EVALUATING HABITAT-ASSOCIATION MODELS FOR THE SALTMARSH SPARROW

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Abstract. Habitat models that associate organisms with features of their environment can help identify areas for planning conservation strategies. These models, however, should be tested with new data before their conclusions are widely accepted. The Saltmarsh Sparrow (*Ammodramus caudacutus*) is a species of growing conservation concern along the Atlantic coast of North America. In a previous study, we developed models for Saltmarsh Sparrow presence and nesting habitat. Sparrow occupancy was best predicted from raw reflective properties of marshes derived from remote sensing, whereas sparrow nesting was best predicted from a classification of marsh plant communities. To test these models, we 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. The models' performance, assessed by the area under a receiver-operating characteristic curve and the deviance of observations from the models' predictions, was significantly better than expected by chance alone. Because sparrows are predicted to occur in many places where they are unlikely to nest, monitoring sparrow presence alone will not identify areas important for their nesting.

Key words: Saltmarsh Sparrow, Ammodramus caudacutus*, presence modeling, saltmarsh, habitat models, remote sensing.*

Evaluación de Modelos de Asociación de Hábitat para *Ammodramus caudacutus*

Resumen. Los modelos de hábitat que asocian a los organismos con rasgos de sus ambientes pueden ayudar a identificar áreas para planificar estrategias de conservación. Estos modelos, sin embargo, deben ser evaluados con datos nuevos antes de que sus conclusiones puedan ser ampliamente aceptadas. *Ammodramus caudacutus* es una especie de preocupación creciente de conservación a lo largo de la costa atlántica de América del Norte. En un estudio previo, desarrollamos modelos de presencia y hábitat de nidificación de *A. caudacutus*. La ocupación de *A. caudacutus* fue predicha mejor a partir de las propiedades reflectivas básicas de los pantanos derivadas a partir de teledetección, mientras que la nidificación de *A. caudacutus* fue predicha mejor a partir de una clasificación de la comunidad de plantas del pantano. Para evaluar estos modelos, monitoreamos una muestra estratificada al azar de sitios para los cuales se había predicho la probabilidad de presencia de *A. caudacutus* y comparamos las observaciones con la probabilidad predicha de presencia y nidificación generada por los modelos. El desempeño de los modelos, evaluado a partir del área debajo de la curva de características de receptor-operador y del desvío de las observaciones de las predicciones del modelo, fue significativamente mejor que lo esperado sólo por azar. Debido a que se predice que *A. caudacutus* esté presente en muchos sitios donde es poco probable que anide, el monitoreo de la presencia únicamente de *A. caudacutus* no permitirá identificar áreas importantes para su nidificación.

INTRODUCTION

Two main reasons for modeling the associations between a species' presence and habitat features are to map predicted distributions and to understand ecological factors that influence ways 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 (Scott et al. 1993) and refine foci of future research when little is known about the species of concern, as with the American fisher (*Martes pennanti*) (Carroll et al. 1999) or Jerdon's Courser (*Rhinoptilus bitorquatus*) (Jeganathan et al. 2004). Increasingly, features of the

environment are described from remotely sensed 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 often not tested by an evaluation of the extent to which they accurately reflect species' distributions.

Applying remote-sensing data to habitat modeling can take two approaches. First, researchers use such data to classify features in the environment that previous studies associated with the organism of interest. With this approach, components of a species' habitat are assumed to be known, and 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. 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 (Lepidoptera). Other studies organize data in ways that describe plant structure and heterogeneity, such as in Gibson et al. (2004), who generated a model of the structural complexity of vegetation by using low-altitude videographic imagery to describe habitat of the Rufous Bristlebird (*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 the Wood Thrush (*Hylocichla mustelina*). These a priori classifications can be used to dissect how individual features influence species' distributions and allow comparisons of species of interest and data sources (Guisan and Zimmerman 2000).

The second approach uses remote-sensing data in a more exploratory way to identify aspects of the landscape 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. To model bird diversity in the Chihuahuan Desert, St-Louis et al. (2009) used the texture of satellite images 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. 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 an 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 from such data. Although habitat models can be evaluated with 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 tidal marshes along the mid-Atlantic and New England coast of eastern North America. Because approximately half of the world population is estimated to breed in southern New England (Dettmers and Rosenberg 2000), the saltmarshes of that region are considered to be especially important for conservation of this species. 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 and Elphick 2011). Because males are not territorial and provide no parental care (Woolfenden 1956, Greenlaw and Rising 1994), and both males and females are frequently found in areas where nesting does not occur (Meiman 2011), the species' presence does not necessarily indicate that conditions are suitable for nesting, even during the peak breeding season. Within the saltmarsh, the plant community subjected to daily tidal inundation is known as the low marsh, while the relatively higher areas of the marsh that flood less frequently are referred to as the high marsh (Bertness and Ellison 1987). Although previous studies have associated Saltmarsh Sparrow nesting with vegetation communities characteristic of the high marsh (Shriver et al. 2007, Gjerdrum et al. 2008b), consistent variables that denote sparrow presence have been harder to determine.

We previously examined a set of alternative models designed to explain variation in the distribution and nesting activity of Saltmarsh Sparrows in Connecticut (Meiman 2011, Meiman et al. 2012). These models examined a wide range of variables generated both in the field and by remote sensing and collectively tested the importance of plant composition, vegetation structure, spectral characteristics of the marsh, the distance from the marsh's upland edge, whether and how marsh restoration had been undertaken at a site, and landscape-level features of the marsh. The model of sparrow presence that best fit the data used a variable derived from raw values of spectral reflectance associated with plots where sparrows did not occur. Nest presence, in contrast, was modeled best with vegetation-structure variables that required data collection on the ground. Recording such 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 and was derived from remote-sensing data, received almost as much support as the best model, and we proposed it as the best option for predicting the distribution of nesting habitat in unstudied areas.

The objective of the current study was to test predictions of the best model for sparrow presence, and the best model based on remote sensing for nest presence, by using data from a new set of sites. We 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 for us to examine the different inferences

and expectations from habitat models based on remote sensing. In addition, the predictive maps derived from the two models provide detailed information about the Saltmarsh Sparrow's current distribution in the center of its geographic range.

METHODS

To generate regional maps of predicted sparrow presence we used a model based on a classification of saltmarsh pixels that provided a fit better than alternative models did (Meiman 2011, Meiman et al. 2012). This classification determined whether each pixel of saltmarsh 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-present pixels") or not found despite at least three point-count surveys and mist-netting sessions ("sparrow-absent pixels"; see Meiman et al. 2012 for details). The model predicted

that higher proportions of sparrow-absent pixels were associated with a lower probability of Saltmarsh Sparrow presence.

We overlaid a grid of 1-ha cells across all of Connecticut's saltmarshes and calculated the proportion of sparrow-absent pixels within each grid cell after removing areas outside the delineated marsh boundary (NOAA 2004). The resulting structure was strongly skewed with most cells having relatively few sparrow-absent pixels (see Results). To ensure that we sampled across a wide spectrum of prediction probabilities, we therefore stratified sampling across three groups of cells: those with <20% sparrow-absent pixels, those with 20–40%, and those with >40%. These three categories approximately corresponded to sites that were almost certain to have sparrows (>95% chance, "high expectation"), those that had a 50–95% chance of having sparrows ("medium expectation"), and those that had a <50% chance of having sparrows ("low expectation") (e.g., Fig. 1a). We generated predictions in WinBugs
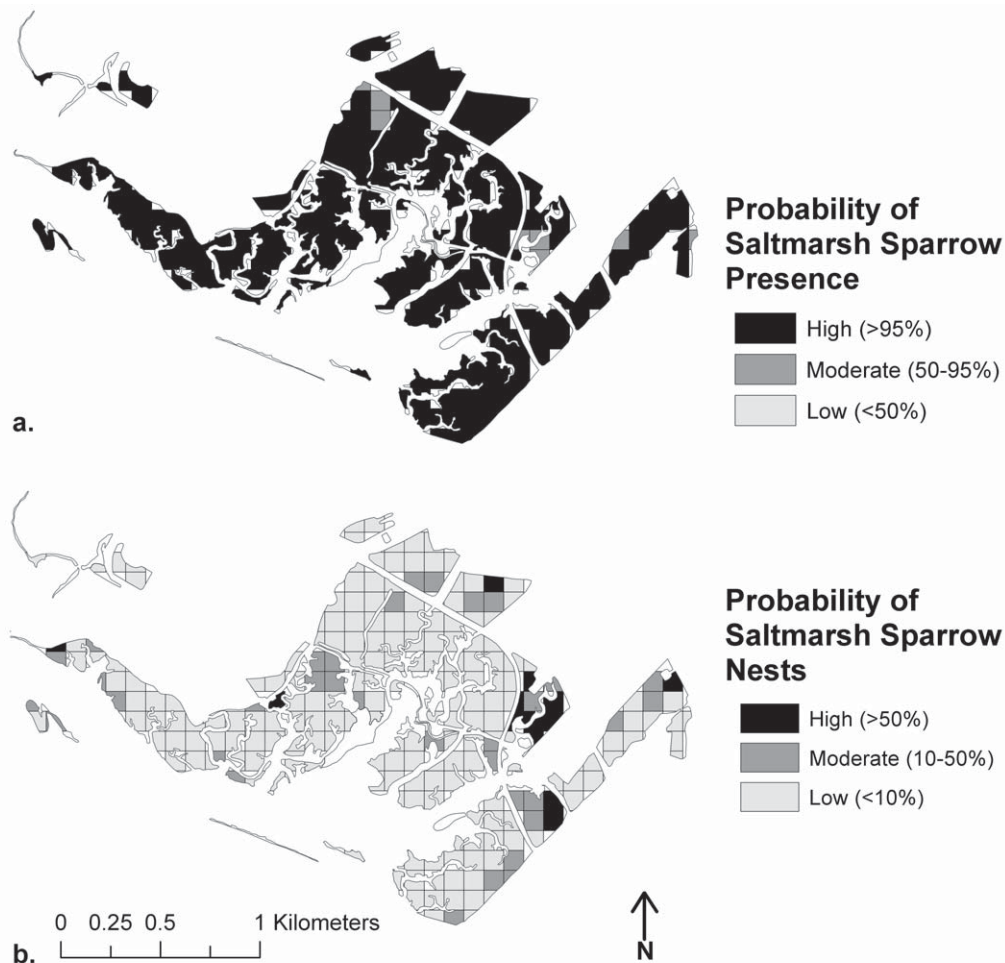

FIGURE 1.   Predictions of Saltmarsh Sparrow habitat in 1-ha grid cells at McKinney National Wildlife Refuge, Great Meadows Marsh, Stratford, CT. This example illustrates a situation in which predictions for Saltmarsh Sparrow presence and nesting are very different. Lighter colors indicate lower predicted probabilities of (a) sparrow presence and (b) sparrow nesting. While a high probability of sparrow presence is predicted for much of Connecticut's saltmarshes, much smaller areas are predicted to be used for nesting. Full map available at http://hydrodictyon.eeb.uconn.edu/people/meiman/.

(Spiegelhalter et al. 2000), in which the uncertainty about model structure as well as uncertainty around parameter estimates could be propagated throughout the process of fitting the model to the predictions.

Randomly sampling 24 cells from each of the three categories, we selected 72 cells to visit during field tests between 25 May and 25 August 2009. In the field, we established 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 number of samples for the categories of high, medium, and low expectation were 26, 23, and 23, respectively. The sampled cells spanned the region from Sherwood Island State Park in Westport to Barn Island Wildlife Management Area in Stonington. We assessed the sparrows' presence by 10-min point counts in each plot. All counts took place after sunrise, between 06:00 and 11:00 EDT, and we recorded all sparrows seen and heard within the plot. After each point count, to reduce the risk that zero counts were due to lack of detection, we slowly walked back and forth throughout the plot. Sites where no sparrows were detected were surveyed repeatedly, at least 2 weeks apart, either until we encountered sparrows or until four visits had been completed. We set the number of surveys required to establish absence after calculating detection probabilities from previous surveys in Connecticut saltmarshes (Elphick and Meiman, unpubl. data). Using data from 40 sites surveyed in 2007 and 2008, we calculated the probability of detecting at least one sparrow in a 5-min point count with PRESENCE 2.0 (Hines and MacKenzie 2004). From the most parsimonious model with the best fit, a constant-probability model, we estimated that four visits to a site reduced the probability of missing sparrows if they were present to less than 5%. Because we used longer (10-min) point counts combined with area searches, the chance of detecting sparrows if present at our survey points should have been very high.

During 2009, we 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 communities (Hoover 2009, Meiman 2011). This data layer was not available for the entire state prior to the field test, so we used the same sampling frame selected for the sparrow-presence model to evaluate the nest-presence model.

After the field season, plant-community data became available for all of our study area (M. Hoover, unpubl. data), and we were able to determine the percentage of high marsh habitat within each of the test cells. This data set allowed us to stratify cells into three groups according to their likelihood, based on the model, of containing nesting birds. Cells with <20% high marsh had a <10% predicted probability of containing a nest ("low expectation"), cells with 20–50% high marsh had a 10–50% predicted probability of containing a nest ("medium expectation"), and cells that consisted of >50% high marsh had >50% predicted probability of containing a nest ("high expectation") (e.g., Fig. 1b).

To determine whether Saltmarsh Sparrows were nesting in the test cells, we watched for birds flying with food or fecal sacs during point counts and subsequent time spent in the plot. After each point count, we also searched for nests by slowly walking back and forth throughout the plot, ensuring that the searcher's path went within 10 m of all parts of each plot, and located nests by noting the point from where birds flushed. At sites where sparrows had been found but where nests had not, we conducted additional searches at approximately 2-week intervals until a minimum of three nest searches had been completed. To evaluate how well we were able to detect nests by this search pattern, we analyzed nest-detection probabilities after the 2009 survey season with the program PRESENCE 2.0 (Hines and McKenzie 2004) and estimated that in plots where sparrows occurred, three visits were sufficient to reduce the probability of missing a nest if it was present to <5%.

We evaluated each model's predictions in three ways. First, we calculated the area under a receiver-operating-characteristic curve (AUC) for each model as a measure of its performance. This curve plots the way in which the rate of false positive results changes relative to the true positive rate for different discrimination thresholds. The AUC is a measurement of a model's performance that does not depend on designating a single 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's 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 models' performances with test data and training data, we also calculated the AUC for the data used to build the models.

Second, we calculated an index of how much the field observations deviated from the predictions. For each cell, we determined the difference between each observation (1 = present, 0 = absent), and the predicted probability (values ranged from 0 to 1). We 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 was randomly assigned to the same predicted probabilities.

Third, to assess each model's ability to predict absences in the low-probability category and presences in the high-probability category, we 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, we 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 a >50% chance of containing nests actually had them.

Finally, we examined the true distribution of the sparrows and nests. We mapped the presences and absences to determine whether (1) they were concentrated in certain areas, (2) prediction errors were concentrated in certain areas, and (3) there were areas where both models generated errors.

RESULTS

On the basis of the presence model, Saltmarsh Sparrows are expected to occur in most of the saltmarsh in the study region. Of the cells for which probability of sparrow presence was predicted, 66% had a high expectation of Saltmarsh Sparrow presence, 28% a medium expectation, and 5% a low expectation. Overall, the mean predicted probability of presence was greater than 95% for most major marsh systems (Fig. 2). 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 10% and 15%, respectively. Yet other sites had more variable predictions. For example, the marshes on the Upper Farm River in Branford had a mean predicted probability of sparrow presence of only 54% with predictions for individual cells that ranged from 2% to 99% (Fig. 2).

We 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. 3a). 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 our 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. 3b). Finally, we examined the model's ability to classify cells correctly. Sparrows were absent at 50% 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.

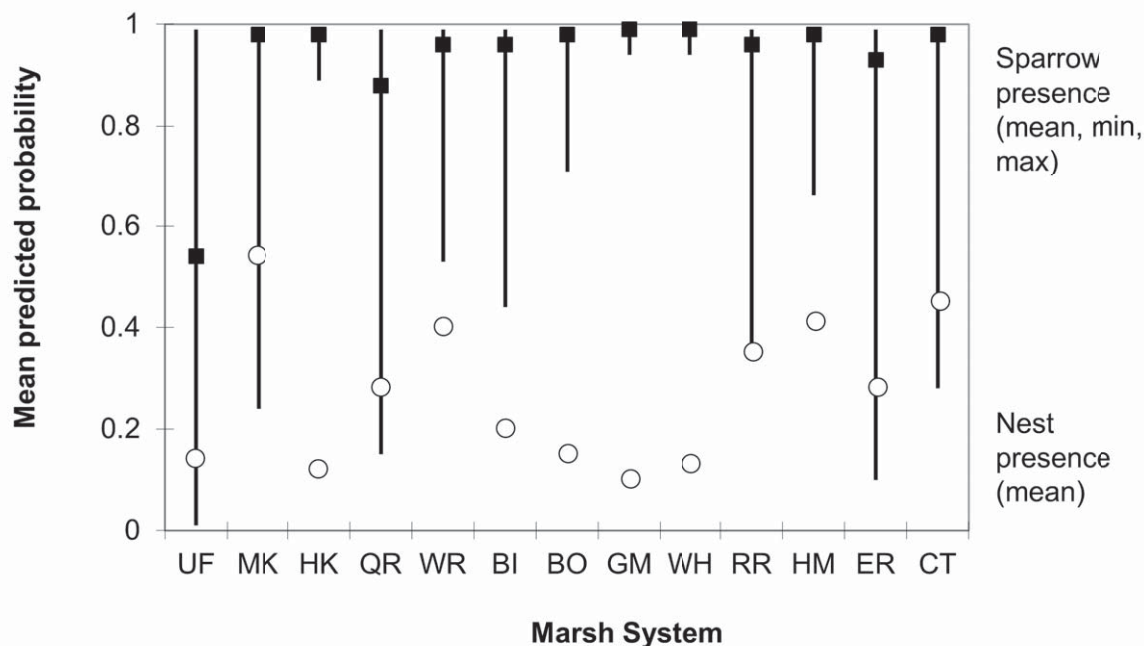The nest model predicted that 43% of the area of saltmarsh in Connecticut had a low probability of sparrows

FIGURE 2. Predicted Saltmarsh Sparrow use of 1-ha cells for larger saltmarsh systems of conservation interest along the Connecticut coast, arranged in order of increasing size. Black squares indicate the marsh-wide mean predicted probability of birds being present within a 1-ha area of marsh. Vertical lines represent the ranges associated with those means. Unfilled circles represent the marsh-wide mean probability of birds nesting within a 1-ha area of marsh. Predicted probabilities of nest presence ranged from 0 to 1 for all marshes, so ranges are not illustrated. UF = Upper Farm River, Branford and East Haven (90 ha); MK = McKinney National Wildlife Refuge, Westbrook (113 ha); HK = Hammock River Marsh, Clinton (123 ha); QR = Quinnipiac River, North Haven (125 ha); WR = West River, Guilford (131 ha); BI = Barn Island Wildlife Management Area, Stonington (136 ha); BO = Back Bay and Oyster River, Old Saybrook (158 ha); GM = Great Meadows Marsh, Stratford (154 ha); WH = Wheeler Marsh, Milford (233 ha); RR = Ragged Rock, Old Saybrook (234 ha); HM = Hammonassett State Park, Madison (288 ha); ER = East River Marsh, Guilford and Madison (337 ha); CT = East Connecticut River, Old Lyme (416 ha).
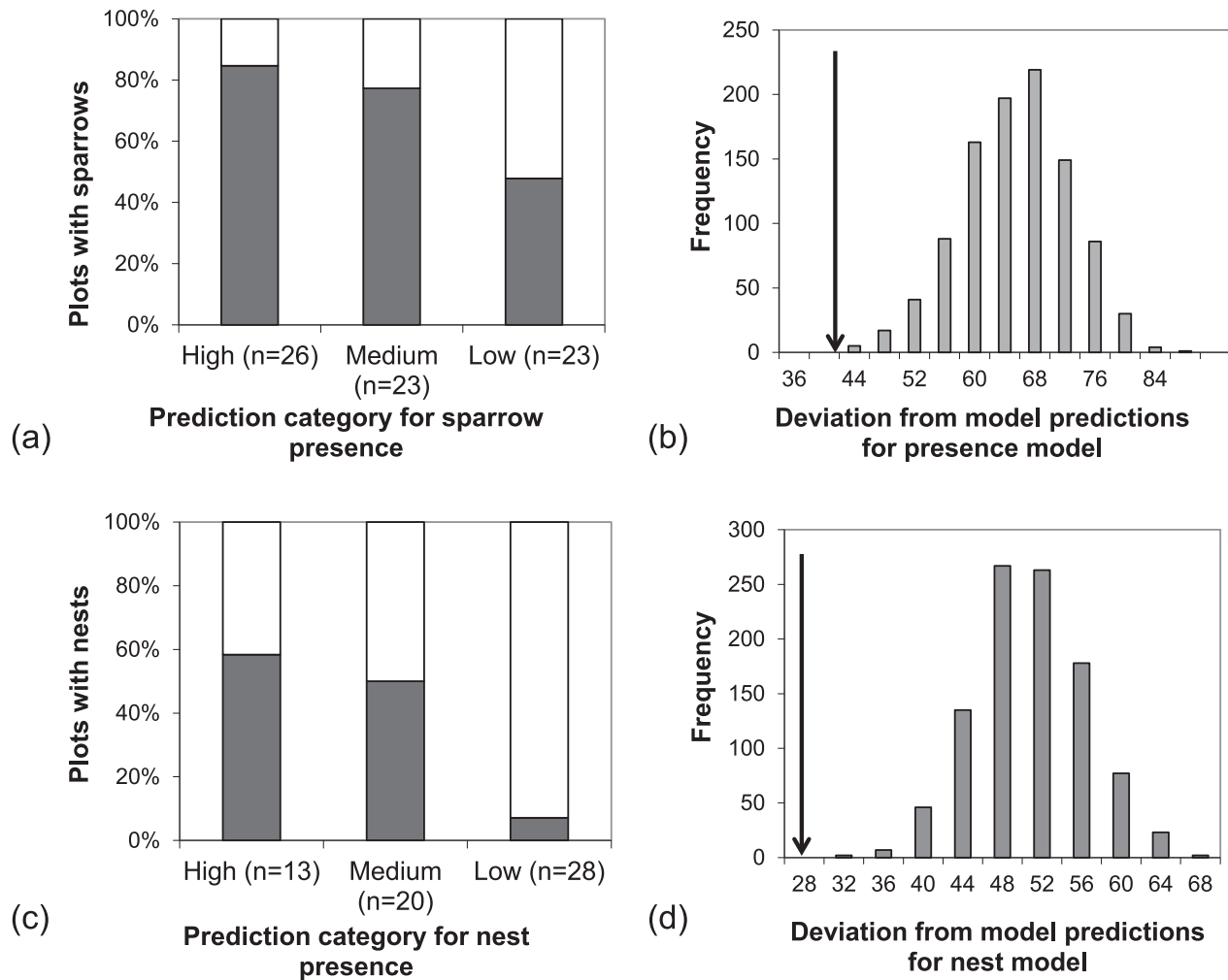
FIGURE 3.   Rates of Saltmarsh Sparrow presence (top panels) and nest presence (bottom panels) compared to predictions. (a) Observed rates of Saltmarsh Sparrow presence in cells predicted to have high (>95%), medium (50–95%), and low (<50%) predicted chances of containing sparrows. Dark gray indicates presence. (b) Deviance from model predictions 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. (c) 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 gray indicates nest presence. (d) Deviance from model predictions 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 (sparrow or nest presence = 1, sparrow or nest absence = 0) and the predicted probability at each site.

nesting, 27% had a medium probability, and 29% had a high probability. Within each of the major marsh systems, some cells were predicted to have a <2% probability of sparrow nests and some cells were predicted to have a >95% probability of nests. The mean predicted probability within a marsh system ranged from 12 to 54% (Fig. 2).

For the test of the nest model, 61 cells met the minimum criterion of at least three visits and were included in subsequent analyses. We found nests in 19 (31%) of these cells, a majority of which were classified as having a high chance of containing nesting birds (Fig. 3c). Only two (7%) 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. 3d). Because only one of the 42 nests we found successfully fledged young (due to high failure rates associated with repeated tidal flooding in 2009; Bayard and Elphick 2011), it was not possible to conduct analyses that would associate levels of reproductive success with the amount of high marsh in a cell.

The presences, absences, and prediction errors for both models were distributed across the entire study region. Combining information from both models showed one cell out of seven that had a high expectation for both sparrow presence and nest presence but had no sparrows. The two models' predictions conflicted (low probability of sparrow presence and high probability of nest presence) for four cells, of which two had both sparrows and nests, one had sparrows but no nests, and one had no sparrows.

DISCUSSION

Predictions generated by the models discriminated between areas with and without sparrows and their nesting 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 fewest. Model deviances and AUC measures indicated that predictions from both models performed better than expected by chance alone. The presence model's predictions were worse with test data than with the original training data, but the performance of the nest model was remarkably similar for both data sets.

Although the models performed well, they were not perfect. Model errors may be caused by errors introduced during processing of the remote-sensing data, leading to habitat misclassification. While many studies that use remote-sensing data have tested the accuracy of processing, the focus of our study was to test whether the results of processing could be used to predict an organism's occurrence, as increasing the precision of a poor predictive variable should not improve a model's performance. Because the pixels were classified from 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 saltmarsh 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 that 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 limited dispersal. Rotenberry and Wiens (2009) used data on habitat associations from 1977 to 1983 to generate models to predict shrubsteppe birds' occupancy in 1997 of the areas on which those models were based. Although bird abundance and distributions in the region remained similar, few of the models performed well. These discrepancies suggest that inferences drawn from predictive distribution maps based on 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 Saltmarsh Sparrow nesting. Minor elevation differences affect the risk of flooding (Gjerdrum et al. 2005, Gjerdrum et al. 2008a, Bayard and Elphick 2011), while several plant species of high marsh contribute to a vegetation structure that is associated with nests (Gjerdrum et al. 2008b). Until a sufficiently detailed GIS layer classifying the marsh community was built, however, the extent to which high marsh can be used as a predictor of sparrow nesting could not be established. We found sparrow nests were consistently absent where the amount of high marsh delineated within a hectare was less than 20% (category of low predicted probability). Areas with greater proportions of high marsh at the 1-ha scale should be considered of higher priority for conservation planning for the Saltmarsh Sparrow than areas with less high marsh, even if sparrows occupy the latter areas.

The map generated from the model for nesting directly links habitat to reproduction and has specific implications for Saltmarsh Sparrow conservation and management. In addition, because the nest model was built with a predefined classification of high marsh, this model is likely transferable to other areas where Saltmarsh Sparrows occur, as long as high marsh is delineated by the same GIS processes and the birds' behavior in selecting nest sites 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 reflective properties different from those of the areas they do occupy. Sparrow occupancy was predicted from these reflective properties with moderately good accuracy in new areas, suggesting that the processes driving the reflective difference occur throughout the region sampled. However, the remote-sensing data used to classify the pixels 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 because of

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 both high and low chances of containing sparrows to test specific hypotheses about environmental conditions that cause reflectance to vary might clarify the underlying biological relationships.

Of the area of saltmarsh in Connecticut, two-thirds was classified as having at least a 95% chance of having sparrows present. In contrast, only 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 is much smaller than the total area where sparrows are likely to be found, monitoring of 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, see also example in Fig. 1) 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 the 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. Our 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). With 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 such as the White-throated Sparrow (*Zonotrichia albicollis,* Tuttle et al. 2006), redtail monkey (*Cercopithecus ascanius*, Stickler and Southworth 2008), and Alaotran gentle lemur (*Hapalemur alaotrensis,* Lahoz-Monfort et al. 2010). These studies all used remote sensing to detect within-class variability not easily detected from 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.

ACKNOWLEDGMENTS

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