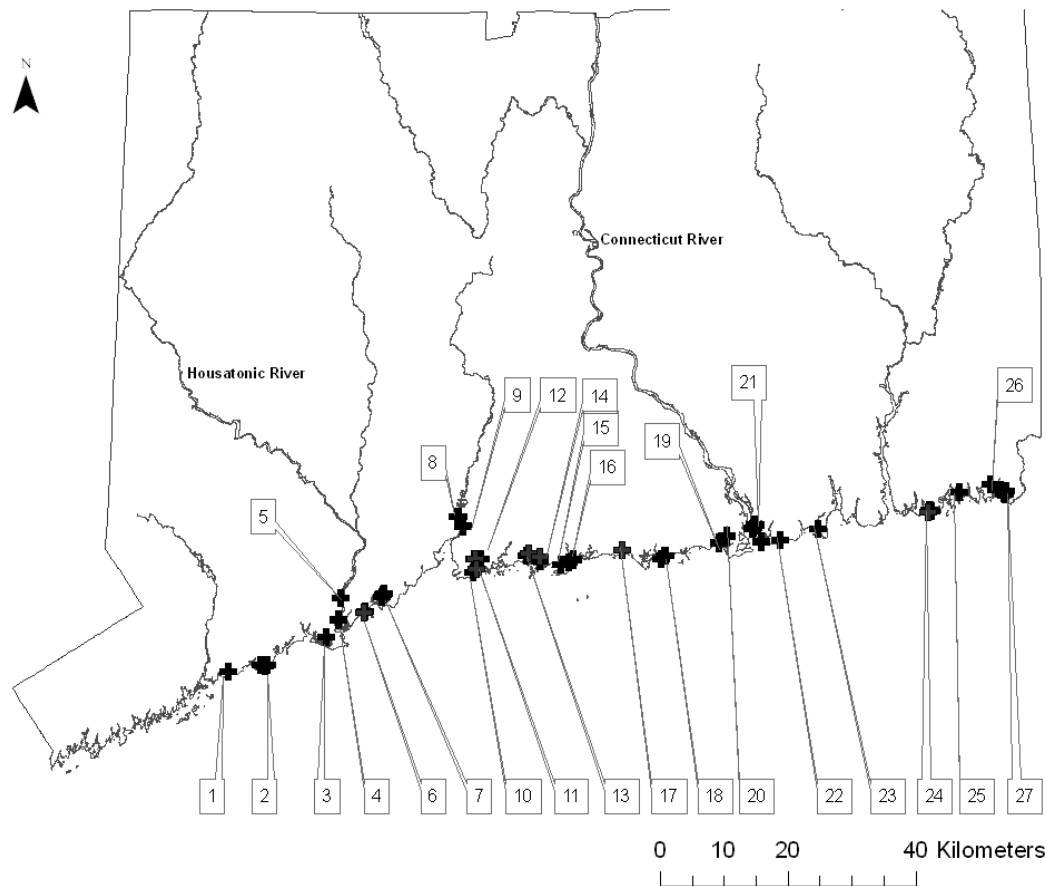
**Fig. 2** Sites surveyed for saltmarsh sparrows and their nests, 2006-2008.  1. Sherwood Island State Park, Westport.  2. Pine Creek, Fairfield.  3. Great Meadows NWR, Stratford.  4. Wheeler Marsh WMA, Milford.  5. Long Island, Stratford.  6. Silver Sands State Park, Milford.  7. Indian River, Milford.  8. Quinnipiac River WMA, New Haven.  9. Hemingway Creek, New Haven.  10. East Haven Land Trust, East Haven.  11. Farm River State Park, East Haven.  12. Upper Farm River, Branford.  13. Stony Creek and Pine Orchard, Branford.  14. Jarvis Creek, Branford.  15. Great Harbor, Guilford.  16. Long Cove and Chaffinch Island Park (West River), Guilford.  17. Fence Creek, Madison.  18. Hammock River, Clinton.  19. Mud/Hagar Creek, Old Saybrook.  20. Upper Oyster River, Old Saybrook.  21. Lieutenant River, Upper Island, and Great Island (Connecticut River), Old Lyme.  22. Mile Creek, Old Lyme.  23. Watt's Island, East Lyme.  24. Groton Long Point, Groton.  25. Cottrell Marsh, Stonington.  26. Paffard Marsh, Stonington.  27. Barn Island WMA, Stonington
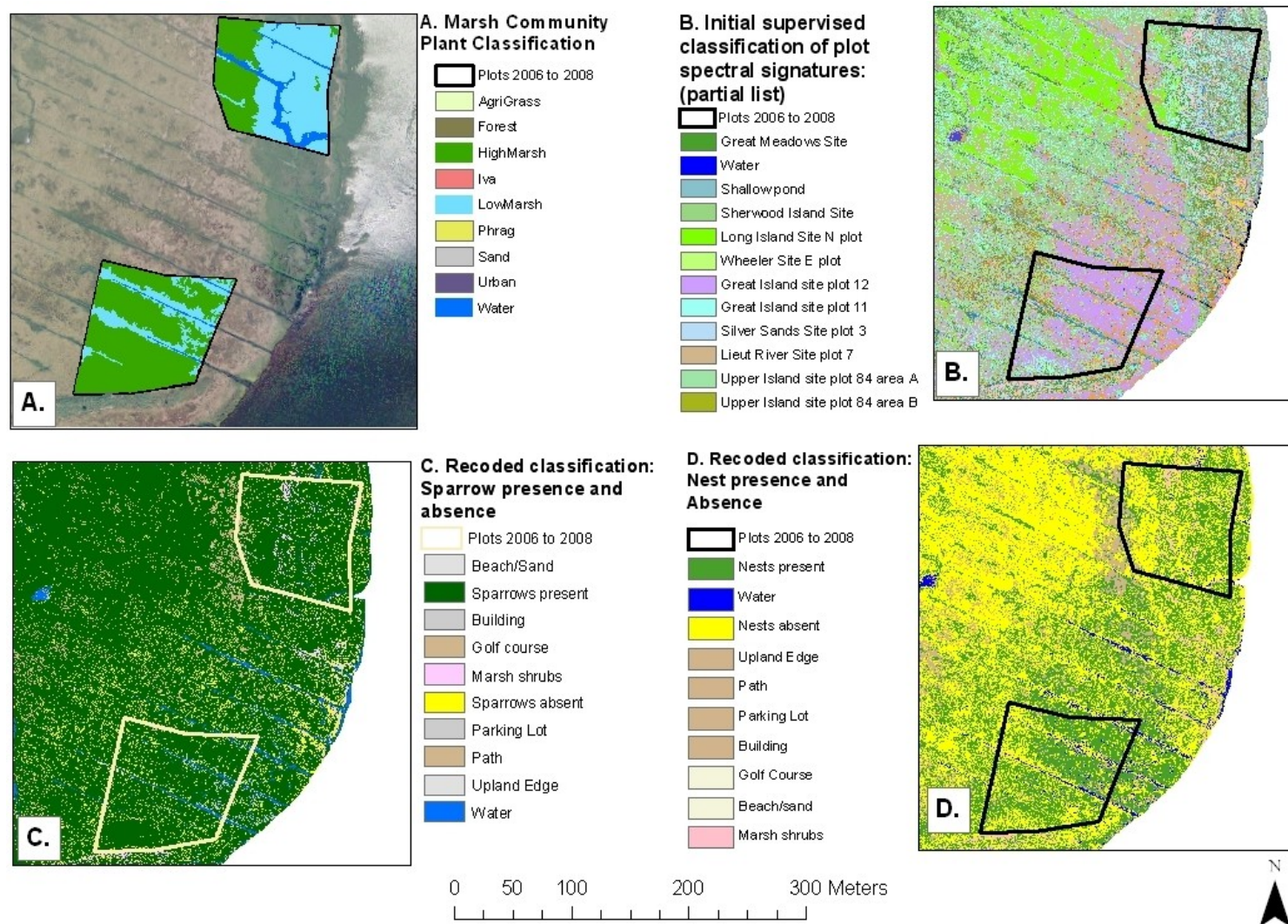
**Fig. 3** Two plots at Great Island in the Connecticut River characterized using remote sensing. **A**. Classification of marsh communities based on plant and elevation data (M. Hoover, unpublished data). **B**. Initial supervised classification based on library of spectral signatures built from all plots sampled in 2006-2008. **C**. Recoded pixel classification for sparrow presence categories: classification of each pixel according to whether saltmarsh sparrows had been detected in the plot on which the initial classification was based. **D**. Recoded pixel classification for nest presence categories: recoded classification of each pixel according to whether saltmarsh sparrow nests had been detected in the plot on which the initial classification was based
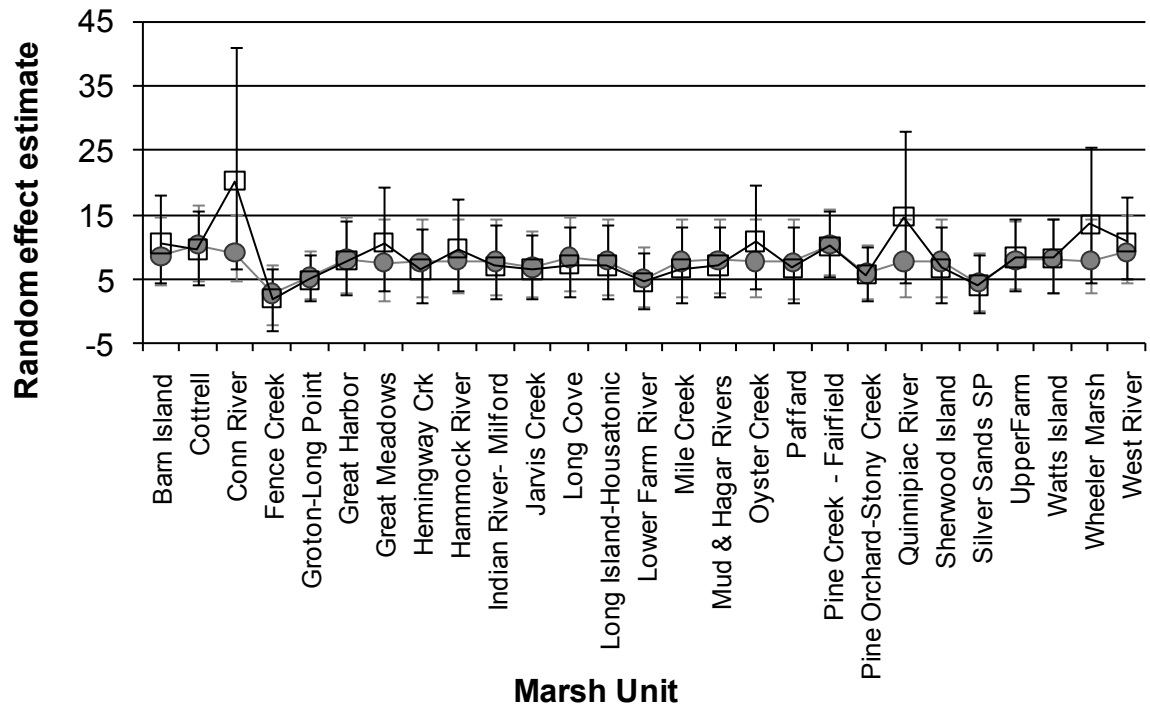
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**Fig. 4** Mean random effect estimates for marsh units from presence model P11, which included sparrow-absent pixels (gray circles), and from presence model P31, which included size + sparrow-absent pixels (open squares). Error bars represent 95% credible intervals around the mean
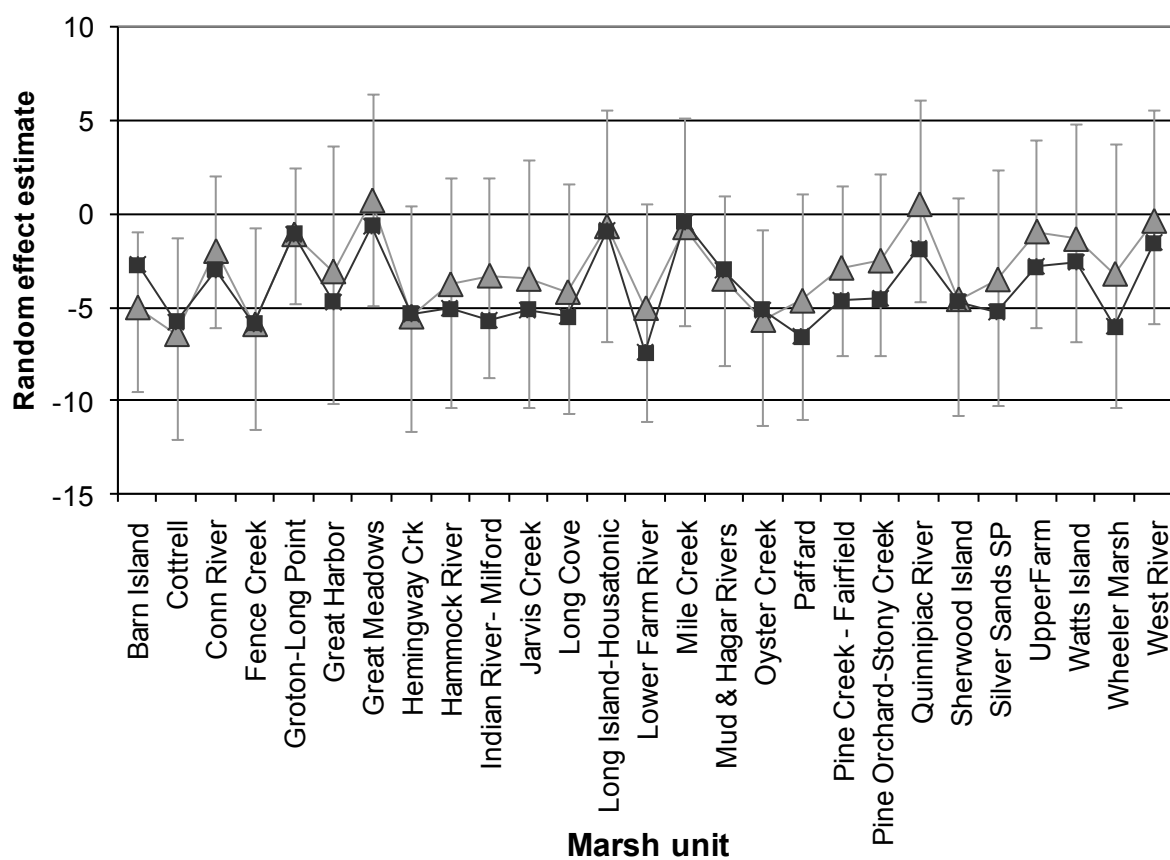
**Fig. 5** Mean random effect estimates for marsh units from nest model N4, which included vegetation structure (gray triangles), and from nest model N9, which included proportion of high marsh (black squares). Error bars represent 95% credible intervals around the mean

**APPENDIX A.  Correction of Elevation Data.**

The means of the digital surface model (DSM) and digital elevation model (DEM) for 1-ha plots declined from west to east along the coast of Long Island Sound (Fig. 6).  To assess how elevation was associated with sparrow presence without this gradient, I determined the relationship between mean elevation and longitude, and predicted the mean elevation of marshes at the longitude of each study plot.  Subtracting the predicted mean elevation from the mean elevation of the DSM gave a relative elevation corrected for the longitudinal gradient.

To accomplish this, I generated a 1-ha cell-size grid over the state-wide marsh polygon data layer (NOAA 2004), and randomly selected 150 samples.  Cells of less than 0.5 ha were discarded, leaving 137 samples.  A mean elevation was calculated for each cell from the DEM (Hoover 2009), and the center of the cell was used as the associated longitude (Fig. 7).  Each degree of longitude was associated with a 0.38 m change in elevation (95% confidence interval 0.29 - 0.47 m).

I used the regression equation generated from the random samples to predict the mean ground-return elevation for the longitude of each saltmarsh sparrow plot location.  I then subtracted the predicted mean elevation from the raw DSM of each plot to calculate an adjusted mean elevation (Fig. 8).
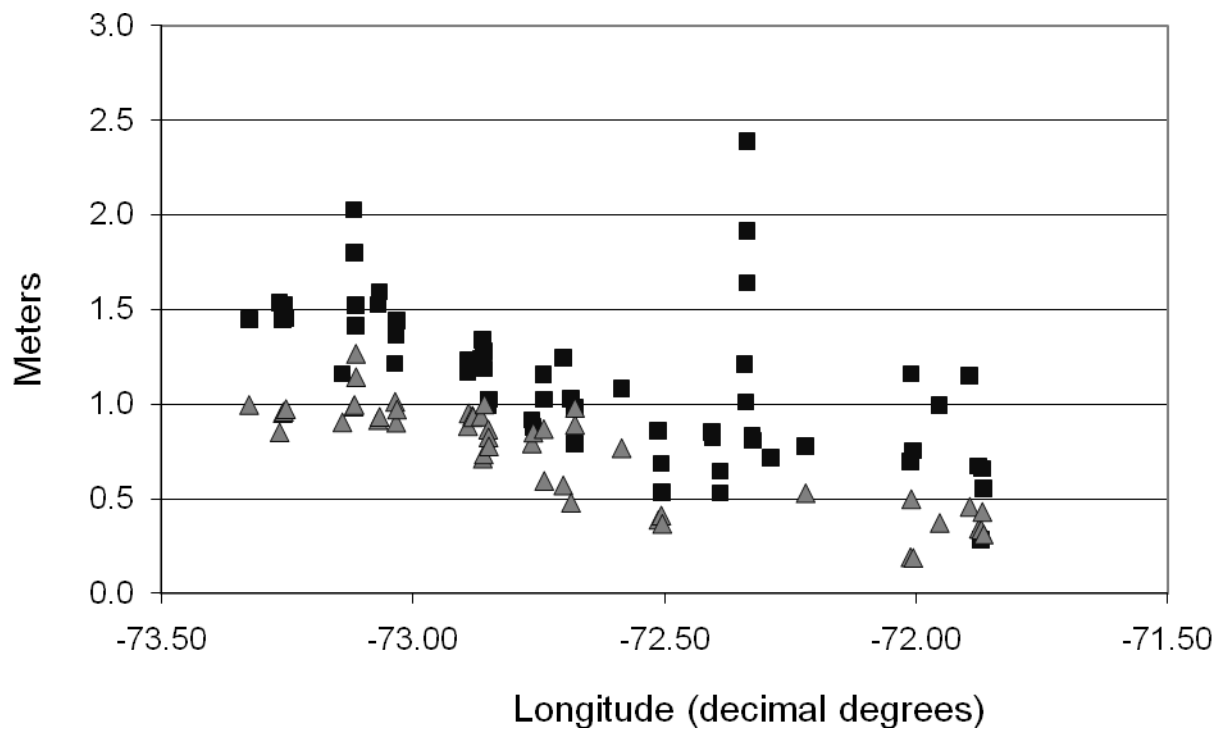
**Fig. 6** Mean elevations of 60 1-ha plots along the Connecticut coast, from west to east. Both the ground-return digital elevation model (DEM, gray triangles) and canopy-height digital surface model (DSM, black squares) data are shown. (The Connecticut River area was not included in the DEM data, so ground-return elevation data at those sites are unavailable.)
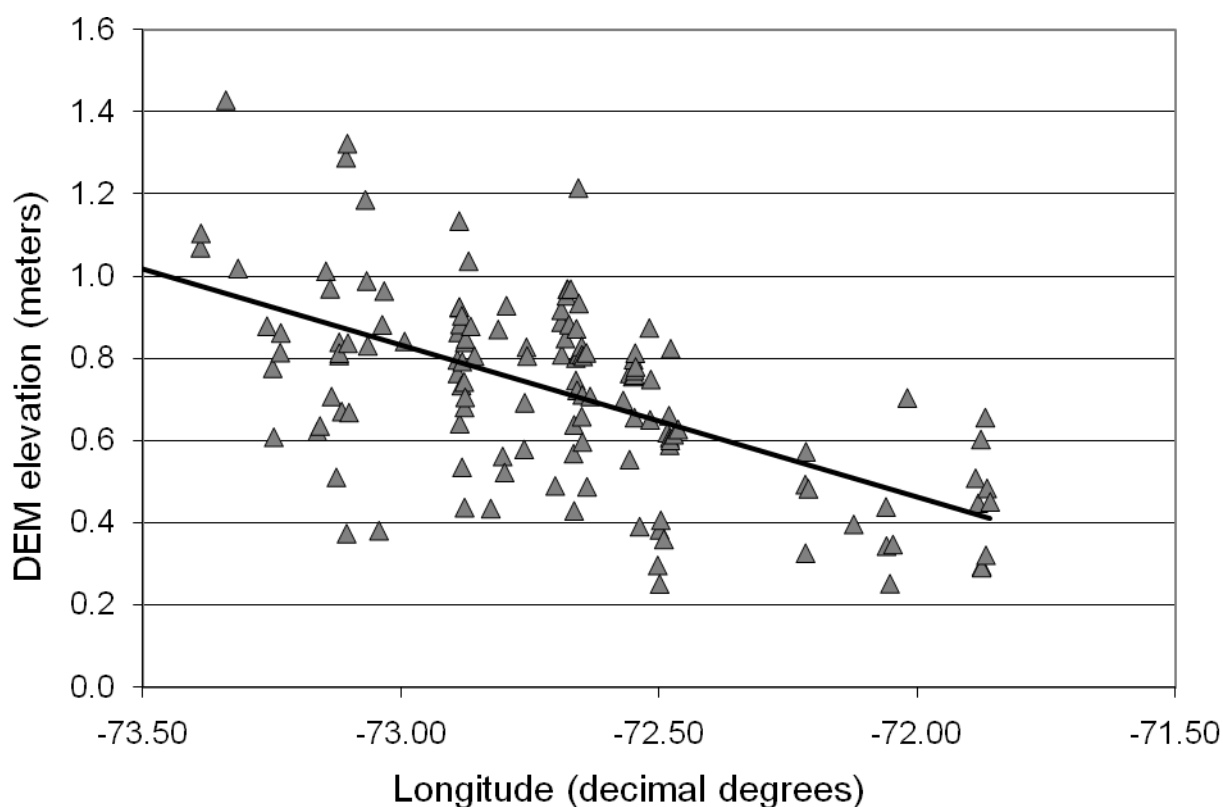
**Fig. 7** A fitted regression line for the mean elevation of 137 randomly-selected 0.5 - 1.0-ha marsh samples in Connecticut using the DEM (ground-return) data. Marshes in the Connecticut River area are not represented. A regression line calculated through the sample estimates that each degree of longitude (83.8 km) along the Connecticut coast was associated with a 0.38 m change in elevation (SE 0.05 m, $r^2$=0.35, p=0.001)
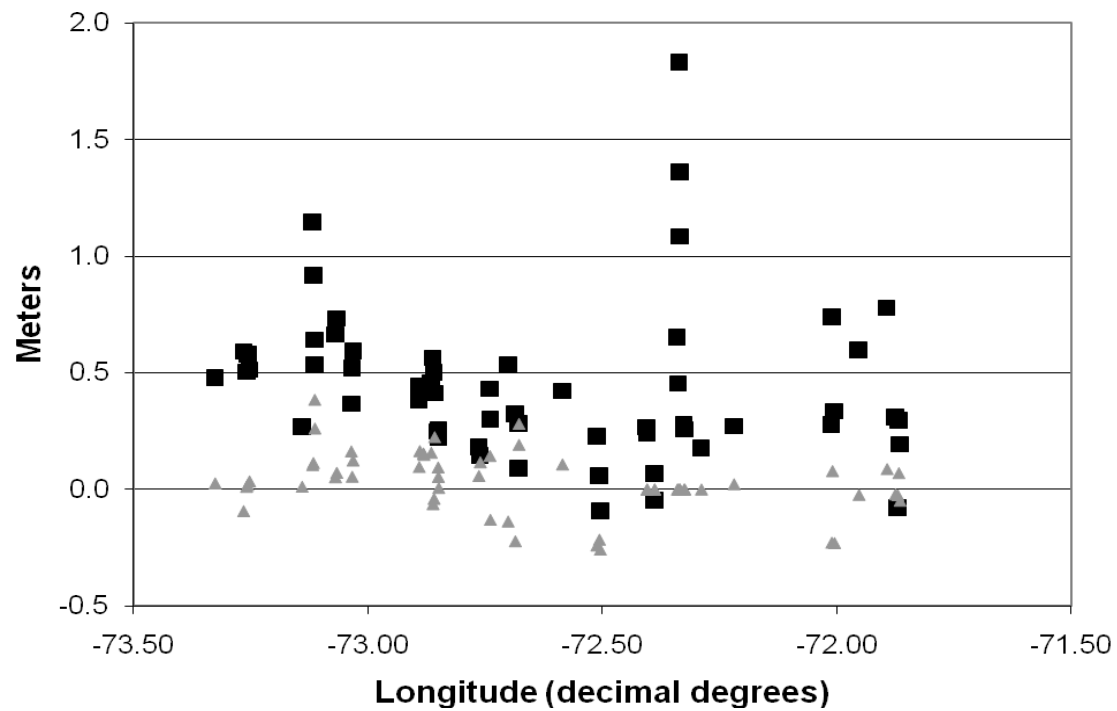
**Fig. 8** Using the regression equation generated from the random sample of 137 plots, I determined the mean ground-return elevation for the longitude of each saltmarsh sparrow plot location. I then subtracted the predicted mean elevation from the raw mean elevation of each plot. The adjusted mean elevations using ground return data (DEM, black squares) are shown with the adjusted mean elevations using the canopy-height data (DSM, gray triangles)

**APPENDIX B.  Generalized WinBUGS Code Used in All Models.**

**model**

```
{
#global intercept prior, included in all models
        global.intercept ~ dnorm(0,0.1)


# for each plot
        for (i in 1:60)
{
        presence[i] ~ dbern(p2[i]) #presence at the site is a Bernoulli distribution


        logit(p[i]) <- marsh.int[marsh[i]]+ slope.plotcharacteristic*plotcharacteristic[i] # the logit
of the probability is a linear relationship that includes a marsh-system random effect plus a
within-marsh characteristic.  I added additional plot characteristics here.
        p2[i]<-max(0.00001,min(0.99999,p[i])) # this line constrains the logit values to improve
stability
        }


#priors for marsh-system and plot-based variable coefficients
        slope.plotcharacteristic~dnorm(0,0.01)
        slope.marshcharacteristic ~dnorm(0,0.01)
#for each of the 27 marsh systems sampled
        for (j in 1:27)
        {
        marsh.int[j] ~ dnorm(marsh.int1[j], 0.1) #random effect of marsh system in which plot is
located (intercept) is normally distributed around the marsh factor, which is determined from the
next line,
        marsh.int1[j] <- global.int + slope.marshcharacteristic*marshcharacteristic[j] #marsh
factor  is determined by the global distribution and a marsh-level variable.  Additional marsh-
level variables were added here.
        }
}
```

# Chapter 2.  An Evaluation of Habitat Association Models of Saltmarsh Sparrow Occupancy and Nesting

**ABSTRACT**

Building habitat models that associate organisms with features of their environment can help identify areas of high or low priority for planning conservation strategies.  These models, however, need to be tested using new data before their conclusions should be widely accepted. Saltmarsh sparrows (*Ammodramus caudacutus*) are a species of growing conservation concern along the Atlantic Coast of North America.  In a previous study, I developed models for the distribution of saltmarsh sparrow presence and nesting habitat.  Sparrow occupancy was predicted using raw reflective properties of marshes, suggesting that the processes driving the reflective difference occur throughout the sampling region.  Sparrow nesting was predicted using a marsh plant community classification. To test these models, I surveyed a stratified random sample of sites for which the probability of sparrow presence had been predicted, and compared the observations to the predicted probability of presence and nesting generated from the models. Model performance, assessed by determining the area under a receiver operating curve and the model deviance, was significantly better than expected by chance alone. Tests of these models confirm that the area where sparrows are predicted to occur is much larger than the area where they are predicted to nest.  Consequently, monitoring sparrow presence will not be sufficient for indicating the most important nesting areas.

## I. INTRODUCTION

Two main reasons for modeling the associations between species presence and habitat features are to map predicted distributions and to understand ecological factors that influence the way that organisms interact with the environment (Wiens and Rotenberry 1981, Young and Hutto

2002). Maps generated from habitat association models then can be used to establish

conservation priorities, such as in GAP analysis (Scott *et al.* 1993), and refine the focus of future

research when little is known about the species of concern, as with the American fisher (*Martes*

*pennanti*) (Carroll *et al.* 1999) or the Jerdon's courser (*Rhinoptilus bitorquatus*) (Jeganathan *et al.*

2004). Increasingly, features of the environment are being described through the use of remote

sensing image data, which are then used to create habitat models. Although remote sensing can

cover larger areas than can be completely sampled on the ground, models derived from remote

sensing are rarely tested by examining the extent to which the model accurately reflects the

distribution of the species.

Applying remote sensing data to habitat modeling can take two approaches. First,

researchers use remote sensing data to classify features in the environment known to be

associated with the organism of interest. With this approach, the components of a species' habitat

are assumed to be known, and the remote sensing data are organized to represent these

components as accurately as possible. Many studies over the last few decades have used this

approach; for instance, Gottschalk *et al.* (2005) reviewed 109 studies that used satellite imagery

to model habitat for birds alone. Frequently, habitat data take the form of land cover types, as in

Klute *et al.* (2002), who modeled eight forest types to describe American woodcock (*Scolopax*

*minor*) habitat, and Debinski *et al.* (1999), who used Landsat data to discriminate between three

forest types and six meadow types to delineate habitat for butterflies. Other studies organize data

in ways that describe plant structure and heterogeneity, such as in Gibson *et al.* (2004), who

generated a model of vegetation structural complexity using low altitude videographic imagery to

model the habitat of rufous bristlebirds (*Dasyornis broadbenti*). Yet another strategy is to

classify topographic details that influence microhabitat conditions or abiotic processes. For

example, Shriner *et al.* (2002) used slope and aspect calculated from digital elevation data to

predict habitat for wood thrushes (*Hylocichla mustelina*). These *a priori* classifications can be

used to dissect how individual features influence species distributions, and allow comparisons between different species of interest and between data sources (Guisan and Zimmerman 2000).

The second approach uses remote sensing data in a more exploratory way to identify which aspects of the landscape are associated with the organism's presence. Subsequent analysis then attempts to link the identified areas with biological processes that can explain the pattern. For example, Hepinstall and Sader (1997) built habitat association maps for 14 species of birds with raw reflectance data, bypassing the effort and errors associated with first generating a land cover classification. Bellis *et al.* (2008) found that variables describing image texture modeled greater rhea (*Rhea americana*) habitat more effectively than did land cover types. In another study, St-Louis *et al.* (2009) used satellite image texture as a surrogate for habitat structure and vegetation variables such as the normalized difference vegetation index (NDVI) derived from raw spectral reflectance as surrogates for plant productivity to model avian biodiversity in the Chihuahua Desert. Because remote sensing data are expected to reflect integration of many habitat features (Fisher 1997), this second approach can be used to evaluate suites of conditions under which the organism occurs.

Both approaches assume that the target organism benefits from the space in which it is usually found (Rotenberry 1981, Gottschalk *et al.* 2005). With increasing reliance on remote sensing data for conservation planning (Elith and Leathwick 2009), it is especially important to test the assumption that there is predictive power to the associations observed in models built using remote sensing data. Although habitat models can be evaluated using approaches such as splitting data sets, jackknifing, or data resampling (Pearce and Ferrier 2000, Elith and Leathwick 2009), the best test of the extent to which a habitat model can be generalized beyond the data on which it is based is its ability to predict the presence of the target species at a completely new set of sites (Fielding and Bell 1997, Henebry and Merchant 2002).

Saltmarsh sparrows (*Ammodramus caudacutus*) breed in salt marshes along the mid-Atlantic and New England coast of eastern North America. Because this species is most

abundant in southern New England (Greenlaw and Rising 1994), the salt marshes of that area are considered to be especially important to its conservation (Dettmers and Rosenberg 2000). Females nest near the ground, which makes the nests vulnerable to tidal flooding (DiQuinzio *et al.* 2002, Shriver *et al.* 2007, Gjerdrum *et al.* 2008a, Bayard 2010, Bayard and Elphick 2011). Males are not territorial and provide no parental care (Woolfenden 1956, Greenlaw and Rising 1994), and both male and female sparrows are frequently found in areas where nesting does not occur (Chapter 1). Consequently, sparrow presence does not necessarily indicate that conditions are suitable for nesting, even during the peak breeding season. As a result, conservation strategies need to account for differences between marsh areas where sparrows occur and those where nesting takes place.

In Chapter 1, I examined a set of alternative models designed to explain variation in the distribution and nesting activity of saltmarsh sparrows. These models examined a wide range of variables generated from both field and remote sensing data, and collectively tested the importance of plant composition, vegetation structure, marsh spectral characteristics, the distance from the marsh's upland edge, whether and how marsh restoration had occurred at a site, and landscape-level features of the marsh. The sparrow presence model that best fit the data used a variable derived from raw spectral reflectance values associated with plots where sparrows did not occur. Nest presence, in contrast, was modeled best using vegetation structure variables that required data collection on the ground. Collecting this type of ground data over large areas, however, is not feasible, so the best nest model cannot generate regional predictions of where nesting habitat exists. An alternative model, which used a measure of the amount of high marsh habitat that was derived from remote sensing data, received almost as much support as the best model, and was proposed as the best option for predicting the distribution of nesting habitat in new areas.

The objective of the current study was to test predictions of the best model for sparrow presence, and the best remote sensing model for nest presence, using data from a new set of sites.

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I surveyed a stratified random sample of marsh conditions for sparrows, and compared the observations to the predicted probabilities of presence and nesting generated from each model. Because the model for presence and the model for nests each used a different approach in linking the sparrows with habitat conditions, evaluating both models offers an opportunity to examine the different inferences and expectations from remote sensing habitat models. In addition, the predictive maps derived from the two models provide detailed information about the current distribution of saltmarsh sparrows in Connecticut.

**II. METHODS**

To generate regional maps of predicted sparrow presence I used a model based on a supervised classification of saltmarsh pixels, which previous work showed to provide a better fit than alternative models (Chapter 1). This classification determined whether each pixel of saltmarsh habitat in the region had spectral characteristics that corresponded to marsh areas in previously surveyed plots where sparrows were either confirmed to be present (designated "sparrow-presence pixels") or not found despite extensive surveys ("sparrow-absent pixels"). The model predicted that increasing proportions of sparrow-absent pixels were associated with a decreasing probability of saltmarsh sparrow presence. The full equation describing this relationship was the following, in which SD refers to the standard deviation for each coefficient:

Logit of predicted probability of sparrow presence within 1 ha = 7.31 (SD 1.5) – 0.17 (SD 0.05) x proportion of sparrow-absent pixels .

A grid of 1-ha cells was overlaid across all of Connecticut's salt marshes, and the proportion of sparrow-absent pixels within each grid cell was calculated. To ensure I sampled areas across a wide spectrum of prediction probabilities, I organized cells into three groups: cells with <20% sparrow-absent pixels, cells with 20-40%, and cells with >40%. These three

categories approximately correspond to sites that are almost certain to have sparrows ("high expectation"), those that have a 50-95% chance of having sparrows ("medium expectation"), or those that have a <50% chance of having sparrows ("low expectation"). I generated predictions using WinBUGS (Spiegelhalter *et al.* 2000), where the uncertainty about model structure as well as uncertainty around parameter estimates could be propagated throughout the model-fitting process to the predictions.

Randomly sampling 24 cells from each of the three categories, I selected 72 cells to visit during field tests between 25 May and 25 August 2009. In the field, I placed 0.5 ha plots within the chosen cells, or as close to the original selection as logistically possible. In two cases, minor shifts in location caused the classification of the sample site to change, such that the final samples for the high, medium, and low expectation categories were 26, 23, and 23, respectively. The sampled cells occurred in 29 marsh systems that ranged from Sherwood Island State Park in Westport, CT to Barn Island Wildlife Management Area in Stonington, CT (Fig. 1A; Appendix C lists the latitude and longitude of all test plots). I conducted 10-min point counts in each plot to determine whether sparrows were present. All counts took place before 11:00, and I recorded all sparrows seen and heard within the plot. After each point count, I slowly walked back and forth throughout the entire plot, and recorded any sparrows not detected during the point count. Sites where no sparrows were detected were repeatedly surveyed, at least two weeks apart, either until I encountered sparrows or until four visits had been completed. I set the number of surveys required to establish absence after calculating detection probabilities from previous survey efforts in Connecticut salt marshes (C.S. Elphick and S. Meiman, unpublished data). Using data from 40 sites surveyed in 2007 and 2008, I calculated the probability of detecting at least one sparrow in a 5-min point count using PRESENCE 2.0 (Hines and MacKenzie 2004). From the most parsimonious model with the best fit, a constant-probability model, I estimated that four visits to a site reduced the probability of missing sparrows if they were present to less than 5%. By using

longer (10-min) point counts combined with area searches, the chance of detecting sparrows if present at my survey points should have been very high.

During 2009, I also surveyed the sampled cells for nests. The best remote sensing model for nest locations used the proportion of high marsh habitat within a 1-ha plot, which was derived from a GIS data layer that delineated plant community classifications (Hoover 2009; Chapter 1). This data layer was not available for the entire state prior to the field test, so I used the same sampling frame selected for the sparrow presence model to evaluate the nest presence model. The full equation describing the relationship between nest density and the amount of high marsh was:

Logit of probability of nest presence within 1 ha = -3.86 (SD 1.07) + 7.88 (SD 2.11) x proportion of high marsh.

After the field season, plant community data became available for all of my study sites and I was able to determine the percentage of high marsh habitat within each of the test cells. This allowed me to classify cells into three groups according to their likelihood of containing nesting birds based on the model. Cells with <20% high marsh had a <10% predicted probability of nest presence ("low expectation"), cells with 20-50% high marsh had a 10-50% predicted probability of nest presence ("medium expectation"), and cells that consisted of >50% high marsh had greater than 50% predicted probability of nest presence ("high expectation") (Fig. 1B).

To determine whether birds were nesting in the test cells, I watched for birds flying with food or fecal sacs during the point counts and subsequent time spent in the plot. After each point count survey, I also searched for nests in the plot by slowly walking back and forth throughout the area in a zig-zag fashion and located nests by noting the point from where birds flushed. At sites where sparrows had been found but where nests had not, I conducted additional searches at approximately 2 week intervals until a minimum of 3 nest searches had been completed. To

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evaluate how well I was able to detect nests using this search pattern, I analyzed nest detection probabilities after the 2009 survey season using the program PRESENCE 2.0 (Hines and McKenzie 2004), and estimated that in plots where sparrows occurred, 3 visits were sufficient to have less than a 5% probability of missing a nest if it was present.

I evaluated each models' predictions in three ways. First, I calculated the area under a receiver operating curve (AUC) for each model as a measure of model performance. This is a single measurement of model performance that does not depend on designating a threshold for prediction of presence (Fielding and Bell 1997), and is relatively robust to differences in prevalence (Manel *et al.* 2001). Values of AUC can range from 0.5, in which the model decisions of positive and negative outcomes are not better than random, to 1.0, in which the model discriminates perfectly between positive and negative predictions. To compare the model performances between test data and training data, I also calculated the AUC for the data used to build the models.

Second, I calculated an index of how much the field data deviated from the predictions. For each cell, I determined the difference between the observation (1 = present, 0 = absent), and the predicted probability (values ranged from 0 - 1). I then took the sum of the deviations and compared it to the distribution of the same deviance indices derived from 1000 dummy datasets, in which the same number of presences were randomly assigned to the same predicted probabilities.

Third, to assess each models' ability to predict absences in the low probability category and presences in the high probability category, I determined how many of the cells that were predicted to have a <50% chance of containing sparrows actually lacked them, and how many cells predicted to have a >95% chance of containing sparrows actually had them. For the nest model, I determined how many cells that were predicted to have a <10% chance of having nests actually lacked them, and how many cells predicted to have >50% chance of containing nests actually had them.

Finally, I examined the actual distribution of the sparrows and nests. I mapped the observed presences and absences to determine whether a) they were concentrated in certain areas, b) prediction errors were concentrated in certain areas, and c) there were areas where both models generated errors.

## III. RESULTS

Based on the presence model, saltmarsh sparrows are expected to occur in most of the saltmarsh habitat in the study region. Of the 3,738 ha of salt marsh for which probability of sparrow presence was predicted, 66% had a high expectation of saltmarsh sparrows presence, 28% a medium expectation, and 5% a low expectation. Overall, the mean predicted probability of presence was greater than 95% for most of the major marsh systems (Fig. 2, Appendix D). Of the marshes where mean predicted probabilities were high, some had uniformly high probabilities across the whole marsh, while others did not. For example, all cells in the Wheeler Marsh at the mouth of the Housatonic River in Milford and in the Hammock River marsh in Clinton were predicted to have presence probabilities of at least 85%. In contrast, the marshes on the East River in Guilford and the Quinnipiac River in New Haven included areas where the probability of sparrow presence was predicted to be as low as 15% and 20%, respectively. Yet other sites had much more variable suitabilities. For example, the marshes on the Upper Farm River in Branford had a mean predicted probability of sparrow presence of 63% with predictions for individual cells that ranged from 2% to 99%.

I detected saltmarsh sparrows in 50 of the 72 cells sampled. As expected, sparrows were most often detected in cells predicted to have a high chance of containing them, and least often detected in cells predicted to have a low chance (Fig. 3). The AUC for the presence model was 0.70, indicating that predictions were better than random, but poorer than that obtained for the training data (0.88). Overall, the deviance between the model's predictions and my field

observations was far lower than expected by chance (43.0 versus a mean of 63.8 for the null distribution, p < 0.001, Fig. 4).

Finally, I examined the model's ability to classify cells correctly. Sparrows were absent at fifty percent of sites classified as having a <50% ("low") chance of containing sparrows, and sparrows were present at 85% of sites classified as having a >95% ("high") chance of containing sparrows.

The nest model predicted that 43% of the marshes across Connecticut had a low probability of sparrows nesting, 27% had a medium probability, and 29% had a high probability. Within each of the major marsh systems, cells occurred that had <2% predicted probability of sparrow nests as well as cells predicted to have >95% probability of nests. The mean predicted probabilities within marsh systems ranged from 12 to 54% (Fig. 2, Appendix D).

For the test of the nest model, 61 cells met the minimum criterion of at least three visits and were included in subsequent analyses. I found nests in 19 (31%) of these cells, a majority of which were classified as having a high chance of containing nesting birds (Fig. 5). Only two of the 28 cells predicted to have a low chance of containing nesting sparrows did so. The AUC calculated for the test data was 0.79, compared to an AUC of 0.78 for the training data. The total deviance between the predicted probabilities and the nest presence/absence data was significantly less than expected by chance (28.9 versus a mean deviance of 48.8 for the null distribution, p < 0.001, Fig. 6). Because only one of the 42 nests I found successfully fledged young (due to high failure rates associated with repeated tidal flooding in 2009; Bayard and Elphick 2011), no analysis to examine levels of reproductive success associated with amount of high marsh in a cell was possible. I found no nests at 92% of the sites classified as having a <10% ("low") chance of having nests present, and located nests at 54% of sites classified as having a >50% ("high") chance of containing nests.

The presences, absences, and prediction errors for both models were distributed across the entire study region (Fig. 7, 8). Combining information from both models showed one cell had

a high expectation for both sparrow presence and nest presence but had no sparrows (Sasco Creek in Westport). There were conflicting predictions from the two models (low probability of sparrow presence and high probability of nest presence) for four cells, of which two had sparrows and nests present (Cottrell Marsh in Stonington and Pine Creek in Fairfield), while one had sparrows but no nests (Bluff Point in Groton), and the other had no sparrows (a second plot in Cottrell Marsh in Stonington).

## IV. DISCUSSION

The predictions generated by the models discriminated between areas where sparrows and nesting did and did not occur fairly well. Cells predicted to have a high likelihood of containing sparrows or nests had the most presences, while those predicted to have a low likelihood had the least. Model deviances and AUC measures indicated that predictions from both models were better than expected by chance alone. The presence model predictions were worse using test data than when the original training data were used, but the performance of the nest model was remarkably similar for both data sets.

Although the predictions were quite good, they were not perfect. Model errors may be caused by errors introduced while processing the remote sensing data, leading to habitat misclassification. While many studies that use remote sensing data have tested processing accuracy, the focus of this study was to test whether the processing results could be used to predict an organism's occurrence, as increasing the precision of a poor predictive variable would not lead to improved model performance. Because the pixel classifications were built using presence data, the model may have been overfit to the original plot characteristics. Additionally, the plots used for training data may not have included all salt marsh elements that sparrows avoid, or some marsh elements that sparrows avoid may lack unique spectral characteristics.

Other errors may be due to factors such as competition or population dynamics, which can affect whether an organism is actually found in areas of suitable habitat. For instance, by

varying life history parameters of greater gliders (*Petauroides volans*) in simulated landscapes, Tyre *et al.* (2001) found that habitat elements, which were perfectly delineated in the simulations, were unable to explain more than half of the variability in species occupancy because of the confounding effects of demographic stochasticity and dispersal limitation. In a study by Rotenberry and Wiens (2009), models for shrubsteppe bird species generated using data about habitat associations collected between 1977 and 1983 were used to predict occupancy in 1997, in the same areas that had originally been studied. Although bird abundance and distributions in the region remained similar, few of the models performed well (Rotenberry and Wiens 2009). These discrepancies suggest that the inferences that can be drawn from predictive distribution maps that have been built from remote sensing data depend on how closely the modeled variables relate to critical aspects of the organism's biology (Guisan and Zimmerman 2000, Austin 2002, Van Horne 2002).

High marsh, the predictor variable for the nest model, combined elements of elevation and vegetation composition. Both of these elements previously have been demonstrated to have important associations with sparrow nesting. Minor elevation differences affect the risk of flooding (Gjerdrum *et al.* 2005, Gjerdrum *et al.* 2008a, Bayard and Elphick 2011), while several high marsh plant species contribute to a vegetation structure that is associated with nests (Gjerdrum *et al.* 2008b). Until a sufficiently detailed habitat classification GIS layer was built, however, the extent to which high marsh can be used as a predictor of sparrow nesting could not be established. In this study, sparrow nests were consistently absent where the amount of high marsh delineated within a hectare was less than 20% (low predicted probability class). Areas with greater proportions of high marsh at the 1-ha scale should be considered of higher priority for conservation planning for saltmarsh sparrows than areas with less high marsh, even if sparrows occupy the latter areas.

The map generated using the nesting model directly links habitat to reproduction and has specific implications for saltmarsh sparrow conservation and management. In addition, because

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the nest model was built using a predefined high marsh community classification, this model is likely transferable to other areas where saltmarsh sparrows occur, as long as high marsh is classified in the same way and the birds' nest site selection behavior is similar. Maps of this habitat could then be used to identify priority sites for sparrow conservation and to track the availability of suitable habitat over time.

On the other hand, the reasons why the main predictor variable in the sparrow presence model is ecologically important to saltmarsh sparrows are unclear, making interpretation of the map produced by that model more difficult. The sparrow presence model was built on the premise that areas of marsh that sparrows do not occupy have different reflective properties than the areas they do occupy. Sparrow occupancy was predicted with moderately good accuracy in new areas using these reflective properties, suggesting that the processes driving the reflective difference occur throughout the sampling region. However, the remote sensing data used to generate the pixel classifications were collected under specific conditions of season, time, tide, and resolution  Unless data from other areas are collected under very similar conditions, this model may not work well elsewhere.

Currently it is not known whether areas that are occupied but not used for nesting are needed to sustain sparrow populations. This study highlights two elements that require investigation. The first is to determine what the sparrows do in these areas, and whether it is likely to affect populations if these areas disappear. Second, it is important to determine how the reflective properties of occupied sites relate to saltmarsh sparrow biology. Reflective characteristics may differ due to divergent growth responses of plants that have been subjected to different durations of tidal inundation. Inundation pattern could be associated with sparrow occurrence simply because it affects the amount of suitable foraging habitat, or it could directly affect prey resources. Targeting areas predicted to have high versus low chances of containing sparrows to test specific hypotheses about environmental conditions that cause the different reflectance properties might clarify the underlying biological relationships.

Of the saltmarsh area in Connecticut, two-thirds was classified as having at least a 95% chance of having sparrows present.  In contrast, 29% of the saltmarsh area was predicted to have a high (>50%) chance of containing nesting sparrows.  Because the total area where reproduction is likely to occur is much smaller than the total area where sparrows are likely to be found, monitoring saltmarsh sparrow populations should focus primarily on the areas where there is a high chance of nesting. Methods that simply record whether the species is present will not be adequate for inferring whether there is any associated reproductive behavior.  In addition, the wide disparity between the predictions for sparrow presence and sparrow nesting at several marsh systems (Fig. 2) warrants a closer examination of the reasons for sparrow activity in some of these areas.

One reservation that has been expressed in the application of remote sensing data to habitat model building is that the form used in the model can be several steps removed from a proximal causes of presence or absence (Henebry and Merchant 2002, Van Horne 2002).  However, directly linking elements identified in remote sensing to how an organism interacts with its environment requires prior knowledge about the organism.  This study used the association of remote sensing data with saltmarsh sparrow presence because previous work had shown that prior knowledge was insufficient to explain and predict distribution patterns (Gjerdrum et al. 2008b).  By generating a map that details the distribution of a useful predictor variable, the differences between areas with and without the species can be more closely examined.  This strategy has been adopted for regional assessment of habitats associated with the occurrence of a variety of species (e.g., white-throated sparrows *Zonotrichia albicollis,* Tuttle et al. 2006; redtail monkey *Cercopithecus ascanius,* Stickler and Southworth 2008; Alaotran gentle lemur *Hapalemur alaotrensis* Lahoz-Monfort et al. 2010).  These studies all used remote sensing to detect within-class variability not easily detected using general land cover classes.  Because remote sensing can be used to detect both direct and indirect mechanisms that affect presence and reproduction, it is a useful tool for conservation planning.

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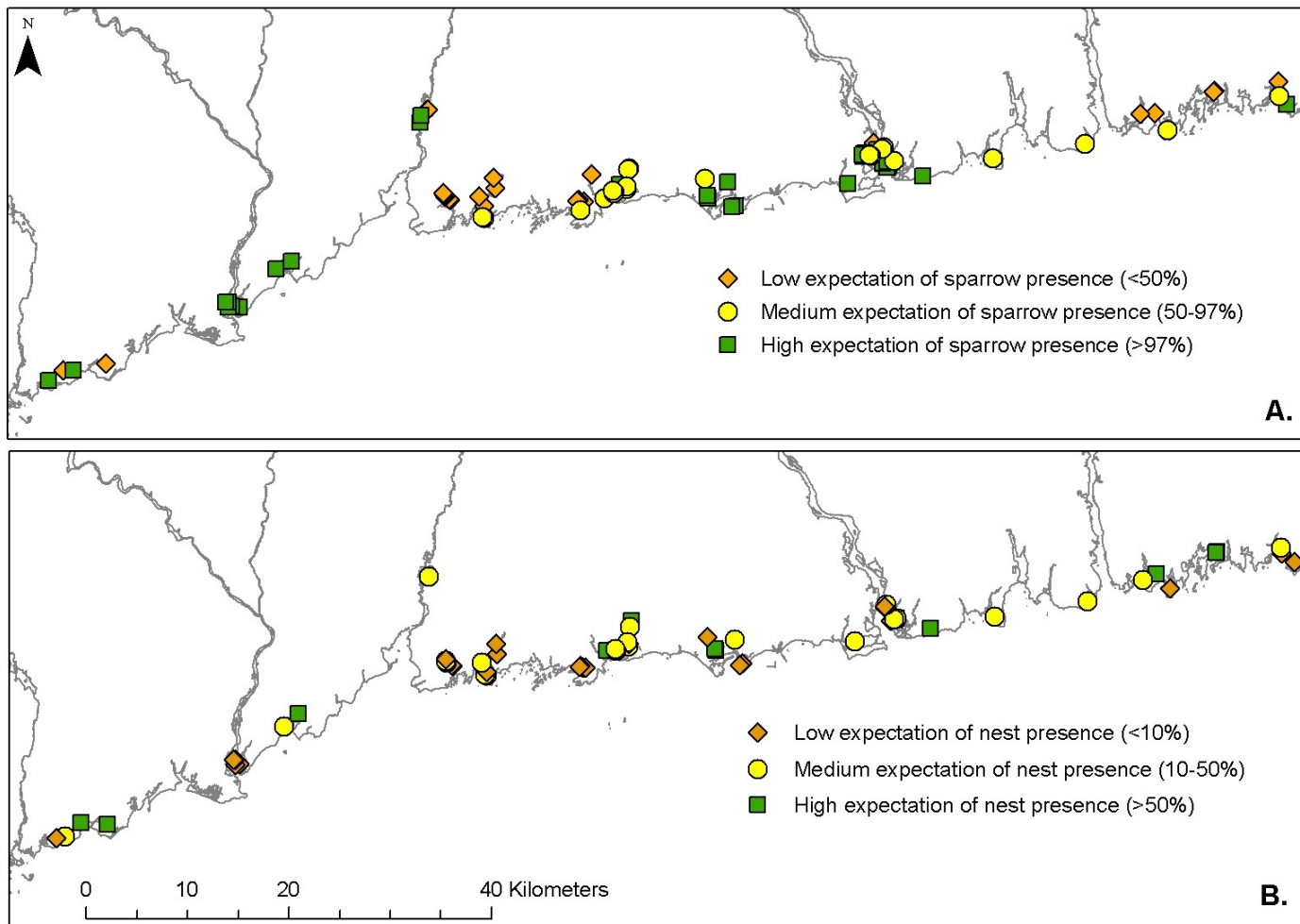
**Fig. 1A** Locations and predicted probability categories of the 72 cells used to evaluate the saltmarsh sparrow habitat model in Connecticut in 2009. Cells were randomly sampled from the three categories of predicted presence probability. **B**. Predicted probability of saltmarsh sparrow nest presence at 61 of the 2009 survey locations for which sampling was sufficient to establish presence or absence of nests. Categories of expected nest presence were assigned after the field surveys had been conducted
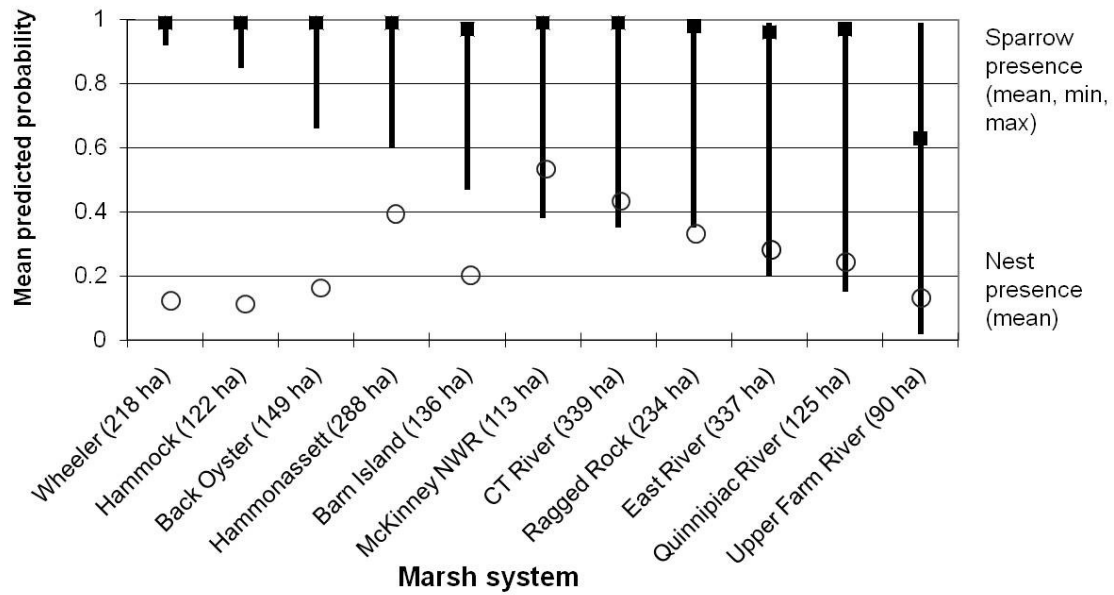
**Fig. 2** Predicted probabilities of sparrow presence (black squares indicate marsh-wide mean, lines represent the range from min to max) and nest presence (open circles) in the largest (>90 ha) marsh systems studied. Nest presence prediction probabilities for all marshes ranged from 0 to 1, and so ranges were not illustrated
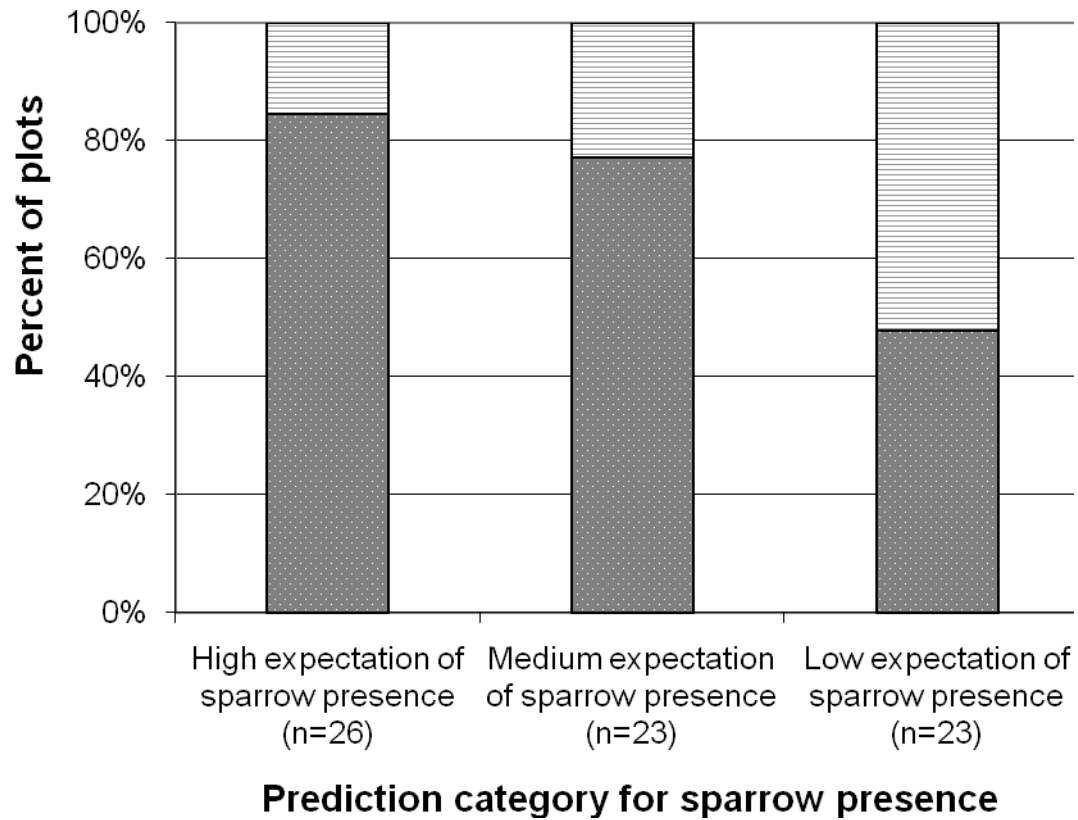
**Fig. 3** Observed saltmarsh sparrow presence rates in cells predicted to have high (>95%), medium (50-95%), and low (<50%) predicted chances of containing sparrows. Dark gray indicates sparrow presence, and pale gray indicate sparrow absence
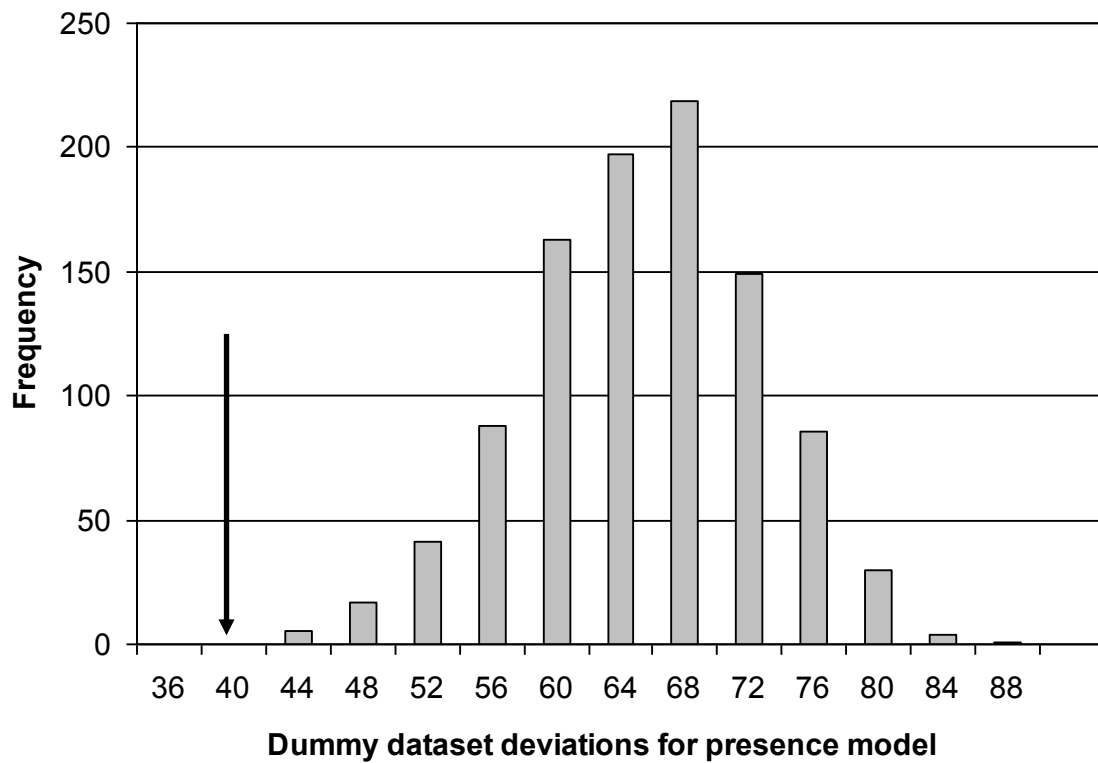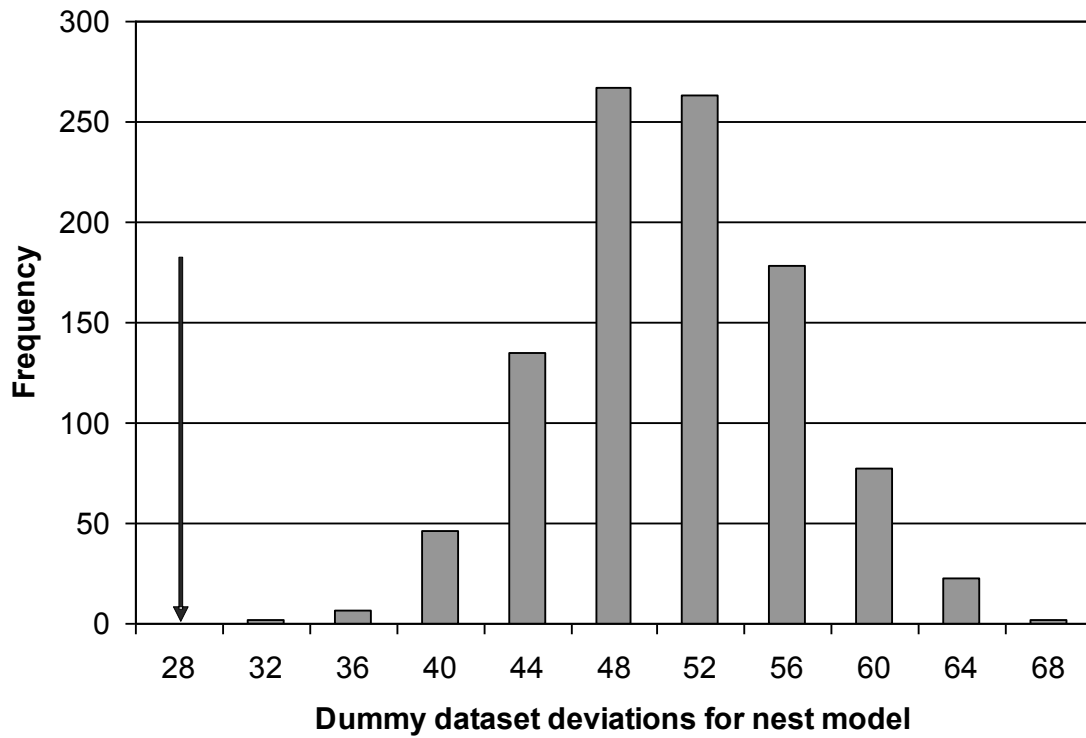
**Fig. 4** Deviance of observed data (indicated by arrow) relative to deviations from 1000 dummy datasets that had the same number of sparrow presences randomly distributed across sampled sites. Deviances were calculated as the sum of the differences between the observed data (sparrow presence = 1, sparrow absence = 0) and the predicted probability of presence at each site
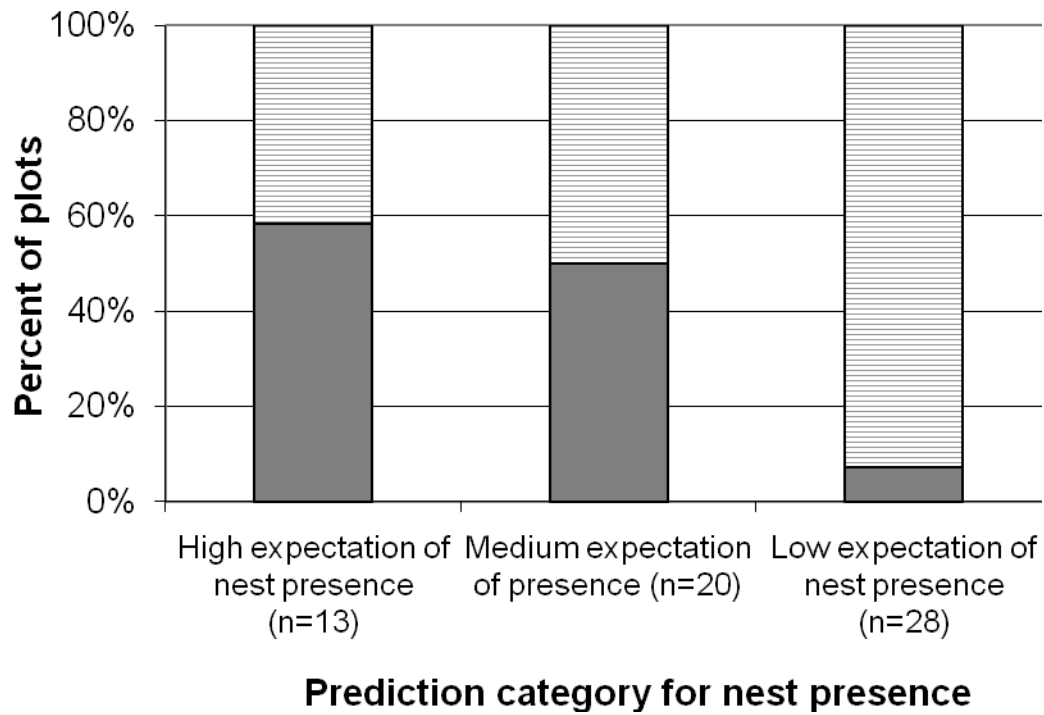
**Fig. 5** Proportion of sampled cells with nesting saltmarsh sparrows for cells with high (>50%), medium (10-50%), and low (<10%) predicted chances of supporting nesting. Dark grey indicates nest presence, and pale gray indicate no nests were found

**Fig. 6** Deviance of observed data (indicated by arrow) relative to deviations from 1000 dummy datasets that had the same number of nest presences randomly distributed across sampled sites. Deviances were calculated as the sum of the differences between the observed data (nest presence = 1, nest absence = 0) and the predicted probability of presence at each site
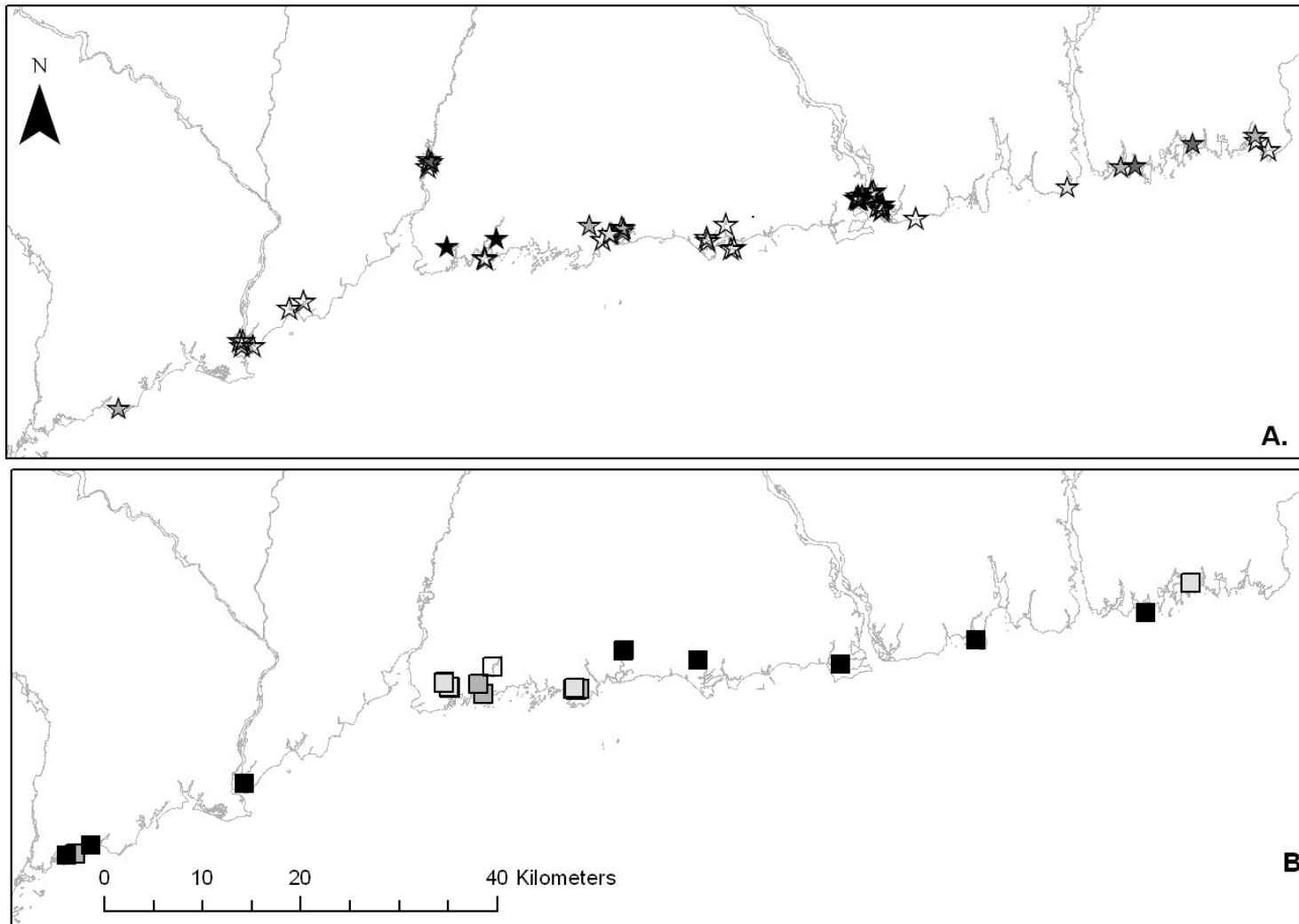
**Fig. 7** Maps showing magnitude of sparrow presence prediction errors for each sampled cell. Darker colors indicate greater deviances between the model predictions for each site and the observations. Panels show accuracy of predictions for (A) the presence of sparrows, (B) the absence of sparrows
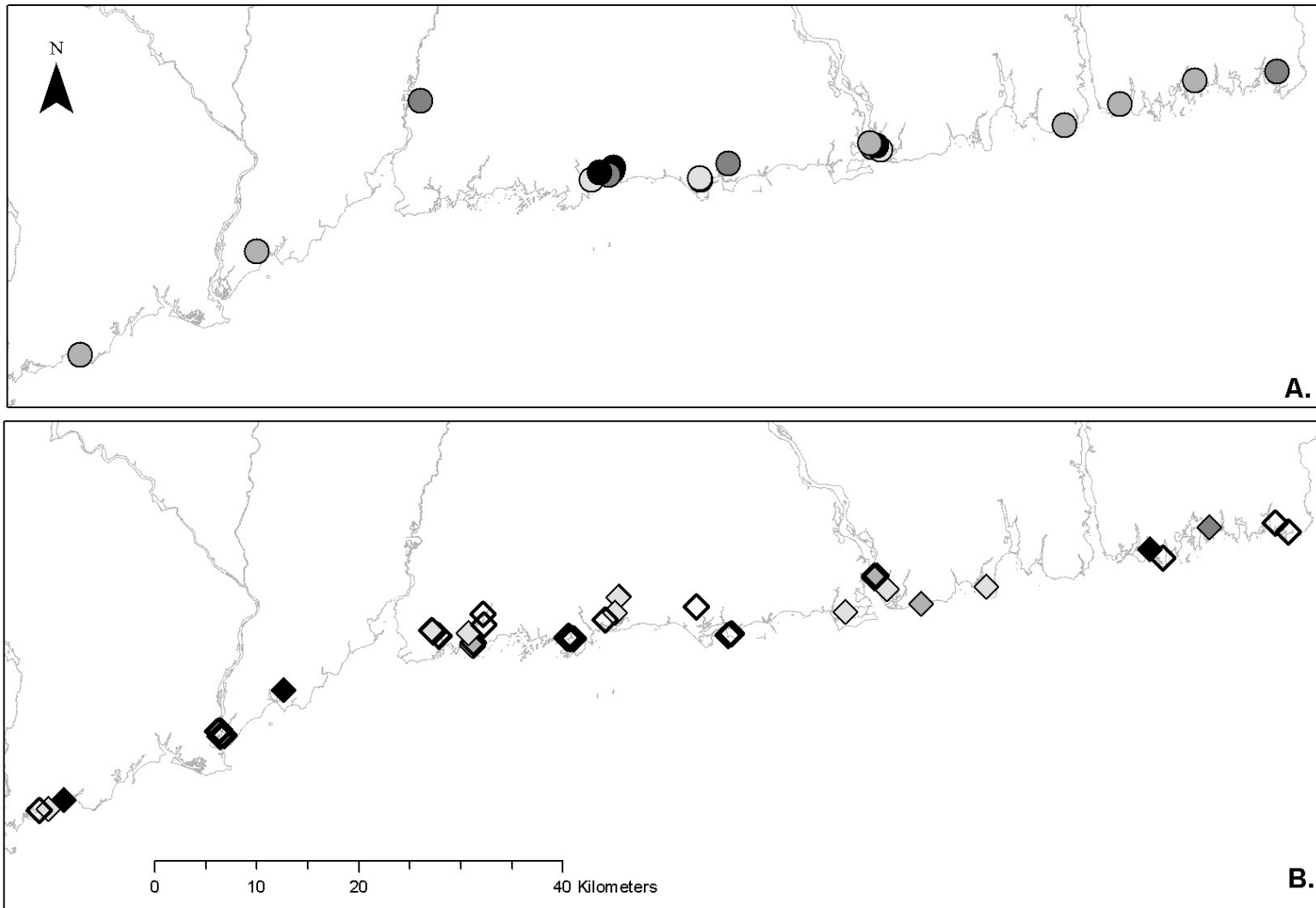
**Fig. 8** Maps showing magnitude of sparrow nest prediction errors for each sampled cell. Darker colors indicate greater deviances between the model predictions for each site and the observations. Panels show accuracy of predictions for (A) the presence of saltmarsh sparrow nests, and (B) the absence of saltmarsh sparrow nests

## APPENDIX C.  Test plot locations

| ID | Site | Town | Latitude | Longitude |
|---|---|---|---|---|
| 1153 | Sherwood Island | Westport | 41.11895248 | -73.32664681 |
| 1207 | New Creek | Westport | 41.1203009 | -73.3158565 |
| 1257 | Sasco Creek | Westport | 41.12810166 | -73.29755449 |
| 1299 | Pine Creek | Fairfield | 41.12579351 | -73.26562446 |
| 2385 | Wheeler | Milford | 41.18588447 | -73.11641259 |
| 2492 | Wheeler | Milford | 41.18097321 | -73.11407441 |
| 2500 | Wheeler | Milford | 41.1859033 | -73.1137034 |
| 2713 | Wheeler | Milford | 41.18200908 | -73.10927238 |
| 3079 | Wheeler | Milford | 41.18091831 | -73.10069132 |
| 3477 | Settler's Cove Condo | Milford | 41.21414509 | -73.05596285 |
| 3571 | Indian River (West) | Milford | 41.22087731 | -73.03847406 |
| 4591 | Quinnipiac River | North Haven | 41.34186769 | -72.88294735 |
| 4598 | Quinnipiac River | North Haven | 41.34768801 | -72.88165235 |
| 4639 | Quinnipiac River | North Haven | 41.34454695 | -72.8811919 |
| 4693 | Quinnipiac River | North Haven | 41.34571743 | -72.8789568 |
| 4929 | Upper Farm River | East Haven | 41.27051643 | -72.86360354 |
| 4952 | Upper Farm River | East Haven | 41.2677936 | -72.86211899 |
| 4956 | Upper Farm River | East Haven | 41.26932278 | -72.86283409 |
| 5038 | Upper Farm River | Branford | 41.26559177 | -72.85671484 |
| 5056 | Upper Farm River | Branford | 41.26488919 | -72.85557676 |
| 5242 | Branford River-Lower | Branford | 41.26713669 | -72.82144373 |
| 5261 | Indian Neck | Branford | 41.25638192 | -72.81778387 |
| 5291 | Indian Neck | Branford | 41.25557412 | -72.81575149 |
| 5296 | Indian Neck | Branford | 41.25854621 | -72.81590444 |
| 5452 | Branford River | Branford | 41.28321897 | -72.80388339 |
| 5476 | Branford River | Branford | 41.2739791 | -72.80247174 |
| 6037 | Great Harbor | Guilford | 41.26099954 | -72.70581045 |
| 6058 | Great Harbor | Guilford | 41.26187033 | -72.70458472 |
| 6103 | Great Harbor | Guilford | 41.25999517 | -72.70224425 |
| 6147 | Great Harbor | Guilford | 41.26010934 | -72.69869913 |
| 6307 | Farmview Rd | Guilford | 41.2842388 | -72.68853755 |
| 6565 | Chittenden Park | Guilford | 41.27010381 | -72.67332219 |
| 6695 | East River | Guilford | 41.27635751 | -72.66346592 |
| 6714 | East River | Madison | 41.27452035 | -72.66227982 |
| 6736 | East River | Madison | 41.27547003 | -72.66114968 |
| 7012 | East River | Madison | 41.2815445 | -72.64896625 |
| 7052 | East River | Madison | 41.27774359 | -72.64789327 |
| 7055 | East River | Madison | 41.28034647 | -72.64715452 |
| 7182 | Guilford Salt Meadows Sanctuary | Guilford | 41.29514731 | -72.64508864 |
| 7231 | Guilford Salt Meadows Sanctuary | Guilford | 41.29586353 | -72.64365048 |
| 7738 | Upper Hammonassett | Madison | 41.28472226 | -72.55431477 |
| 8032 | Cedar Island Marina | Clinton | 41.26731383 | -72.54508674 |
| 8036 | Cedar Island Marina | Clinton | 41.26936999 | -72.54599311 |
| 8408 | Clinton Cemetary | Clinton | 41.2812968 | -72.52198517 |
| 8457 | Hammock River | Clinton | 41.25895904 | -72.51748282 |
| 8517 | Hammock River | Clinton | 41.26000993 | -72.51358641 |
| 9748 | Old Saybrook | Old Saybrook | 41.27655374 | -72.38048483 |
| 10121 | Ragged Rock | Old Saybrook | 41.30189106 | -72.36233319 |

**Appendix C.** Test plot locations (cont).

| ID | Site | Town | Latitude | Longitude |
|----|------|------|----------|-----------|
| 10202 | Ragged Rock | Old Saybrook | 41.30049205 | -72.36069542 |
| 10204 | Ragged Rock | Old Saybrook | 41.30221293 | -72.36034389 |
| 10207 | Ragged Rock | Old Saybrook | 41.30385171 | -72.36023848 |
| 10316 | Ragged Rock | Old Saybrook | 41.30103237 | -72.3581045 |
| 10388 | Ragged Rock | Old Saybrook | 41.30461413 | -72.35521441 |
| 10494 | Upper Island | Old Lyme | 41.30632958 | -72.34462184 |
| 10495 | Upper Island | Old Lyme | 41.30729122 | -72.3446537 |
| 10541 | Upper Island | Old Lyme | 41.30815486 | -72.34214364 |
| 10652 | Great Island | Old Lyme | 41.29361477 | -72.33777913 |
| 10862 | Great Island | Old Lyme | 41.2898668 | -72.33291905 |
| 10870 | Upper Island | Old Lyme | 41.2951953 | -72.33351647 |
| 10997 | Great Island | Old Lyme | 41.29165211 | -72.33086551 |
| 11003 | Upper Island | Old Lyme | 41.29603366 | -72.33073335 |
| 11616 | Mile Creek | Old Lyme | 41.28173228 | -72.29146971 |
| 12079 | Black Pt Road | East Lyme | 41.29516257 | -72.21477427 |
| 12309 | Waterford Town Beach Park | Waterford | 41.30602473 | -72.10539733 |
| 12461 | Bluff Point | Groton | 41.32298333 | -72.03914753 |
| 12542 | Bluff Point | Groton | 41.32357209 | -72.02230741 |
| 12651 | Groton - Long Point | Groton-Long Point | 41.31500956 | -72.00731546 |
| 16109 | Cottrell | Stonington | 41.34062764 | -71.951445 |
| 16118 | Cottrell | Stonington | 41.34153516 | -71.95054939 |
| 16640 | Barn Island | Stonington | 41.34748505 | -71.87460507 |
| 16652 | Barn Island | Stonington | 41.34231691 | -71.87397687 |
| 16858 | Barn Island | Stonington | 41.33407848 | -71.85956527 |

**APPENDIX D. Mapped predictions of sparrow presence and nest presence for major marsh systems in Connecticut.**

D1. Barn Island Wildlife Management Area, Stonington, CT
D2. Bluff Point State Park, Groton, CT
D3. Connecticut River (east side), Old Lyme, CT
D4. Connecticut River (west side), Old Saybrook, CT
D5. McKinney National Wildlife Refuge, Salt Meadow Unit, Westbrook, CT
D6. Hammock River and Hammonassett State Park, Clinton and Madison, CT
D7. East River and West Rivers, Madison and Guilford, CT
D8. Lower Housatonic River, Milford and Stratford, CT
D9. McKinney National Wildlife Refuge, Great Meadows Marsh, Stratford, CT
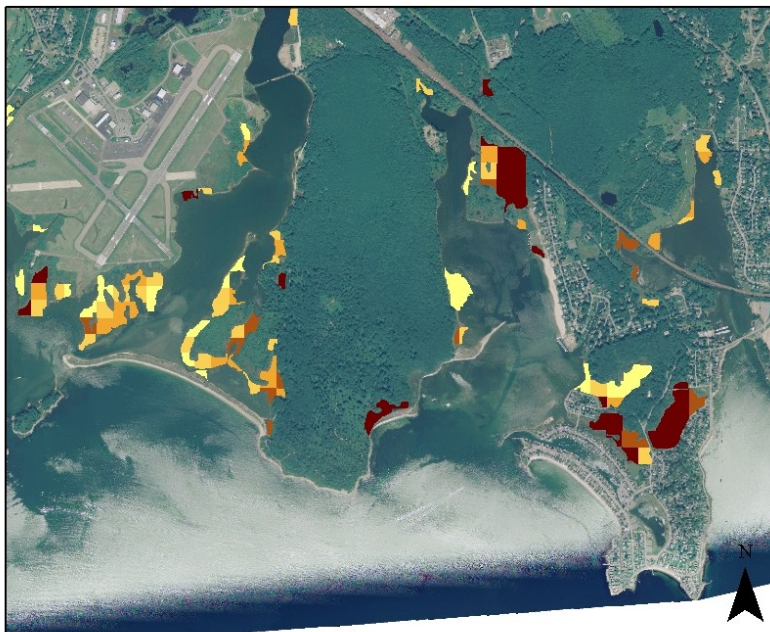D10. Sasco Creek and Sherwood Island State Park, Westport, CT
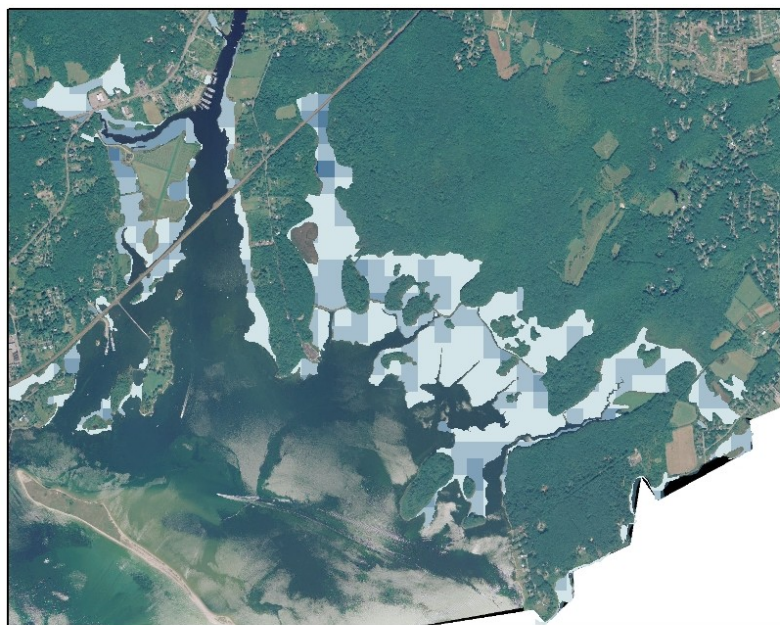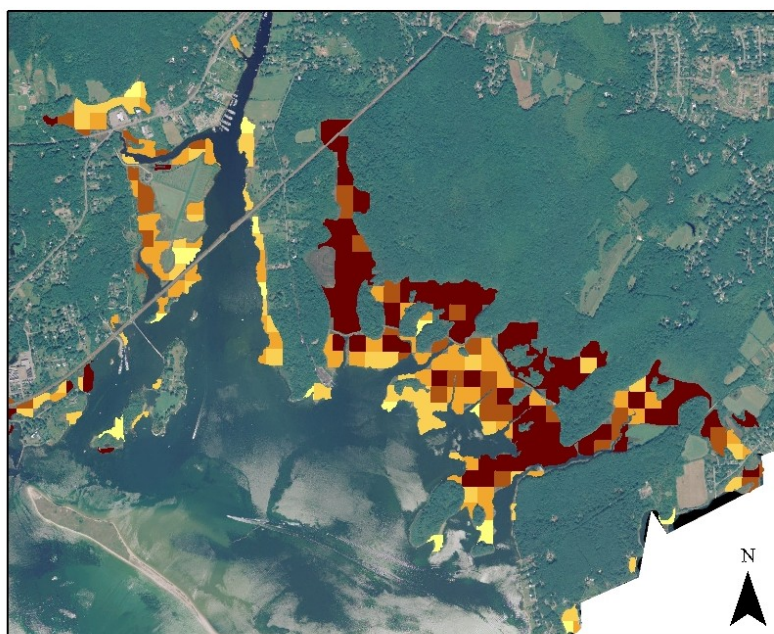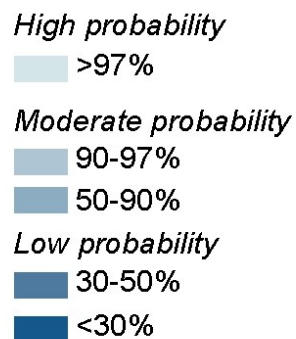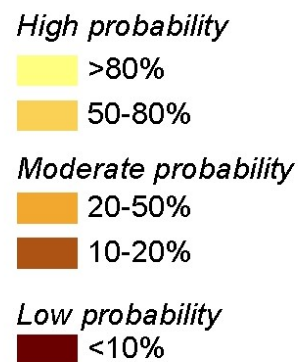
**D1** Saltmarsh sparrow habitat at Barn Island Wildlife Management Area in Stonington, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**D2** Saltmarsh sparrow habitat at sites near Bluff Point State Park in Groton, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**Predicted probability of saltmarsh sparrow presence**

*High probability*
- >97%

*Moderate probability*
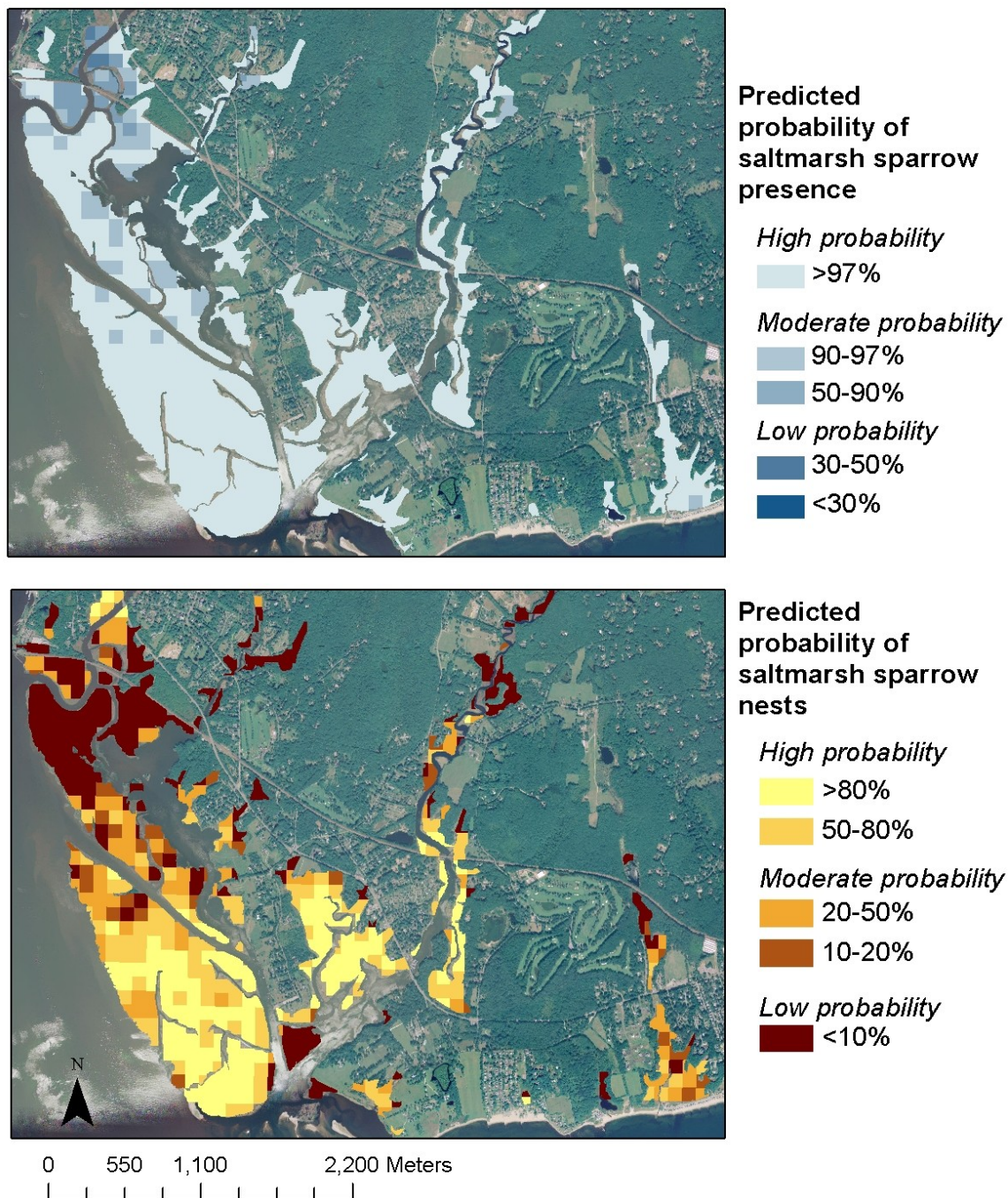- 90-97%
- 50-90%

*Low probability*
- 30-50%
- <30%

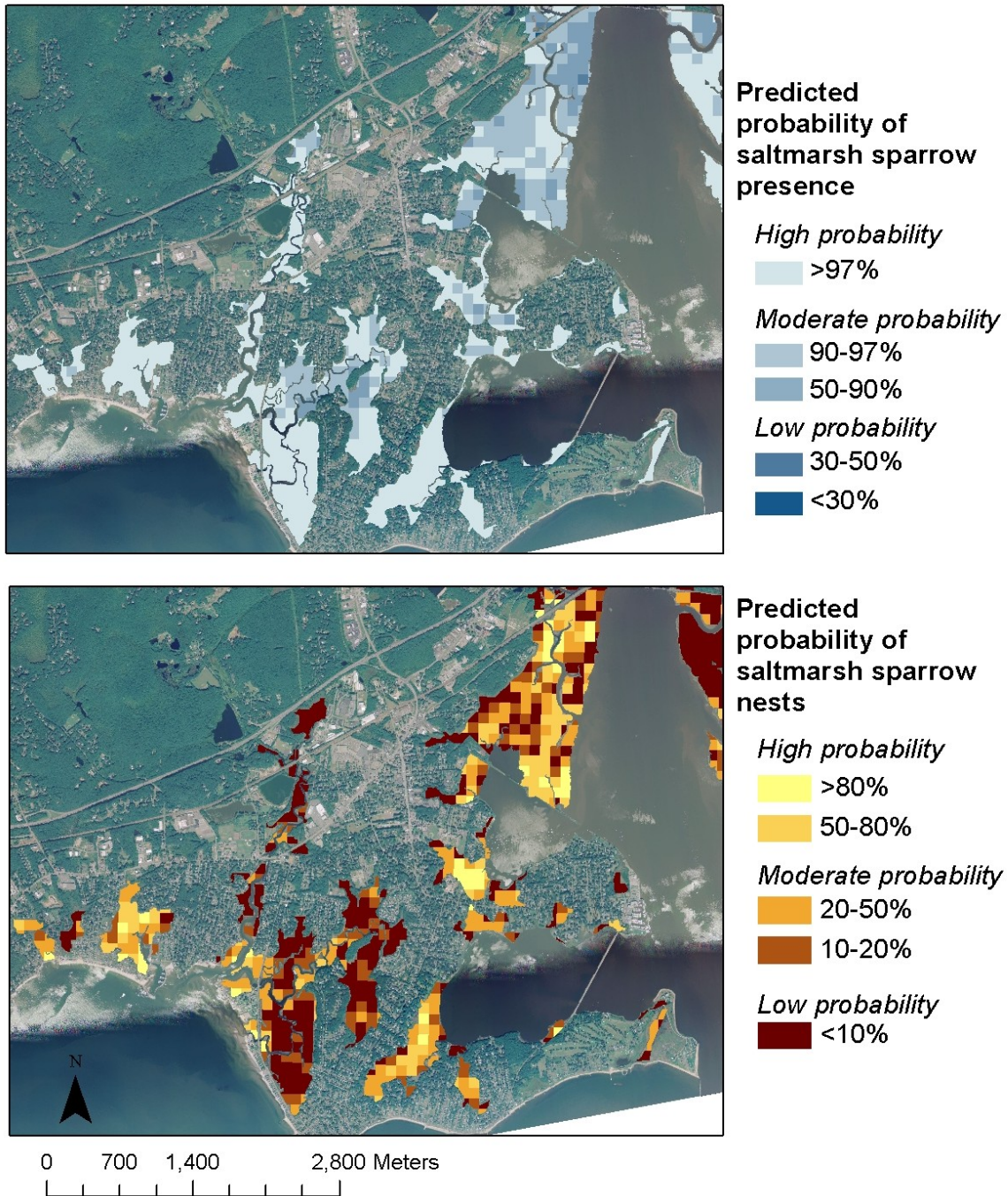**Predicted probability of saltmarsh sparrow nests**

*High probability*
- >80%
- 50-80%

*Moderate probability*
- 20-50%
- 10-20%

*Low probability*
- <10%

N

0    550    1,100    2,200 Meters

**D3** Saltmarsh sparrow habitat on the east side of the Connecticut River mouth in Old Lyme, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**D4** Saltmarsh sparrow habitat on the west side of the Connecticut River mouth in Old Saybrook, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**Predicted probability of saltmarsh sparrow presence**

*High probability*
>97%

*Moderate probability*
90-97%
50-90%

*Low probability*
30-50%
<30%

**Predicted probability of saltmarsh sparrow nests**

*High probability*
>80%
50-80%

*Moderate probability*
20-50%
10-20%

*Low probability*
<10%

N

0    500   1,000          2,000 Meters
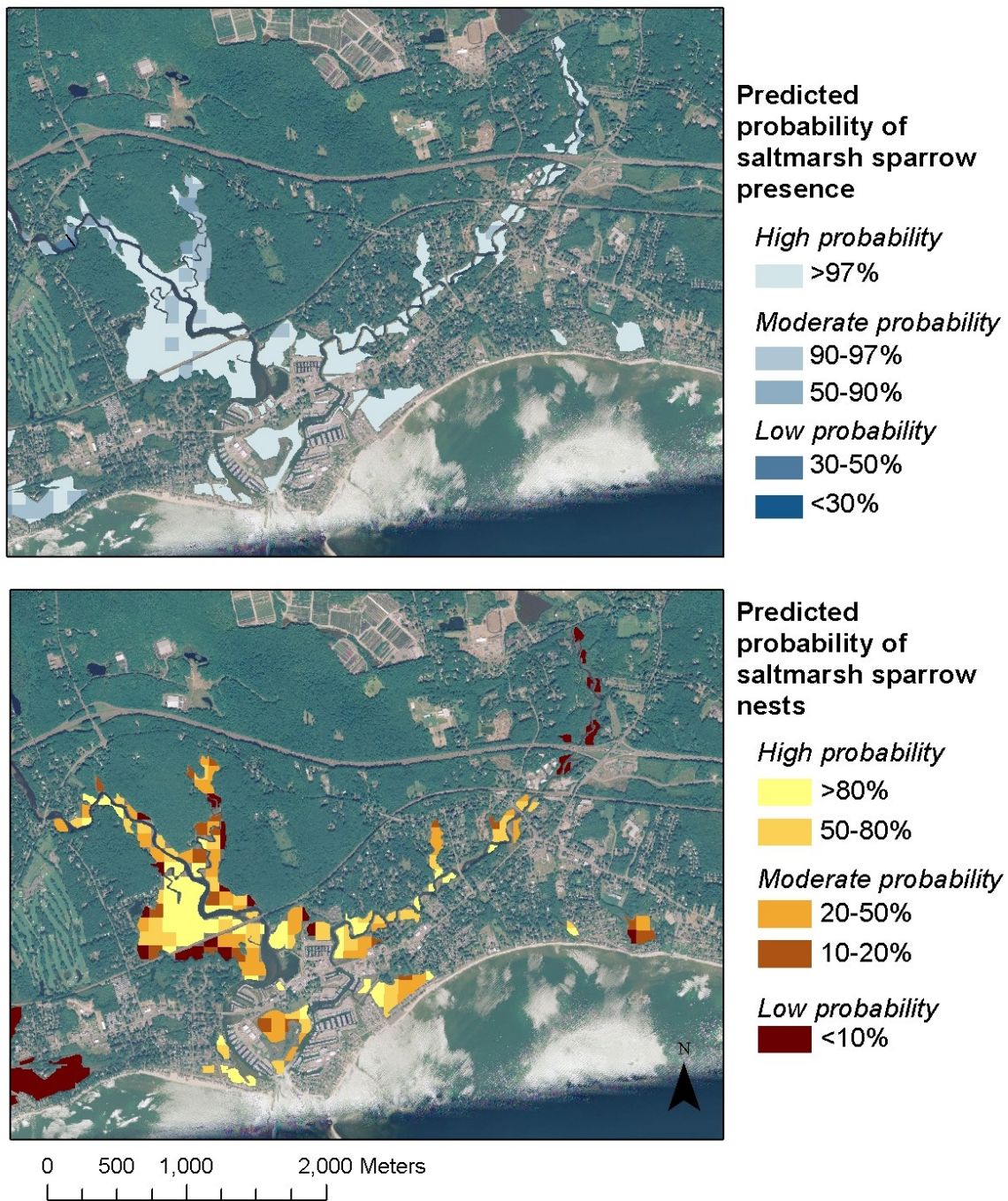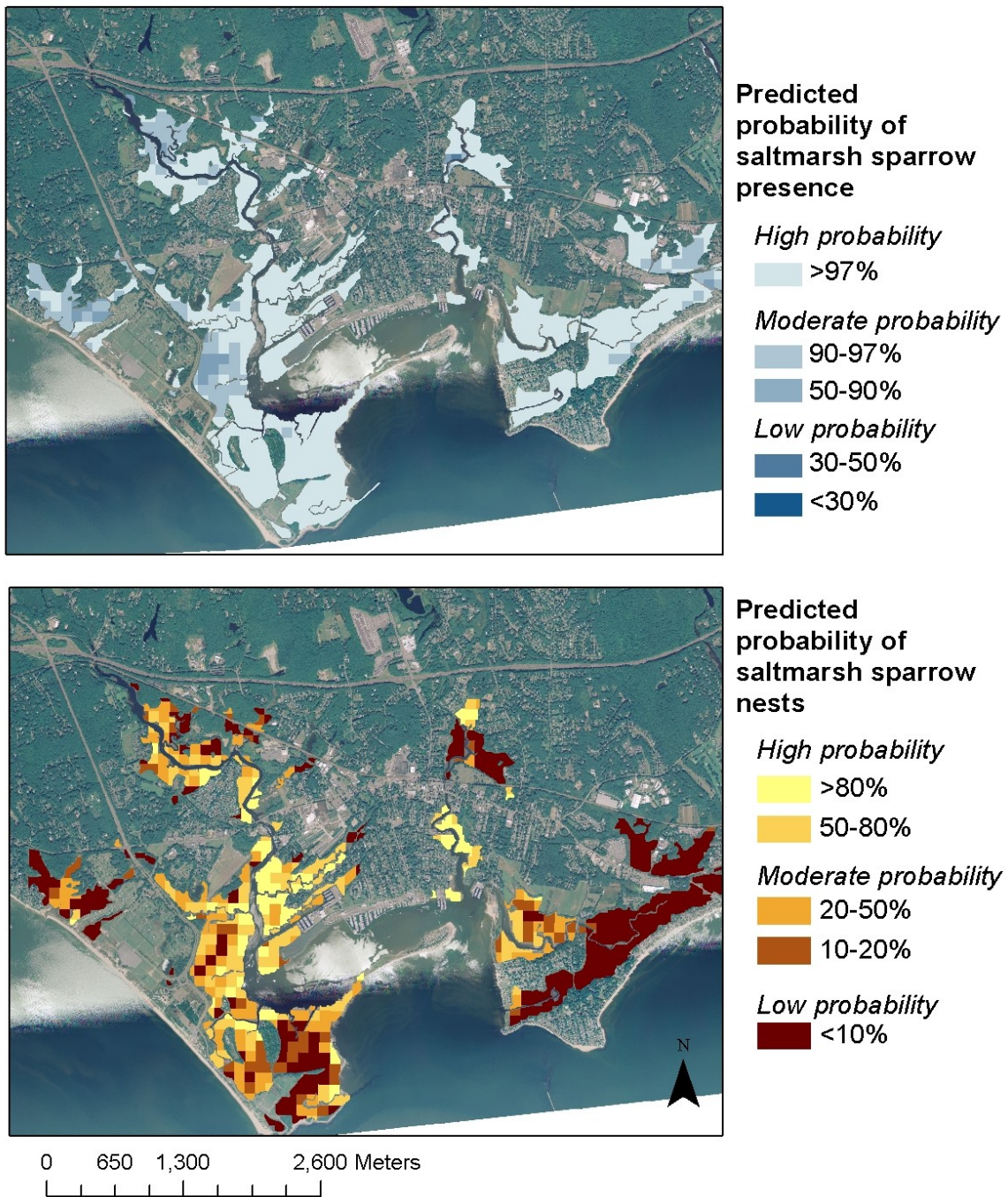
**D5** Saltmarsh sparrow habitat at McKinney National Wildlife Refuge Salt Meadow Unit in Westbrook, CT.  Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**Predicted probability of saltmarsh sparrow presence**

*High probability*
>97%

*Moderate probability*
90-97%
50-90%

*Low probability*
30-50%
<30%

**Predicted probability of saltmarsh sparrow nests**

*High probability*
>80%
50-80%

*Moderate probability*
20-50%
10-20%

*Low probability*
<10%

0    650    1,300    2,600 Meters

**D6** Saltmarsh sparrow habitat at the Hammock River and Hammonassett State Park in Clinton and Madison, CT.  Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting
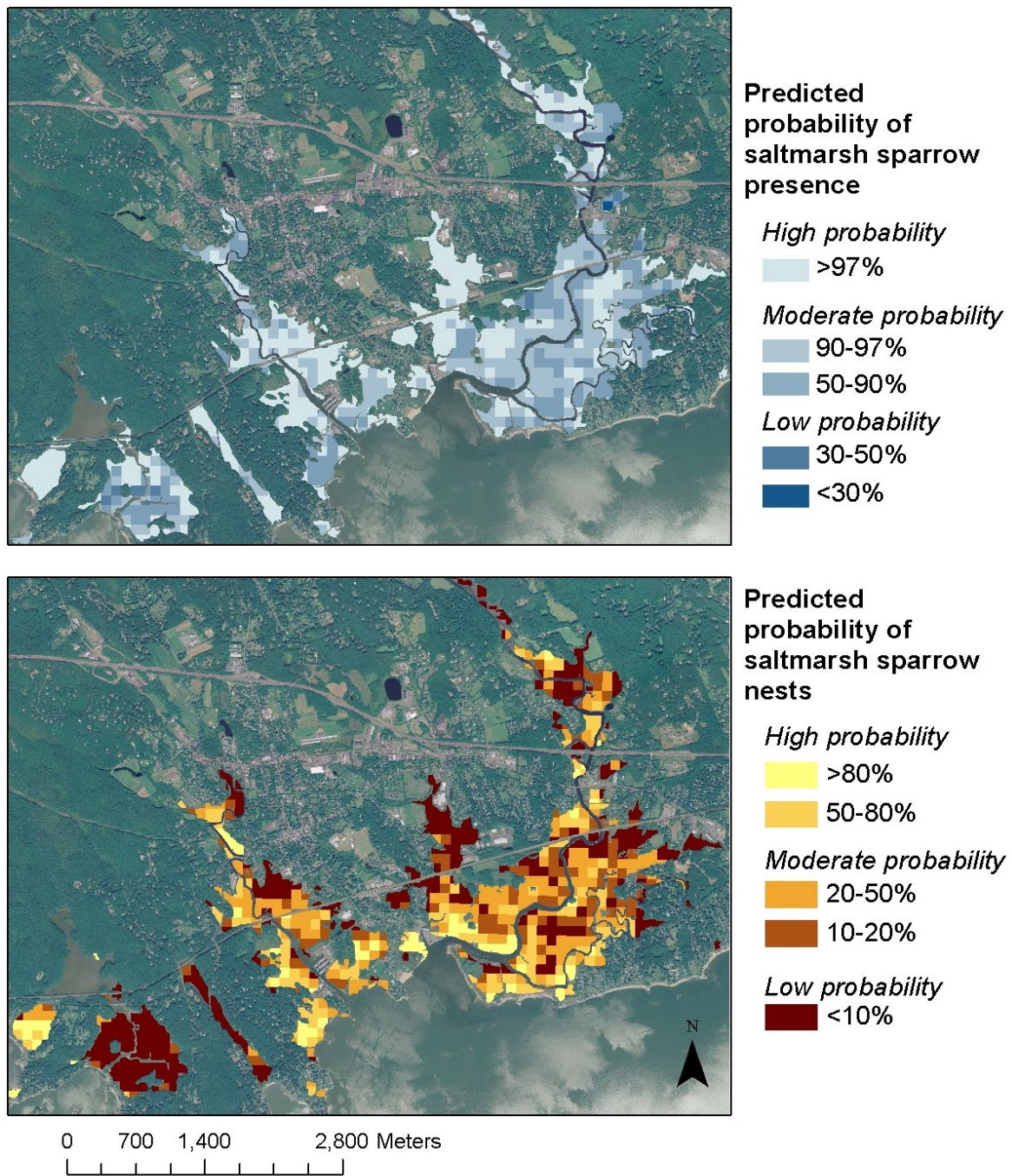
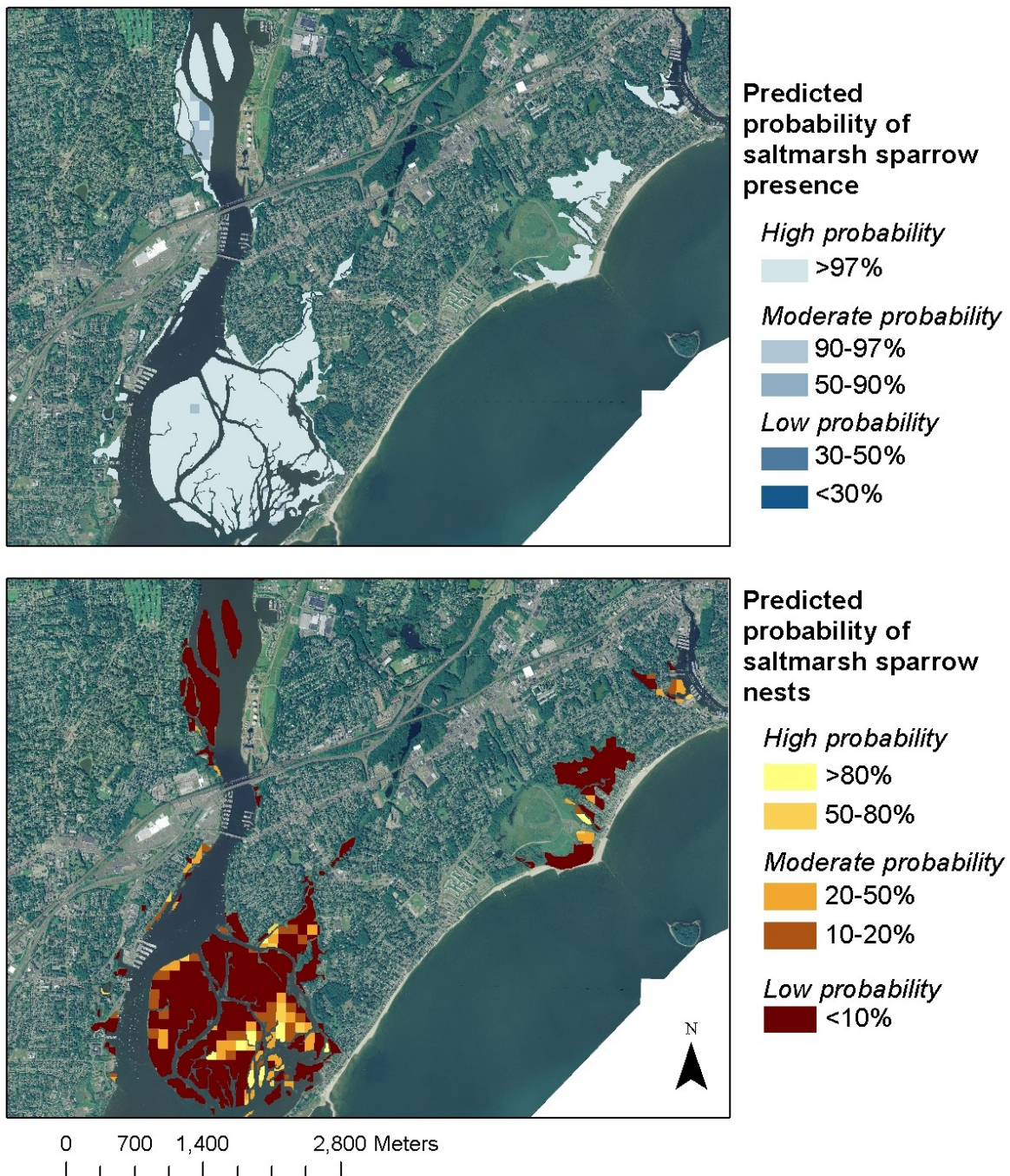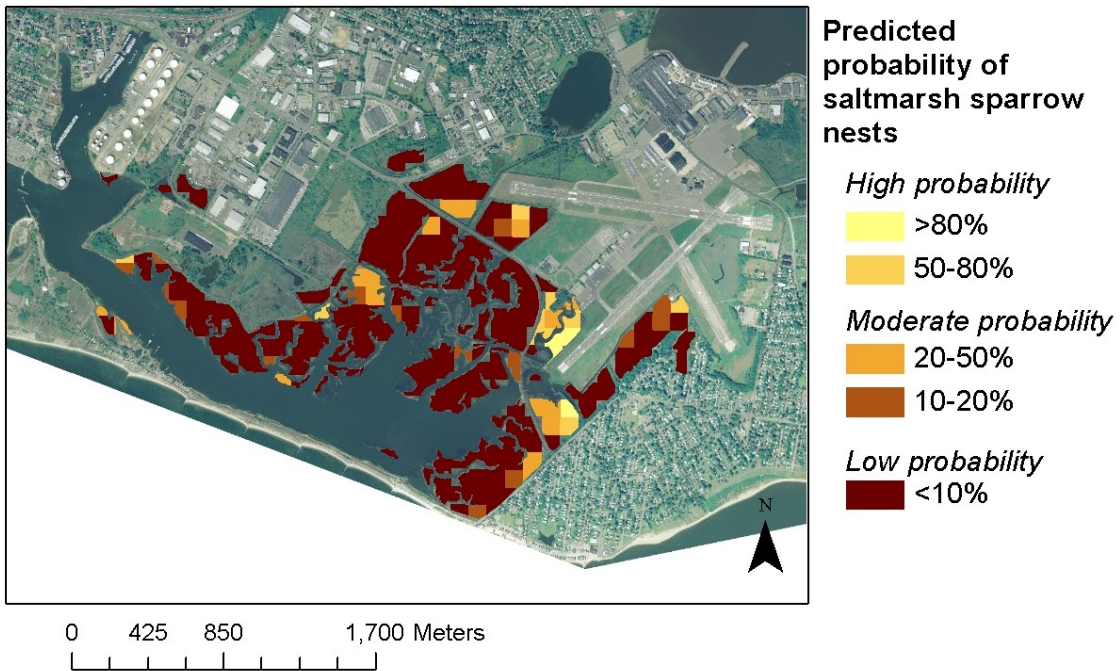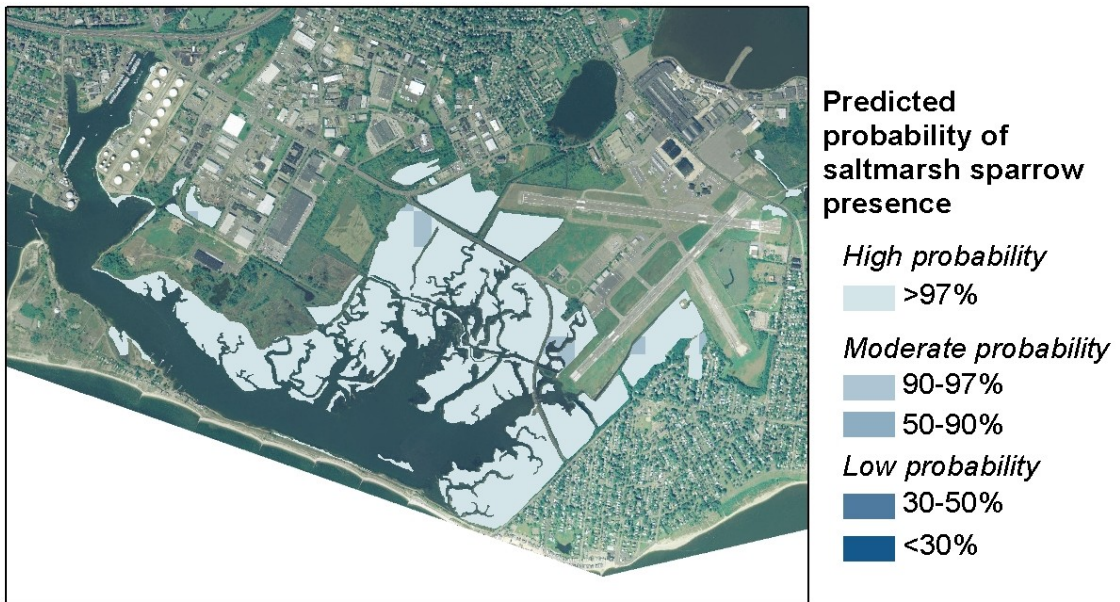**Predicted probability of saltmarsh sparrow presence**

*High probability*
>97%

*Moderate probability*
90-97%
50-90%

*Low probability*
30-50%
<30%

**Predicted probability of saltmarsh sparrow nests**

*High probability*
>80%
50-80%

*Moderate probability*
20-50%
10-20%

*Low probability*
<10%

0    700    1,400    2,800 Meters

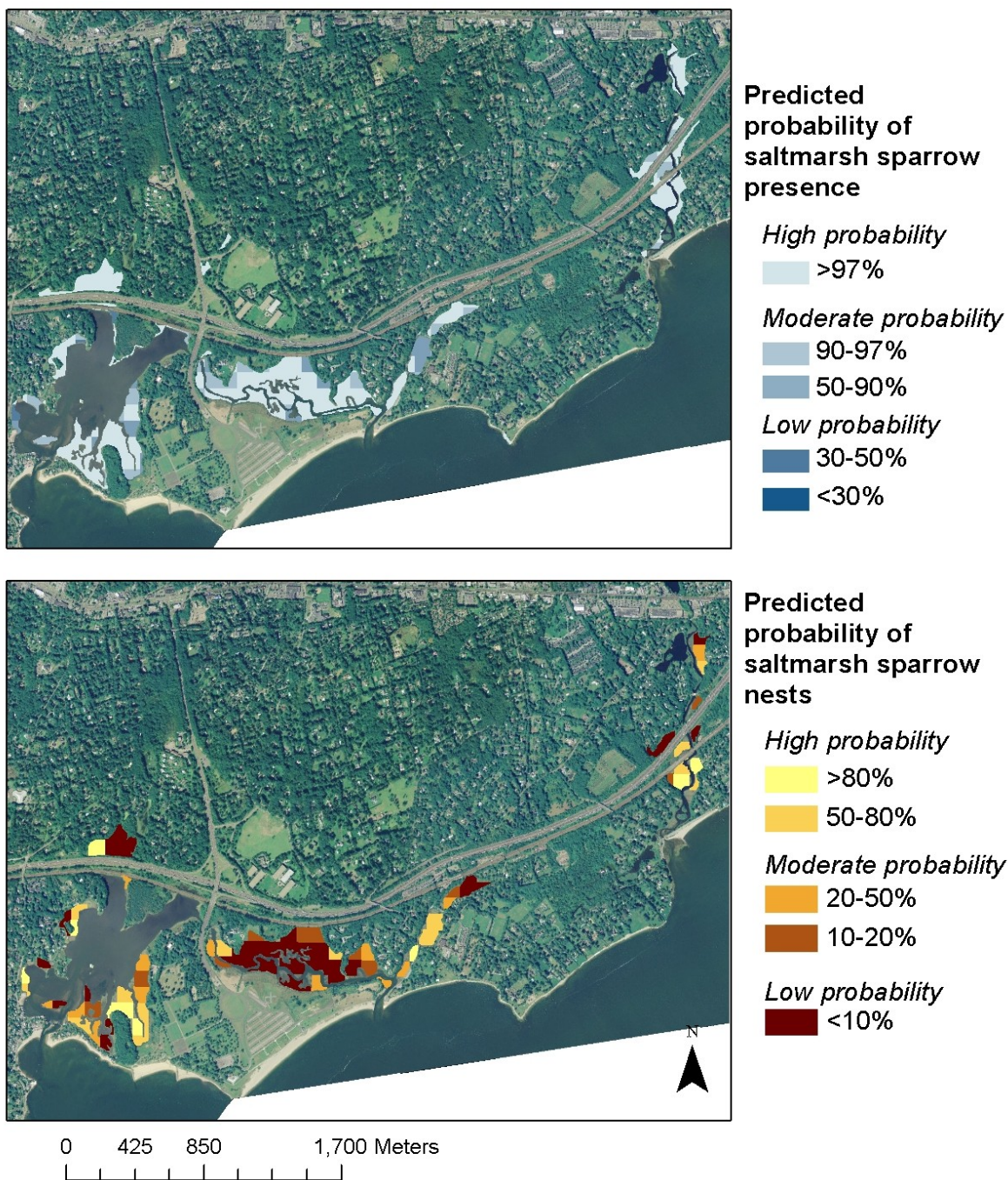**D7** Saltmarsh sparrow habitat at the East and West Rivers in Madison and Guilford, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**D8** Saltmarsh sparrow habitat along the lower Housatonic River in Milford and Stratford, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**Predicted probability of saltmarsh sparrow presence**

*High probability*
>97%

*Moderate probability*
90-97%
50-90%

*Low probability*
30-50%
<30%

**Predicted probability of saltmarsh sparrow nests**

*High probability*
>80%
50-80%

*Moderate probability*
20-50%
10-20%

*Low probability*
<10%

N

0    425    850         1,700 Meters

**D9** Saltmarsh sparrow habitat at McKinney National Wildlife Refuge, Great Meadows Marsh, Stratford, CT.  Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting

**Predicted probability of saltmarsh sparrow presence**

*High probability*
>97%

*Moderate probability*
90-97%
50-90%

*Low probability*
30-50%
<30%

**Predicted probability of saltmarsh sparrow nests**

*High probability*
>80%
50-80%

*Moderate probability*
20-50%
10-20%

*Low probability*
<10%

0    425    850         1,700 Meters

**D10** Saltmarsh sparrow habitat from Sasco Creek to Sherwood Island State Park, Westport, CT. Darker colors indicate decreasing probability predicted for (top) sparrow presence, and (bottom) sparrow nesting