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HOW WELL CAN WE MODEL NUMBERS AND PRODUCTIVITY OF SALTMARSH SHARP-TAILED SPARROWS (*AMMODRAMUS CAUDACUTUS*) USING HABITAT FEATURES?

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ABSTRACT.—Habitat models are often used to describe species distributions, but they need to be tested to evaluate their predictive performance. We investigated the importance of model evaluation in a study of habitat selection by Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*), a species of conservation concern in eastern North America. We estimated the number of birds, nests, and fledglings produced in thirty 1-ha study plots spread across multiple marshes and used an information-theoretic approach to select among explanatory habitat models. Model performance was evaluated using both the original data set and data from another 30 plots from the same set of marshes. Our models indicate that both female and male Saltmarsh Sharp-tailed Sparrows increase in abundance as one moves away from the marsh's upland edge and in areas where there is deep thatch and uniform vegetation height. In contrast to the results for adult birds, number of nests and production of fledglings were positively associated with Saltmeadow Rush (*Juncus gerardii*). These models suggest that where adults spend the most time is influenced by the vertical structure of the vegetation but that nesting activity is determined more by plant compositions that indicate subtle variations in marsh elevation. Despite the fact that we found good internal consistency for our models during model evaluation, model performance worsened considerably when used to make predictions about new sites. Thus, although our study identifies several new factors influencing habitat selection in Saltmarsh Sharp-tailed Sparrows, it also highlights the need to be cautious when making predictions from habitat models. *Received 8 February 2007, accepted 17 November 2007.*

Key words: *Ammodramus caudacutus*, habitat use, model validation, productivity, Saltmarsh Sharp-tailed Sparrow, statistical models.

¿Cuán Bien Podemos Modelar los Números y la Productividad de *Ammodramus caudacutus* Utilizando las Características del Hábitat?

RESUMEN.— Frecuentemente se utilizan modelos de hábitat para describir las distribuciones de las especies. Sin embargo, estos modelos deben ser probados para evaluar su poder de predicción. Investigamos la importancia de la evaluación de modelos en un estudio sobre selección de hábitat en *Ammodramus caudacutus*, una especie del este de Norteamérica en estado de conservación preocupante. Estimamos el número de aves, de nidos y de volantones producidos en 30 parcelas de 1 ha distribuidas en varios humedales, y utilizamos una aproximación basada en la teoría de la información para seleccionar los mejores modelos de hábitat explicativos. El desempeño de los modelos fue evaluado utilizando los datos originales y los de otras 30 parcelas del mismo conjunto de humedales. Nuestros modelos indicaron que las abundancias de hembras y machos de *A. caudacutus* aumentaron con la distancia a los bordes en las partes altas de los humedales y en áreas donde existe una capa profunda de materia orgánica y vegetación de altura uniforme. De modo contrastante a los resultados obtenidos para las aves adultas, el número de nidos y la producción de volantones estuvieron relacionados positivamente con la presencia de *Juncus gerardii*. Estos modelos sugieren que el lugar donde los adultos pasan la mayor parte del tiempo está influenciado por la estructura vertical de la vegetación, pero que la actividad de anidación está más determinada por la composición de las plantas, la cual indica variaciones sutiles en la elevación del humedal. A pesar de que encontramos buena consistencia interna para nuestros modelos durante la evaluación, el desempeño de los modelos empeoró considerablemente cuando éstos eran usados para hacer predicciones sobre sitios nuevos. Por lo tanto, a pesar de que nuestro estudio identifica varios factores nuevos que influencian la selección de hábitat en *A. caudacutus*, también resalta la necesidad de tener cautela al hacer predicciones a partir de modelos de hábitat.

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A DETAILED KNOWLEDGE of a species' habitat needs is often required for effective population management. Statistical models are commonly used to examine species–habitat relationships when presence–absence (Franco et al. 2000, Karl et al. 2000, Luck 2002a) or abundance (Maurer 1986, Latham et al. 1997, Franco et al. 2000) are correlated with known habitat features. Models that attempt to predict productivity are less common (Heglund 2002) but are especially important, because the best breeding habitat does not necessarily support the most individuals (Fretwell 1972, Van Horne 1983, Vickery et al. 1992, Sutherland 1996, Bock and Jones 2004). Ideally, identification of species–habitat associations can be used to detect new areas that could support individuals, to identify which areas will produce the most offspring, to predict the consequences of environmental change, or to evaluate the effects of land-use decisions (Scott et al. 2002). Even apparently well-supported models (i.e., those with high Akaike weights), though, might produce poor predictions if the full suite of influential habitat factors are not fully known or if habitat alone is insufficient to explain species distributions. Before such models can be applied, therefore, their predictive power should be evaluated to avoid misdirected management decisions. When using a single data set to develop and evaluate a model, jackknife or bootstrap techniques are commonly used, but these approaches test only the model's internal consistency (Guisan and Zimmermann 2000). Obtaining new data to compare with model predictions, though less common, is needed to determine how well models will perform when extended to new circumstances (Fielding and Haworth 1995, Guisan and Zimmermann 2000).

We determined how breeding Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*) respond to habitat variation and used this information to develop and test predictive models that could provide practical information for saltmarsh bird conservation. The Saltmarsh Sharp-tailed Sparrow is the only bird species found exclusively in saltmarshes (Greenberg 2006). Its breeding range extends along the Atlantic Coast from Maine to Virginia (Greenlaw and Rising 1994), and it has been estimated that half the world population breeds in the coastal marshes of southern New England (Dettmers and Rosenberg 2000). Saltmarsh Sharp-tailed Sparrows are nonterritorial and promiscuous and do not form pair bonds; males occupy overlapping home ranges in which they search for receptive females, which then provide all the parental care (Greenlaw and Rising 1994).

Saltmarsh Sharp-tailed Sparrows are ranked as high conservation priorities both nationally and regionally (U.S. Fish and Wildlife Service 2002, Rich et al. 2004) and are considered globally vulnerable to extinction (BirdLife International 2004). This concern is based on their limited range and specialized habitat use. Salt marshes along the Atlantic Coast have suffered considerable habitat loss, fragmentation, and modification (Rozsa 1995, Zedler and Adam 2002), and the effects of these changes are exacerbated by reduced sparrow densities in smaller marshes (Benoit and Askins 2002, Shriver et al. 2004). Continuing threats to these habitats include the spread of the invasive Common Reed (*Phragmites australis*), sea-level rise, and coastal erosion (Zedler and Adam 2002).

The number of Saltmarsh Sharp-tailed Sparrows detected varies considerably both within and among marshes (Benoit and Askins 2002, Shriver et al. 2004; C. Elphick et al. unpubl. data).

Past studies have provided information on broad species distributions and general patterns of habitat use in Saltmarsh Sharp-tailed Sparrows, and it is well documented that they breed primarily in high marsh habitats dominated by Saltmeadow Cordgrass (*Spartina patens*; Brawley et al. 1998, Benoit and Askins 1999, DiQuinzio et al. 2002, Shriver 2002, Shriver et al. 2004). Detailed information on the causes of variation in numbers and productivity within the areas that the species occupies, however, is lacking. Previously, we examined nest-site microhabitat and patterns of nest success (Gjerdrum et al. 2005). Those results demonstrated that flooding during high spring tides is the major cause of nest loss (see also Greenberg et al. 2006), and successful nesting requires building nests that are unlikely to be washed out during high tides (Gjerdrum et al. 2005, Humphreys et al. 2007, Shriver et al. 2007). Habitat selection at the scale of individual nests, however, can be hard to relate to management actions, which typically occur at a larger spatial scale. In the present study, therefore, we examined the relationships between habitat features and the numbers and productivity of Saltmarsh Sharp-tailed Sparrows at a scale similar to that at which management decisions (e.g., concerning removal of Common Reed or alteration of tidal flow) occur. We also tested whether current knowledge of habitat use is sufficient to understand how Saltmarsh Sharp-tailed Sparrows will respond to habitat changes. Specifically, our objectives were to determine (1) how numbers and productivity of Saltmarsh Sharp-tailed Sparrows vary in response to habitat conditions and (2) whether numbers and productivity of Saltmarsh Sharp-tailed Sparrows can be accurately predicted on the basis of known habitat associations. To do this, we (1) used an information-theoretic approach to identify relationships between habitat variables and occurrence and productivity of Saltmarsh Sharp-tailed Sparrows at 30 study plots in marshes along the Connecticut coast and (2) tested the generality of the resulting models at 30 additional plots.

Methods

Study site.—The study was conducted during 2002–2004 at 12 marshes along the coast of Connecticut (Fig. 1). Using random points taken from grids overlaid onto U.S. Geological Survey topographic maps, we set up sixty 1-ha study plots across the 12 sites on which to focus our research activities. Areas dominated by Common Reed were excluded from the marsh areas from which our plots were selected, because our study species is not known to nest in dense stands of this introduced species (Benoit and Askins 1999). If a large, deep channel (>5 m across) crossed a plot, we moved the location to the nearest point where we could gain access to the entire plot without having to cross a channel. In larger marshes, pairs of nearby plots were sampled simultaneously. Vegetation within our study areas consisted primarily of Saltmeadow Cordgrass, Smooth Cordgrass (*S. alterniflora*), Saltgrass (*Distichlis spicata*), and Saltmeadow Rush (*Juncus gerardii*). These species produce a grassy sward that is dense but quite short, with the tallest stems in a plot averaging only 40 cm (Gjerdrum et al. 2005) and most of the vegetation somewhat shorter.

Bird sampling.—Each plot was visited five times at approximately two-week intervals from June to August to conduct systematic surveys. On each visit we set up an array of six two-panel
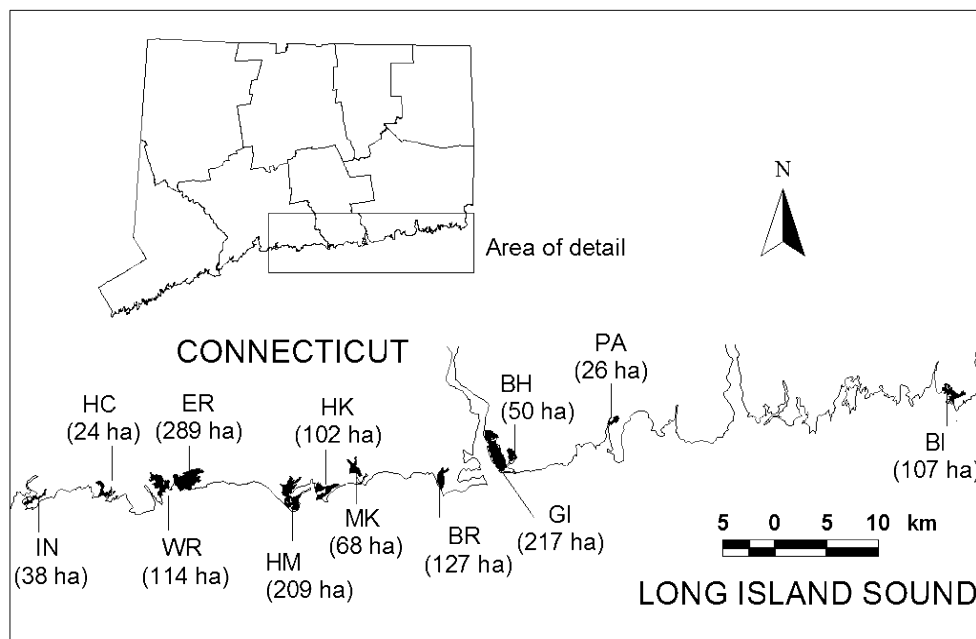
Fig. 1. Locations of saltmarsh study sites in Connecticut during 2002–2004. IN = Indian Neck (0 and 2 plots for model building and model testing, respectively); HC = Hoadley Creek (1, 1); WR = West River (0, 4); ER = East River (9, 3); HM = Hammonasset (4, 6); HK = Hammock River (3, 1); MK = Menunketesuck River = (3, 4); BR = Back River (2, 0); GI = Great Island (3, 5); BH = Black Hall River (1, 1); PA = Patagansett River (1, 1); and BI = Barn Island (3, 2).

mist nets across the plot to capture birds present within the plot's boundaries. Net locations were varied among visits to maximize coverage within each plot. We flushed birds into nets by systematically walking across the plot, following channel edges and moving toward the nets, at ~30-min intervals. Mist netting occurred in the mornings, and each visit lasted ~4 h. All captured birds were fitted with a numbered metal leg band and up to three plastic color bands, to allow for individual recognition. We determined sex of adult birds by the presence of a brood patch (females) or an enlarged cloacal protuberance (males) (Pyle 1997).

Nest searching and monitoring.—On each date that banding occurred, we also conducted a thorough search of the plot to look for nests. Searches involved walking back and forth across the entire plot, investigating any spots from which birds flushed and watching for activities such as transport of food or fecal sacs. In addition to intensive searches, we looked for nests every three to five days when checking the status of known nests. The simple, almost two-dimensional vegetation structure made nest searches and mist-net placement straightforward and easier to standardize than in more complexly structured habitats. The temporal distribution of nest discovery dates in relation to initiation dates suggests that almost all nests in our plots were found (see below).

All nests were marked with a flag placed 5 m away, such that the nest lay on a line between the flag and the plot center; this system enabled us to find nests again easily while reducing the risk of identifying their location to predators. Nests were checked every three to five days, and the number of fledglings present on the last visit before fledging was assumed to be the number that fledged (98% of successful nests were visited within three days of the predicted fledge date).

Habitat sampling.—Within each plot, we sampled habitat at the center, corners, and midpoints of each side and at nine randomly selected points. Systematically and randomly located points were compared to assess whether randomization, which is more time-consuming, would be necessary in future work. Habitat variables were not significantly different between the two sets of points (Gjerdrum et al. 2005); thus, we calculated plot averages across all 18 points. A 1-m quadrat was placed around each sampling point. We measured the height of the tallest stem at the corners of the quadrat, the depth of the accumulated dead plant material ("thatch depth") in the center of the quadrat, and the density of stems in five randomly located 10 × 10 cm sub-quadrats. We estimated the proportionate abundance of each plant type within the quadrat. Habitat sampling for all 60 plots occurred between mid-July and mid-August; at this time, most females are feeding young and plant growth has slowed, reducing the potential for temporal variation among samples to compromise habitat measures. We used tidal wetland coverages from the Connecticut Department of Environmental Protection (Connecticut State Plane 1927) in ARCVIEW GIS, version 3.2 (ESRI, Redlands, California), and the NEAREST FEATURE extension, version 3.8 (J. Jenness, Flagstaff, Arizona), to calculate the distance from the upland edge of the marsh to each plot's center.

Model building.—Data collected from 30 plots across 10 marshes were used to develop habitat models. We chose these model-building plots randomly from our total set of 60 plots and used the remaining 30 plots to test the model's generality (Fig. 1 gives the distribution of plots across sites). We used four measures as dependent variables: (1) total number of females captured over the course of a breeding season, (2) total number of males captured,

(3) total number of nests found, and (4) total number of birds fledged from those nests. We conducted separate analyses for males and females, because males are nonterritorial and polygynous and provide little parental care (Greenlaw and Rising 1994), which means that their numbers bear an uncertain relationship to the amount of nesting activity in an area. The number of females may better reflect the productivity of a site than the total number of birds. The number of nests provides a direct measure of where females choose to nest, and the number of fledglings indicates which areas produce the most recruits to the population.

Our initial set of predictor variables were the distance from a plot's center to the nearest point on the upland edge of the marsh, maximum vegetation height, vegetation stem density, thatch depth, and the percent cover for the five most common plant types; Saltmeadow Cordgrass, short-form Smooth Cordgrass, tall-form Smooth Cordgrass, Saltgrass, and Saltmeadow Rush. For each plot, we used the mean value for each habitat variable across sampling points. The standard deviations for vegetation height and density were also calculated to test whether the structural heterogeneity of the habitat was important. We also included plot location (i.e., marsh site) as a blocking factor in multivariate models, to test for inherent differences among marshes.

First, we examined simple correlations (Pearson or Spearman rank, as appropriate) between predictor variables and each dependent variable. To account for any geographic effects, or seasonal variation in the structure or composition of the habitat, we evaluated the effects of plot location (i.e., the marsh in which the plot lay) and habitat sampling date on each predictor variable. Next, on the basis of our studies of nest-site microhabitat (Gjerdrum et al. 2005, Humphreys et al. 2007), we created a set of candidate models designed to examine the effects on each dependent variable of (1) vegetation structure (termed STRUCT in model descriptions), (2) vegetation composition (COMP), (3) distance from the plot to the marsh's upland edge (DIST), and (4) the site at which the plot was located (MARSH). Before proceeding with the multivariate analysis, we calculated pairwise correlations and variance inflation factors and eliminated variables that contributed to collinearity among predictor variables (Zuur et al. 2007). In each group of collinear variables, we retained the variable that was most strongly correlated with the dependent variables. After addressing collinearity, models testing for a STRUCT effect included variables for vegetation density, thatch depth, and variation in maximum vegetation height. Models testing for a COMP effect included measures of the percent cover for short Smooth Cordgrass, tall Smooth Cordgrass, Saltgrass, and Saltmeadow Rush.

All 15 models comprising different combinations of STRUCT, COMP, DIST, and MARSH were compared for each dependent variable. To increase parsimony in the final models, we also considered reduced versions of the STRUCT and COMP models when these sets of variables appeared in the best-supported models. STRUCT was reduced in two ways: STRUCT-DEN retained only the density variable, whereas STRUCT-HGT retained only the height-variation and thatch-depth variables, which both describe features related to vertical structure in the vegetation. We considered only one alternative COMP model, in which only information on the percent cover of Saltmeadow Rush was retained (COMP-JUNC). This plant was hypothesized to be particularly important, because it is an indicator of the highest portions of the marsh, where nests would be least vulnerable to flooding. Models were compared using Akaike's information criterion for small sample sizes (AIC_c), and Akaike weights (w_i) were used to evaluate the relative likelihood of each model (Burnham and Anderson 2002).

We used SYSTAT, version 8.0 (SPSS, Chicago, Illinois), to develop all models. To meet assumptions of multiple regression, we transformed several variables to reduce skewness and improve the normality, linearity, and homoscedasticity of residuals (Tabachnick and Fidell 2001). Logarithmic transformations ($\log_{10}(y + 1)$) were used for the distance to the upland edge of the marsh, percent cover of Saltgrass, and percent cover of tall-form Smooth Cordgrass; square-root transformations were used for the numbers of nests and fledglings produced.

Testing model predictions.—We evaluated the predictive power of the resulting models using both the initial data set and new data. First, we used a jackknife approach applied to the best-fit model for each dependent variable. Sequentially, we removed one of the 30 plots at a time from the data set, estimated the model coefficients with the remaining data, and obtained a predicted value for the plot that had been dropped. This process was repeated for each plot, and predicted values were compared with observed values. Next, we generated a composite model for each dependent variable using weighted averages for each parameter estimate calculated from those models that received "substantial" support (i.e., $\Delta AIC_{ci} < 2$; Burnham and Anderson 2002). Composite models were used to predict each Saltmarsh Sharp-tailed Sparrow variable for the 30 plots selected for model testing. We then compared the predicted values for each plot to the observed values. For both the jackknife and cross-validation approaches, we tested whether observed and predicted values differed using paired *t*-tests for which a significant difference indicates a bad fit (i.e., rejection of the null hypothesis that the two groups are equal). A nonsignificant result for these tests could arise because of low statistical power, so we also measured the strength of the association between the observed and predicted values using simple correlation coefficients.

Results

Initial analyses.—During the present study, we captured 289 female and 779 male Saltmarsh Sharp-tailed Sparrows during our standardized mist netting and found 166 nests from which 189 nestlings fledged. The date on which egg laying finished could be estimated for 133 nests, and these data show that nest discovery was strongly skewed toward the early part of the nesting period, 86% of nests (115) having been found during incubation or just before egg laying (Fig. 2). Few nests (14%) were found during chick rearing, when the frequent visits by feeding females would be expected to make nests more conspicuous; this result suggests that we found almost all the active nests in our study plots.

The marsh in which a plot was located had a strong effect on habitat measurements ($P < 0.0001$ in all comparisons), justifying the need to include MARSH in our candidate models. By contrast, the date on which we measured habitat was not important ($P > 0.05$ in all comparisons), presumably because we constrained this sampling to a narrow period after peak growth. Pairwise
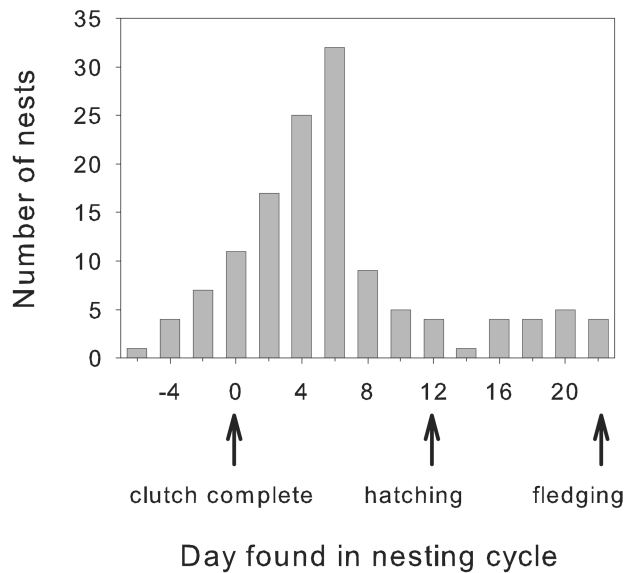
FIG. 2. Timing of nest discovery in relation to nest initiation ($n = 133$ nests). We found 86% of nests during the incubation phase or just before egg laying. Few additional nests were found during the chick-rearing phase, when nests are generally easier to find, which suggests that we successfully located almost all the active nests in our study plots.

comparisons showed that mean vegetation density was correlated with variation in density ($r = 0.79$, $n = 30$) and the amount of Saltmeadow Cordgrass ($r = 0.85$, $n = 30$) and that thatch depth was correlated with vegetation height ($r = 0.72$, $n = 30$). All other pairwise correlations were weak ($r < 0.61$). To avoid collinearity, we used only mean vegetation density and thatch depth in our models and eliminated the three correlated variables from subsequent analyses. All final models described below had variance inflation factors <2 for all variables.

Linking habitat to birds.—Simple correlations (Table 1) show that more female Saltmarsh Sharp-tailed Sparrows were captured in plots where the vegetation was relatively tall and less variable in height, where the thatch layer was deep, and where there was a lower proportion of short-form Smooth Cordgrass. Male densities were highest farther from the upland edge of the marsh, where vegetation height was less variable and where there was more Saltgrass and Saltmeadow Rush. Nest densities were higher at greater distances from upland edges, where vegetation density was higher and more variable and where there was a higher proportion of Saltmeadow Cordgrass and Saltmeadow Rush but less tall-form Smooth Cordgrass. More fledglings were produced in plots where vegetation density was high and where there was more Saltmeadow Rush but less tall-form Smooth Cordgrass.

Given the initial model set, the number of females captured in a plot was best explained by models containing vegetation structure (STRUCT), with or without the distance to upland edge (DIST). Both models had similar support, with $\Delta AICc_i < 4$ (Table 2A). Reducing the STRUCT model to include only measures of vegetation height (STRUCT-HGT) resulted in improved models in both cases, and the two reduced models collectively shared the bulk (80%) of the Akaike weights. The averaged model

TABLE 1. Correlations between habitat variables and measures of the numbers and nesting activity of Saltmarsh Sharp-tailed Sparrows. Only correlations with $P < 0.25$ are listed.

Habitat variable	Correlation coefficient	P
(A) Females captured		
Distance to marsh edge[a]	0.32	0.08
Vegetation height[a]	0.41	0.02
SD vegetation height[a]	−0.45	0.01
Thatch depth[a]	0.43	0.02
Percent Saltgrass[a]	0.26	0.17
Percent short-form Smooth Cordgrass[a]	−0.39	0.03
(B) Males captured		
Distance to marsh edge[a]	0.46	0.01
Vegetation height[a]	0.28	0.13
SD vegetation height[a]	−0.42	0.02
Vegetation density[a]	0.27	0.14
Thatch depth[a]	0.28	0.13
Percent Saltgrass[a]	0.39	0.03
Percent short-form Smooth Cordgrass[a]	−0.27	0.15
Percent tall-form Smooth Cordgrass[a]	−0.27	0.15
Percent Saltmeadow Rush[b]	0.37	0.04
(C) Nests		
Distance to marsh edge[a]	0.36	0.05
Vegetation density[a]	0.60	0.0004
SD vegetation density[a]	0.54	0.002
Percent Saltmeadow Cordgrass[a]	0.49	0.006
Percent tall-form Smooth Cordgrass[a]	−0.43	0.02
Percent Saltmeadow Rush[b]	0.71	<0.0001
(D) Fledglings		
Distance to marsh edge[a]	0.24	0.21
Vegetation density[a]	0.38	0.04
SD vegetation density[a]	0.30	0.10
Percent Saltmeadow Cordgrass[a]	0.25	0.19
Percent Saltgrass[a]	0.31	0.10
Percent tall-form Smooth Cordgrass[a]	−0.54	0.002
Percent Saltmeadow Rush[b]	0.61	0.0004

[a]Pearson's correlation coefficient.
[b]Spearman's rank correlation coefficient.

used to calculate the number of females in test plots was as follows: females captured = $3.416 + 1.924$(DIST) $+ 0.571$(THATCH) $- 0.240$(SDHT), which indicates that the number of females increases where there is deep thatch and uniform vegetation height and that female numbers increase as one moves away from the marsh's upland edge. The inclusion of vegetation density in models with $w_i > 0.01$ (Table 2A) suggests that higher stem densities may also be related, albeit weakly, to high numbers of females.

The predictor variables used in our best model for the number of males captured were the same as those in the top models for females: distance to the upland edge of the marsh, thatch depth, and the standard deviation of vegetation height. This top model received most of the Akaike weight, and the remainder was distributed broadly across several other models, the best of which all combined some measure of vegetation structure with the distance variable (Table 2B). Given its strong support, we used only the top model as our predictive equation: males captured = $-4.053 + 9.185$(DIST) $+ 0.913$(THATCH) $- 0.527$(SDHT).

TABLE 2. Ranking of the top models explaining Saltmarsh Sharp-tailed Sparrow numbers. Ranking is based on the smallest AIC_c value; k is the number of parameters in the model; w_i is the Akaike weight; only models with $w_i > 0.01$ are shown.

Model[a]	Log-likelihood	k	ΔAIC_{ci}[b]	w_i
(A) Females captured				
STRUCT-HGT	−26.21	4	0.00	0.45
DIST, STRUCT-HGT	−25.00	5	0.49	0.35
STRUCT	−26.15	5	2.78	0.11
DIST, STRUCT	−24.92	6	3.48	0.08
(B) Males captured				
DIST, STRUCT-HGT	−55.77	5	0.00	0.60
DIST, STRUCT	−55.76	6	3.14	0.13
DIST	−60.16	3	3.20	0.12
STRUCT	−58.51	5	5.49	0.04
STRUCT, COMP	−51.47	9	5.92	0.03
(C) Nests				
COMP-JUNC	10.82	3	0.00	0.47
DIST, COMP-JUNC	11.85	4	0.62	0.35
STRUCT-DEN	9.60	3	2.44	0.14
STRUCT	10.22	5	6.78	0.02
COMP	11.41	6	7.54	0.01
(D) Fledglings				
COMP-JUNC	−0.38	3	0.00	0.82
COMP	2.27	6	3.43	0.15
DIST, COMP	2.30	7	6.81	0.03

[a]Model definitions: DIST = distance from the center of the plot to the upland edge of the marsh; STRUCT = thatch depth, standard deviation of the vegetation height, and vegetation density; STRUCT-HGT = thatch depth and the standard deviation of the vegetation height; STRUCT-DEN = vegetation density; COMP = relative percent of Saltgrass, short-form Smooth Cordgrass, tall-form Smooth Cordgrass, and Saltmeadow Rush; COMP-JUNC = relative percent of Saltmeadow Rush.

The best model describing the number of nests included just the amount of Saltmeadow Rush. Adding DIST produced a model that received almost as much support, and these models jointly received most of the Akaike weights (Table 2C). Averaging the two top models resulted in an equation that indicates that the number of nests increases in relation to the abundance of Saltmeadow Rush and the distance of a plot from the marsh edge: nests (square-root transformed) = 0.612 + 0.529(DIST) + 0.072(JUNCUS).

The number of fledglings produced in a plot was also best explained as an increasing function of the amount of Saltmeadow Rush (Table 2D). With w_i = 0.82, this model was clearly better than all the others considered, and so we used it to predict the number of fledglings produced in our test plots: fledglings (square-root transformed) = 0.625 + 0.104(JUNCUS). Other models for fledgling production that received minimal support simply added other measures of plant composition and the distance from the marsh's upland edge.

Testing model predictions.—Overall, our final models had relatively good internal consistency but were far less good at predicting conditions in a broad set of new plots (Table 3 and Fig. 3). For all four Saltmarsh Sharp-tailed Sparrow variables, jackknifed data sets produced predicted values that were not consistently different from the observed values (power to detect a "large" effect; i.e., $d = 0.8$, with $\alpha_2 = 0.05$: $1 - \beta > 0.8$; after Cohen 1988). Additionally, there were significant correlations between predicted and observed numbers, with a moderate amount of variation explained in all cases (Table 3).

When models were cross-validated with data from new sites, however, we found little support for our predictions (Table 3 and Fig. 3). Predicted numbers of females and nests were significantly higher than their paired observed values, and there were also signs of overestimation by our best model for the number of males. Moreover, correlations between predicted and observed values were poor for all variables when tested with our independent plot data and essentially nonexistent for the number of females and the number of fledglings (Table 3).

DISCUSSION

Habitat modeling serves two general purposes. First, the development of statistical models that relate habitat features to bird numbers or demographic measures can provide important information about a species' needs and habitat selection, which in turn can guide land management and protection (Scott et al. 2002). Second, when the identified habitat relationships are sufficiently influential to allow models to make accurate predictions about habitat use, they can be used to provide shortcuts to the identification of good habitat and to forecast the consequences of future habitat changes (Rushton et al. 2004). Below, we discuss the specific habitat needs of our study species and general issues concerning the evaluation of predictive habitat models.

The main result of our model comparisons was that numbers of both female and male Saltmarsh Sharp-tailed Sparrows are best explained by variables associated with vegetation height and the distance from the marsh's upland edge, whereas the best models for number of nests and fledgling production contained the amount of Saltmeadow Rush as the key predictor variable.

TABLE 3. Results from our evaluation of four models of Saltmarsh Sharp-tailed Sparrow breeding activity, using jackknife and cross-validation approaches to test model predictions. No difference between observed and predicted values in paired *t*-tests and significant correlations between observed and predicted values indicate that a model is performing well.

|	Jackknife (internal consistency)		Cross-validation (external validity)	
Dependent variable	Paired *t*-test	Correlation	Paired *t*-test	Correlation
Females captured	$t_{29} = 0.003$, $P = 0.99$	$r = 0.56$, $P = 0.001$	$t_{29} = −3.53$, $P < 0.0001$	$r = 0.09$, $P = 0.63$
Males captured	$t_{29} = −0.03$, $P = 0.98$	$r = 0.51$, $P = 0.004$	$t_{29} = −2.54$, $P = 0.09$	$r = 0.36$, $P = 0.05$
Nests	$t_{29} = −0.005$, $P = 0.97$	$r = 0.58$, $P = 0.001$	$t_{29} = −1.22$, $P < 0.0001$	$r = 0.38$, $P = 0.04$
Fledglings	$t_{29} = −0.004$, $P = 0.98$	$r = 0.56$, $P = 0.001$	$t_{29} = −0.32$, $P = 0.34$	$r = 0.06$, $P = 0.73$
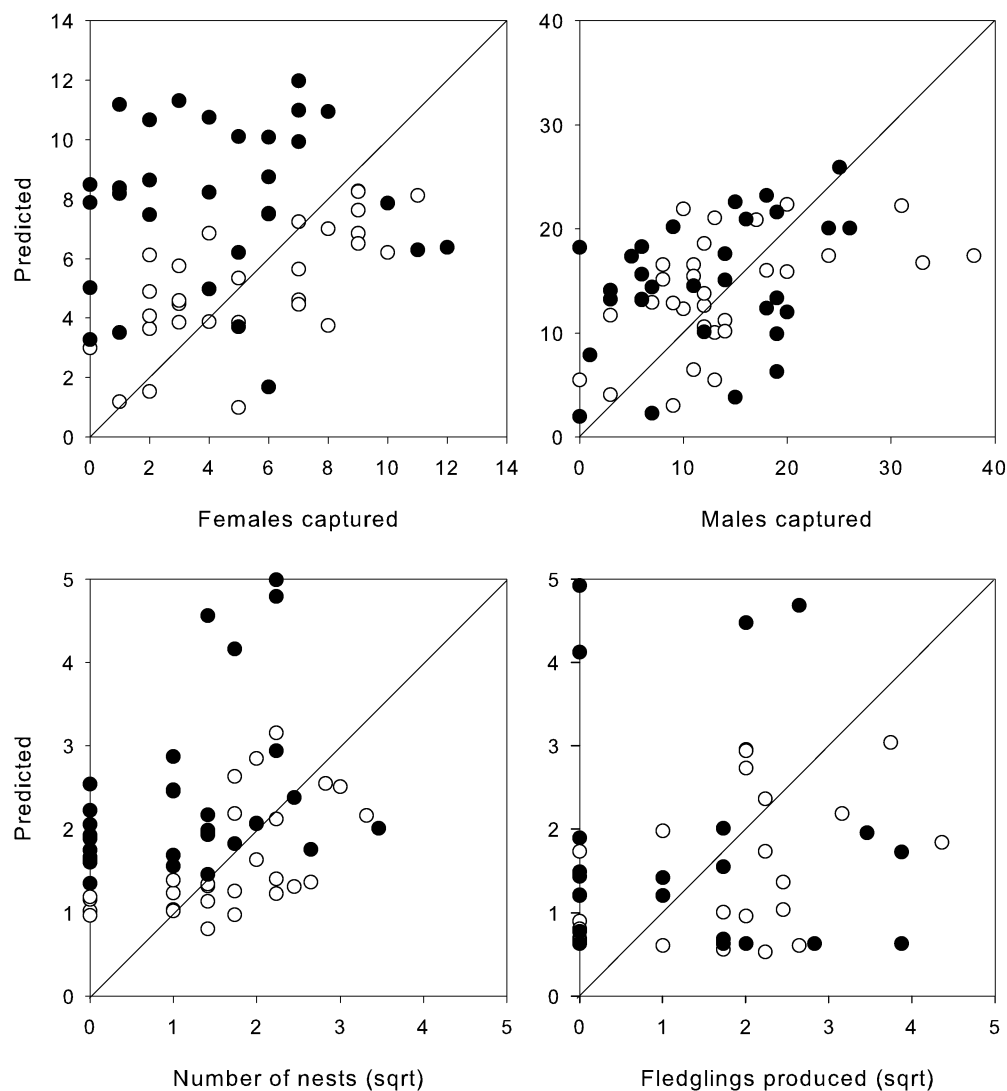
Fig. 3. Comparison of observed values for four measures of breeding activity in Saltmarsh Sharp-tailed Sparrows, with predicted values based on jackknifed estimates for the 30 plots used for model-building (open symbols) and cross-validation estimates for an additional 30 plots (solid symbols). The solid line indicates the line of best fit where all predictions are perfect.

More birds were found in plots with deeper thatch and more uniform vegetation heights. Given that maximum vegetation height is highly correlated with thatch depth, this variable may also be a cue used by Saltmarsh Sharp-tailed Sparrows when deciding which sections of marsh to occupy. The model results also indicate that the influence of the distance from the uplands may be somewhat greater for males than for females. One reason for this difference may be that females, but not males, have to trade this factor off against the tendency for higher-elevation nesting habitat, which is less prone to flooding and found nearer to upland marsh edges. In contrast to the results for adult numbers, number of nests and fledgling production were greater in areas where Saltmeadow Rush was more common. The distance from the upland edge, and to a lesser extent vegetation density, also appeared in supported models for the number of nests, which suggests that these variables may play a secondary role in indicating which sectors of marsh will have the most nests.

The relationship between both nesting density and fledgling production and the occurrence of Saltmeadow Rush is not surprising, given the ecology of the saltmarsh system. This plant has a low tolerance for high soil salinity and grows in high marsh habitat with minimum exposure to tidal water (Niering and Warren 1980). As such, Saltmeadow Rush should be a good indicator of where in a marsh the risk of nest flooding is lowest. Previous studies have demonstrated a positive association between numbers of Saltmarsh Sharp-tailed Sparrows and the presence of Saltmeadow Cordgrass (Reinert and Mello 1995, Brawley et al. 1998), another plant of the high marsh. In the present study, the amount of Saltmeadow Cordgrass was highly correlated with vegetation density and, thus, was dropped from the analyses to avoid multicollinearity. The fact that its close correlate, density, appeared only in models with relatively low weights, and not in any of the informative models for productivity, suggests that the amount of Saltmeadow Cordgrass provides little information on habitat use at

the scale of our study. At the coarser scale of identifying where high marsh occurs, Saltmeadow Cordgrass is clearly informative, but because this plant is ubiquitous and dominant in high marsh (Niering and Warren 1980, Reinert and Mello 1995, Brawley et al. 1998), we believe that the less common Saltmeadow Rush will be a much better indicator of the very best habitat for Saltmarsh Sharp-tailed Sparrows, because it provides the resolution to distinguish among areas of high marsh that differ in their propensity for flooding.

Our finding that a different suite of variables predicted areas of high nesting activity than predicted areas of high density is supported by surveys that show that Saltmarsh Sharp-tailed Sparrow counts are poorly correlated with nest density (C. Elphick et al. unpubl. data). Presumably, the cause of this mismatch is related to the fact that this species is nonterritorial and lacks long-term pair bonds (Greenlaw and Rising 1994), thereby eliminating certain constraints on space use. Nonetheless, it is unclear why birds of both sexes should congregate in areas different from those where most females nest. A full understanding of this phenomenon will require new information on the movement patterns of individual birds within marshes.

Although our results show clear links between certain habitat features and our measures of numbers and productivity of Saltmarsh Sharp-tailed Sparrows, the models generally predicted the activity of Saltmarsh Sharp-tailed Sparrows at new plots poorly, even though the test data came from the same set of marshes. The habitat models developed for all four Saltmarsh Sharp-tailed Sparrow variables appeared robust when applied to the original data set, but they did not perform well in cross-validation tests and systematically overestimated the number of females, males, and nests that occurred in new plots (Fig. 3).

The poor predictive ability of models may have resulted from our failure to include all important habitat variables or to account for key interactions or model structures, or from possible limitations in the ability of birds to assess habitat accurately. Another explanation is that habitat features alone do not explain species distributions. Landscape characteristics, for instance, have important influences on the distribution of many species (Freemark et al. 1995), including saltmarsh sparrows (Benoit and Askins 2002, Shriver et al. 2004, Hanson and Shriver 2006). Similarly, it is well established that behavior and social interactions can influence settlement patterns (e.g., Fretwell 1972). Territoriality can depress bird numbers below expected levels in high-quality habitat. In addition, site fidelity, which is relatively high for our study species (Greenlaw and Rising 1994, DiQuinzio et al. 2002), results in birds continuing to use sites even after habitat quality has declined (Wiens et al. 1986). Conspecific attraction (Reed and Dobson 1993) could also be important, because it can cause both absences from apparently suitable habitat and higher-than-expected numbers in areas where birds settle. Saltmarsh Sharp-tailed Sparrow nests, for instance, are often clustered (the species has been described as "colonial"; Murray 1969) in ways that are not obviously related to habitat.

Combining data collected at the scales of individual birds, study plots, and entire marshes is complex, because the level of replication differs among scales. This problem could be overcome through the use of hierarchical models that account for the nested structure of the data and the spatial behavior of individuals

(e.g., Cushman and McGarigal 2004, Gelfand et al. 2006, Latimer et al. 2006) and, thereby, better account for the complex manner in which birds decide where to settle. For researchers, the challenge in implementing such models will be to ensure adequate replication at the highest hierarchical level.

Habitat models such as those developed here have proved useful for understanding and describing the distribution of many species (Scott et al. 2002). For instance, our model provides detailed information on the specific habitat features that indicate where in the high marsh the best conditions for Saltmarsh Sharp-tailed Sparrows lie. This specific information was not previously available to managers, and it reinforces the importance of protecting the very highest portions of the high marsh, as indicated by the presence of Saltmeadow Rush—especially those portions that do not lie right along the upland boundary. This observation is important, given the threats to high-marsh vegetation from Common Reed invasion and changing interactions with competing native plants, both of which are affected by nutrient enrichment caused by upland development (Bertness et al. 2002). Moreover, our results indicate that Common Reed control activities that lower marsh elevations probably will not restore marshes to conditions suitable for nesting Saltmarsh Sharp-tailed Sparrows.

Although habitat models can provide useful information about relationships between a species and ecological conditions, models are most useful in an applied context when they can accurately predict species responses (Rushton et al. 2004). Even though many authors have advocated the collection of independent data sets to develop and then evaluate models (Fielding and Haworth 1995, Guisan and Zimmermann 2000, Luck 2002b, Vaughan and Ormerod 2003), tests are often not conducted. Although it is perhaps counterintuitive, it is clear from our results and those of others (e.g., Wiens 2002) that even models with apparently good internal consistency will not always provide good predictions. High Akaike weights, too, are not necessarily good indicators of model quality, because they are calculated only in relation to the set of models compared (Burnham and Anderson 2002), as exemplified by comparing the high w_i for our best fledgling model with its very low predictive power. We suspect that mismatches between apparent model validity and predictive power may be the norm, because field studies frequently face logistical constraints that prevent random sampling from the entire population of sites about which one wishes to make inferences. This general problem will be exacerbated if field studies are more likely to be conducted at high-quality sites, which seems likely, given that these are the sites where large data sets can be gathered most efficiently and quickly. An alternative analysis of the data presented here showed that when data from only the sites with the largest populations were used for model building, model predictions worsened (C. Elphick et al. unpubl. data).

As conservation biologists and managers increasingly use habitat models to infer species abundance and productivity, they face two challenges. First, there is a need to move beyond models that incorporate habitat features alone, because other types of information influence decisions about where individuals settle. Second, if models are to be used for prediction, it is imperative that they be thoroughly evaluated using a variety of techniques, including application to independent data sets (Luck 2002b, Vaughan and Ormerod 2003).

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