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# Differences in Habitat at Two Spatial Scales Fail to Predict Differing Occurrences of Three Species of Wintering Ammodramus Sparrows in South Carolina Salt Marshes

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**Differences in Habitat at Two Spatial Scales Fail to Predict Differing Occurrences of Three Species  
of Wintering *Ammodramus* Sparrows in South Carolina Salt Marshes**

Kimberly A. Trinkle

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Submitted in Partial Fulfillment of the  
Requirements for the Degree of Master of Science in  
Coastal Marine and Wetland Studies in the  
College of Science  
Coastal Carolina University  
2013

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## Abstract

Salt marshes have low levels of vertebrate diversity yet extremely high rates of endemism. Two of these endemic species are the Saltmarsh (*Ammodramus caudacutus*) and Seaside Sparrow (*A. maritima*); the closely related Nelson's sparrow (*A. nelsoni*) winters exclusively on salt marshes. A previous winter study found that individual sparrows of all three species were highly faithful to specific banding sites, and that the relative abundances of the three species differed by site. I hypothesized that the reason sparrow assemblages varied among sites was that the three species' winter habitat requirements were different. All three species winter in salt marshes, but detailed habitat requirements of each species are largely unknown. Studying the relationship between habitat and abundance could improve predictions of how changes to the marsh habitat caused by sea level rise and coastal development will affect wintering sparrows. I sampled wintering sparrow populations by mist-netting throughout the winter at 18 sites in South Carolina. I also measured habitat data on a landscape scale and at the scale of vegetation cover in small plots. I built regression models to investigate the relationship between species abundance and habitat. I found that both sparrow assemblage and habitat composition differed among the five marshes and 18 sites. The habitat-driven models' performance was either not significantly different from or was significantly worse than null models which estimated sparrow assemblage structure from capture effort at each site combined with study-wide and site-specific capture rates for each species. The similarities in sparrow assemblages at sites shared by the present study and a previous study indicate that patterns in relative abundance are stable from year to year; yet poor model performance indicates that these patterns cannot be predicted by habitat as measured in this study alone.

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## Introduction

Salt marsh ecosystems are globally rare, yet particularly well-developed along the eastern coast of North America (Greenberg et al. 2006). One unique characteristic of saltmarshes is their high rate of vertebrate endemism. Greenberg et al. (2006) identified 25 terrestrial vertebrate species endemic to coastal marshes, five of which depend solely on saltmarshes for the completion of their entire life cycle. Two of those saltmarsh obligate species are the Seaside Sparrow (*Ammodramus maritimus*) and Saltmarsh Sparrow (*A. caudacutus*) (Greenberg et al. 2006). One subspecies of the closely related Nelson's Sparrow (*A. nelsoni subvirgatus*) also depends entirely on salt marshes during its life cycle. Two other subspecies of Nelson's Sparrow (*A. n. nelsoni*, *A. n. alterus*) breed inland but depend on salt marshes in winter (Shriver et al. 2011). During the non-breeding season (approximately Oct-April), all three species co-occur in salt marshes along the Atlantic coast from Virginia to Florida and along the Gulf of Mexico (Greenlaw and Rising 1994; Post and Greenlaw 2009; Cristol et al. 2011; Shriver et al. 2011).

Because of threats to salt marshes, these three species are listed as species of conservation concern (U.S. Fish and Wildlife Service 2008). Threats to coastal wetlands include destruction and degradation caused by human development. An estimated 30-40% of estuarine wetlands have been destroyed by development and agriculture (Greenberg et al. 2006). Humans can also affect estuarine marshes by introducing invasive species, either accidentally or intentionally. Spread of invasive vegetation is of special concern because these plants can replace native vegetation used by salt marsh specialist species like *Ammodramus* marsh sparrows. For example, Saltmarsh Sparrows were less abundant in stands of the invasive common reed, *Phragmites australis*, when compared to plots with native vegetation (Benoit and Askins 1999).

In addition to human development, sea-level rise resulting from climate change poses a major threat to salt marshes and salt marsh obligate species like the Seaside and Saltmarsh Sparrow. Over the past century, global sea level rose 1.8 mm/yr, with that rate increasing to 3.0 mm/yr over the past decade (Rosenweig et al. 2007). Global sea levels are expected to rise a further 0.18 to 0.59 meters by the end of this century (Bernstein et al. 2007). Such rises in sea level are likely to result in vegetation shifts, with



*Spartina alterniflora* replacing *Spartina patens* in the high marsh, decreasing habitat (especially high marsh refuges) for Seaside and Saltmarsh Sparrows throughout their breeding ranges and for all three species throughout their winter ranges (Erwin et al. 2006). Rising sea levels are also likely to result in more extreme flooding during spring tides and storms, which already have catastrophic consequences on sparrow nesting success (Shriver et al. 2007; Bayard and Elphick 2011).

Salt marshes may persist despite a rise in sea level if the rate of marsh sediment deposition is equal to or greater than the rate of local sea-level rise (Kennish 2001). Sea levels in South Carolina are rising at a rate of 3.2 mm/yr to 4.1 mm/yr (NOAA 2010) with marsh sediment accretion rates ranging from 1.3 mm/yr to 4.5 mm/yr (Kennish 2001), meaning that some South Carolina salt marshes may be able to keep pace with local sea-level rise. If marsh sediment deposition rates are equal to or greater than the rate of sea-level rise, the marsh can either expand laterally or shift inland (Orson et al. 1985). However, the marsh may still be threatened as coastal development can block this landward shift (Wilson et al. 2007). As the opposing forces of sea-level rise and coastal development converge on marshes, it is likely that marshes will undergo changes in both size and composition within the next century, with portions of low marsh being converted to open water and areas of high marsh changing to low marsh (Titus et al. 1988). In addition to causing habitat shifts, sea-level rise is likely to result in a net loss of total salt marsh area. Craft et al. (2008) modeled marsh change using mean (52 cm) and maximum (82 cm) estimates of sea-level rise over the next century along the southeast coast and found that marsh loss is expected to range from 20% (mean sea-level rise scenario) to 45% (maximum sea-level rise scenario). Sea-level rise and human disturbance will alter salt marshes not only on a smaller scale (e.g. vegetation shifts within a marsh), but also on a landscape scale. These landscape-level changes may be related to marsh size and isolation, amount of open water, amount of high and low marsh, and amount of development in and around marshes. These changes will impact salt marsh obligates such as Seaside and Saltmarsh Sparrows as well as species like the Nelson's Sparrow which spend a considerable amount of time in salt marshes (Craig and Beal 1992; Shriver et al. 2004).

*Ammodramus* marsh sparrow abundance can be related to landscape parameters. For example, both Seaside and Saltmarsh Sparrows are more abundant in larger marshes within their breeding ranges (Benoit and Askins 2002; Shriver et al. 2004). Additionally, sparrows may be less abundant in marshes with more areas of open water during the breeding season since they depend on dense vegetation in the high marsh for ground nesting (Craig and Beal 1992). Marsh sparrows are also affected by isolation of marshes (possibly caused by increased development along coastlines), with Nelson's and Saltmarsh Sparrows occurring more frequently in less isolated marshes during the breeding season (Shriver et al. 2004). Human disturbance in and around marshes can also affect sparrow populations; Nelson's Sparrow occurrence is negatively related to road density (Shriver et al 2004) while Seaside Sparrow nest density and success is lower in marshes containing mosquito ponds and ditches (Pepper and Shriver 2010). In the post-breeding and winter season, mudflats and exposed edges of intertidal creeks in the low marsh may serve as important sources of invertebrate food for sparrows (Greenlaw and Rising 1994; Post and Greenlaw 2006; Hill 2008; Post and Greenlaw 2009; Shriver et al. 2011).

In order to be able to predict how changes to marsh size, extent, and vegetation will affect *Ammodramus* sparrows, the birds' current habitat requirements must be known at every life stage. Previous studies discovered important information regarding marsh sparrow habitat use during the breeding and post-fledgling seasons, which can potentially help land planners manage salt marshes for the conservation of *Ammodramus* sparrows on breeding grounds (Gjerdrum et al. 2005; Hill 2008; Shriver et al. 2010; Meiman 2011). However, it is also important to know about sparrow winter habitat requirements, especially since habitat use can differ depending on season or life stage (Hill 2008; Sillet and Holmes 2008; McClure et al. 2012).

Even though knowledge of the breeding ecology of *Ammodramus* marsh sparrows is increasing, there is little knowledge of their winter ecology. Data gained from winter habitat studies can be used in models predicting the occurrences of Seaside, Saltmarsh, and Nelson's Sparrows at different marshes within their winter ranges. Identification of habitat variables associated with the abundance of each species will not only increase knowledge of these species' winter ecologies but can also be combined with

models of habitat change caused by sea-level rise to predict how sea-level rise will affect wintering populations of marsh sparrows.

Two recent studies investigated the biology of wintering *Ammodramus* sparrows (Winder et al. 2012; Shaw 2012). A 2010-2011 winter banding study on sparrow site fidelity conducted in South Carolina revealed a pattern where different proportions of each species were captured at different sites (some of which were located in the same marsh and separated by less than 2 km) in consecutive years (Shaw 2012).

These observations led to the questions being investigated by the present study: 1) Are the differences in relative abundance related to differences in habitat between sites, and 2) Can occurrences of *Ammodramus* marsh sparrows be predicted based on habitat characteristics at the banding site? In order to investigate these questions, I quantified habitat using aerial photographs and performed vegetation surveys at 18 marsh sites along the South Carolina coast to measure habitat at each banding site. From that analysis I generated two separate sets of multiple regression models: one set related the relative abundances of each species to habitat variables, and the other set related capture rate of each species to habitat variables. I then investigated whether these regressions were able to predict the sparrow distribution at new sites. To test the performance of the relative abundance and capture rate models, I compared the predictions made by the habitat models to the predictions made by the null models which predicted sparrow occurrence at each site using study-wide relative abundances and capture rates.

## **Methods**

### *Study Sites*

I chose study sites by viewing aerial photographs of candidate high marsh sites in South Carolina marshes using Google Earth. From the aerial map searches, I found a total of 133 possible sites in six marshes which appeared suitable for banding during the winter. “Suitable” sites were mostly small patches of high marsh surrounded by a matrix of low marsh; I reasoned that large numbers of individuals would become concentrated at these sites during high tides. I also considered strips of high marsh between upland and low marsh because birds may also become concentrated in these areas, but also

because inclusion of these sites allowed me to investigate whether these marsh-edge sites attracted a different mix of sparrows than sites near the center of marshes. Both types of sites had a similar aerial appearance to sites where a previous study had success capturing sufficient numbers of birds (Shaw 2012). Of those 133 sites, I chose 9 banding sites between the North Carolina border (approx. 33°51'40.43"N, 78°33'9.83"W) and Bulls Bay, SC (33° 1'27.01"N, 79°31'0.36"W) based on logistics and accessibility. Many of the 133 sites were eliminated because they were not accessible (i.e. were on private land or blocked by intertidal creeks); several because there were no good places to set nets, and others were eliminated because they were accessible by boat only and my access to boats could be unpredictable. The Town of Kiawah Wildlife Biologist, Aaron Given, banded at 18 additional sites on Kiawah Island (approx. from 32°37'55.32"N, 80° 2'2.88"W to 32°34'58.07"N, 80° 8'36.45"W). I randomly chose nine of those Kiawah sites for habitat and banding analyses. The five marshes were (with approximate areas and number of banding sites in parentheses) Waties Island (470 ha, two banding sites), Huntington Marsh (1140 ha, two sites), North Inlet (3825 ha, four sites), Cape Romain National Wildlife Refuge (12,110 ha, one site), and Kiawah Island (3650 ha, nine sites). The distribution of the study marshes along the SC coast is presented in Figure 1.

### *Habitat Quantification*

I performed a GIS analysis of each site using year 2006 infrared digital orthophoto quarter quadrangles (DOQQs) obtained from the South Carolina Division of Natural Resource's (SCDNR) GIS Database as base layers. I estimated habitat variables including percent cover of open water, low marsh, high marsh, upland, and beach/shell gravel within a 400-m radius and a 70-m radius around the banding site. Other landscape variables measured were latitude, length of inter-tidal creeks and, as a method to distinguish capture sites near the edges of marsh from those more central, distance to nearest tree. I used a "heads-up" digitization method (Bolger et al. 1997; Higanbotham et al. 2004) using the polygon drawing tool in ArcGIS v.9.3 (ESRI, Redlands California) to create habitat layers at map scales of between 1:1,000 and 1:4,000. Such a map scale provided enough detail where boundaries of different habitat types could be viewed and traced easily. It was possible to digitize different habitats using aerial

photos because different marsh features possessed different colors and textures on the images (Higanbotham et al. 2004). In the aerial photographs used in this analysis, open water had a homogenous and smooth dark blue appearance, low marsh had a stippled blue-green-gray color appearance, high marsh was beige and stippled, upland areas appeared red, and inter-tidal creeks appeared as thin, smooth, gray-blue lines.

I quantified land cover at two spatial scales: 1.5 ha (70-m radius from the banding site) and 50 ha (400-m radius from the banding site). Estimates of breeding season home ranges vary from 0.4-5.7 ha (Greenlaw and Rising 1994) to up to 50 ha (Shriver et al. 2010) for Saltmarsh Sparrows, and 0.12 ha to 6.6 ha for Seaside Sparrows (Marshall and Reinert 1990; Post and Greenlaw 2009). I examined both scales (1.5 ha and 50 ha) to determine whether habitat selection was occurring at one scale but not the other or whether some habitat variable was equally important to sparrows at different scales. I also studied both scales because marsh sparrows may use different areas of the marsh depending on tidal level. The 1.5 ha scale in this study was very representative of high marsh roost sites that sparrows use during high tide, while the 50 ha scale included areas of low marsh that sparrows may be using as foraging grounds during low tide. Measuring habitat at both of these scales allowed me to quantify habitat in the two different areas of marsh that sparrows might be using.

Because individual plant species could not be identified from aerial photographs, and including more detailed habitat information can improve model function (McClure 2012), I performed ground vegetation sampling so that percent composition of each plant species could be considered for statistical modeling. I sampled vegetation at 15 randomly selected locations exposed at low tide within a 70-m radius of the banding site and at 30 more randomly selected locations exposed at low tide from the 70-m radius out to a 400-m radius of each banding site. If I could not reach a vegetation plot because of a tidal creek blocking access, I sampled the closest point possible. Within a 1-m<sup>2</sup> quadrat centered on each sampling location, I visually estimated and recorded percent cover of each plant species as well as of bare ground. Vegetation sampling occurred from July 2011 through July 2012. Because sparrows are likely to select high marsh vegetation on the basis of structure rather than based on what species a plant is, I

combined plant species into several categories to simplify analyses and reduce the amount of redundancy in my vegetation variables. Those vegetation classes were: low grass (consisting of *Salicornia* spp., *Limonium carolinianum*, *Distichlis spicata*, and *Batis maritima*), high grass (consisting of *Juncus roemerianus* and *Spartina patens*), and woody shrub (consisting of *Borrchia frutescens* and *Iva frutescens*).

#### *GIS Accuracy Assessment*

To determine digitizing error, I compared vegetation plot compositions to their GIS classifications. If a vegetation plot consisted of at least 50% *S. alterniflora* and bare ground combined, it was considered low marsh, while a vegetation plot containing less than 50% bare ground and *S. alterniflora* combined was considered high marsh. The percentage of vegetation plots accurately classified in GIS out of the total number of plots surveyed on the ground was used as a measure of digitizing accuracy. The results of this assessment only determined my accuracy of discerning between areas of high and low marsh using GIS because vegetation plots were only at areas that sparrows would use, meaning either low or high marsh. Because other features like upland and open water were distinctive in appearance on the aerial photographs used for digitization, comparisons of on-the-ground points and GIS classifications of these features were not performed unless there was uncertainty about their location.

#### *Capture Methods*

Banding occurred from October 2011 through April 2012 on days with an early morning (0700 hr-1100 hr) spring high tide (1.3 m to 1.9 m above MLLW). During each banding visit, mist nets were placed in the high marsh (Plentovich et al. 1998), where sparrows seek refuge from rising water levels during high tides. I used nets measuring 2 m x 12 m or 2 m x 6 m with a 30-mm mesh size on 3.1-m metal poles to catch birds. The number of nets set at each site depended on the size of the vegetation patch where birds were concentrated, but ranged from two to six and were usually arranged in a “U” or “V” shape along the edge of a patch of high marsh vegetation. Birds were flushed into nets from their high tide roost sites when researchers walked through patches of high marsh vegetation and caused

disruption by clapping or hitting the vegetation with a stick or pole. I visited sites along the Grand Strand (i.e., from Waties Island SC to Bulls Bay SC) approximately once every two months, allowing for each site to be visited at least three times from October 2011 to April 2012. Kiawah Island sites were visited once each from January 2012 through April 2012 by biologist Aaron Given, who used similar capture methods (pers. comm.). Because Aaron and I visited our sites different numbers of times, I quantified the number of individuals at a site by calculating new captures per visit. At sites I visited multiple times, I continued to catch new birds at approximately the same rate as the first visit, so standardizing the number of new captures by the number of visits to each site allowed our results to be comparable.

Upon capture, I fitted each sparrow with a USFWS aluminum leg band. Birds were then identified to species, with Nelson's Sparrows identified to subspecies using a morphological key developed by Greenlaw and Woolfenden (2007). For each sparrow, I recorded measurements of culmen length, wing length, tarsus length, and body weight. Additionally, I assigned furcular and abdominal fat scores as well as pectoral muscle scores to each bird using a scoring system developed by Ray Danner (unpublished manuscript). Photographs of each bird were taken for confirmation of identification of species and subspecies. All banding was performed with a sub-permit under Dr. Chris Hill (Federal Banding permit #22990) and with approval from IACUC (Coastal Carolina University, protocol #2011.02).

#### *Data Analysis*

I compared the relative abundances of species between marshes and sites using a chi-square test ( $\alpha=0.05$ ). I used two measures of abundance, relative abundance and new captures per visit, to describe sparrow assemblages in this study. Both provide slightly different information and have different advantages and limitations. Relative abundance can provide information about the possible habitat preference of a species compared to other species but is restrictive in that all values must add up to 100%. Use of relative abundance at sites with small sample sizes can skew the dataset since all sites in this project were given equal weight in analyses. For example, I captured only four sparrows at the site I named Huntington South, all of which were Saltmarsh Sparrows. The capture of a small number of only

Saltmarsh Sparrows resulted in a low capture rate for Saltmarsh Sparrows at this site, yet a high (100%) relative abundance. The 100% relative abundance of Saltmarsh Sparrows heavily weights this site in favor of this species, even though only four were captured there during the entire winter, which is the smallest capture total of any of the 18 sites. Because the variance was so high at Huntington South and several other sites where a small number of sparrows were captured, it was difficult to predict assemblages based solely on relative abundance. I determined the relative abundance for each species by calculating the percent of the total *Ammodramus* sparrow catch at a site that were Saltmarsh Sparrows, Seaside Sparrows, and Nelson's Sparrows. Other species were very rarely captured, and were excluded from analyses. New captures per visit is not restrictive to a final sum (all values do not have to add up to 100%), but appears to depend on site characteristics (whether or not the site is the only patch of high ground in a large swath of low marsh). New captures per visit (hereafter referred to as "capture rate") included individuals that were either un-banded or recaptures from previous years (i.e., any bird that was not a within-season recapture). Within-season recaptures were not considered in this study because I wanted to obtain an estimate of the total abundance of birds at each site for the entire winter. Marsh sparrows have high rates of within season site fidelity coupled with extremely low rates of movement between sites during the winter (Shaw 2012). Because of the low rates of movement between high tide roost sites during the winter, counting a within-season recapture each time it was encountered would inflate the number of individuals at a banding site. Examining both relative abundance and capture rate provided a more comprehensive picture of the relationship between habitat and species abundance.

### *Model Building*

To build and test regression models, I randomly chose 12 of the 18 banding sites to build the models ("model-building sites"), with the remaining 6 sites ("test sites") used to test the predictive ability of the models. I constrained the choice of model-building and test sites so that each group included half northern sites (Waties Island to Cape Romain) and half southern (i.e., Kiawah Island) sites because previous work (Greenlaw and Rising 2007) had shown that relative abundances of these species varied with latitude on the Atlantic coast. I divided my model-building sites and test sites unevenly (12:6)



because winter habitat requirements for the three sparrow species are unknown and I wanted to have as much information as possible to build the predictive models. I built regression models to predict relative abundances of each species from habitat information, and in a second analysis built models to predict capture rates of each species from habitat information. Each predictive model was built using a modified Regression with Empirical Variable Selection (“REVS”) method detailed by Goodenough et al. (2012). I chose this technique because it has been shown to be a robust way to choose informative models from a large set of independent variables (Goodenough et al. 2012). The final candidate models were compared using Akaike’s Information Criterion (AIC).

In an attempt to avoid overfitting or producing an overly complex model, I modified the procedure to limit the maximum number of predictors in any one model to five; this should have allowed for inclusion of enough variables with predictive power in the final model while reducing the chance that an overly complex model would be produced. Because of the small sample size relative to the number of predictor variables, I used AIC corrected for small sample size (AIC<sub>c</sub>) for model selection.

#### *Assessing models that predict relative abundance*

After model building was complete, I applied the relative abundance regression models to habitat data at the six test sites to obtain a predicted relative abundance of each sparrow species at each site. At each site, I then multiplied the relative abundance predicted by the habitat-driven model times the number of sparrows actually caught at that site – if the habitat based model predicted 20% Saltmarsh Sparrows at a site where I had captured 35 total sparrows, the model was considered to have predicted that 7 Saltmarsh Sparrows would be caught at that site. I constructed a null model for relative abundance by calculating the percent of the study-wide total catch that were Saltmarsh Sparrows, Seaside Sparrows, and Nelson’s Sparrows. I then calculated the number of individuals of each species I would expect to find at a given site by multiplying those study-wide relative abundances times the total number of sparrows found at that site. I compared the number of sparrows predicted under each model to the actual capture totals to obtain an error value. I compared the errors of both the habitat-driven model and relative abundance null model using a one-tailed paired t-test ( $\alpha=0.05$ ) to determine if habitat-driven models performed

significantly better than null models (i.e., had a lower error rate). For each species, I evaluated the performance of all top-ranked habitat-driven models ( $\Delta AIC_c < 2$ ). I evaluated three Saltmarsh Sparrow models, two Seaside Sparrow models, and one Nelson's Sparrow model.

*Assessing models that predict capture rate of each species*

In a separate analysis, I applied the capture rate regression models to predict the number of sparrows of each species captured at the six test sites, given the netting effort at each site. I calculated the predicted number of individuals of each species at each site by multiplying the predicted capture rate from the habitat-driven model by the number of times I visited that site. To construct a null model, I multiplied the study-wide capture rates of each species by the number of times each site was visited. I compared the number of sparrows predicted under each model to the actual capture totals to obtain an error value. I compared the mean errors of both the habitat-driven model and capture rate null model using a paired t-test ( $\alpha=0.05$ ) to determine if the habitat-driven model performed better (i.e., had a lower error rate). I evaluated the performance of all top-ranked habitat-driven models ( $\Delta AIC_c < 2$ ). I evaluated three Saltmarsh Sparrow models, one Seaside Sparrow model, and one Nelson's Sparrow model.

Because the two sets of habitat-driven models for predicting relative abundance or capture rate performed either worse than or not significantly different from their respective null models for all three species at novel sites, yet relatively well at the model-building sites, I built separate habitat-driven models (one set for relative abundance, and one set for capture rate) from all 18 sites to determine if adding six additional sites to the model building process yielded any additional information regarding a meaningful relationship between habitat and relative abundance or capture rate. A model built out of 18 sites including the same predictors as a model built from 12 sites would indicate that those predictors had a relationship to the sparrow data, which may have been strengthened by including additional sites in the model. In addition, I further explored the data by plotting variables that were kept in both the 12- and 18-site models against either relative abundance or capture rate. I used these plots to visually explore whether the addition of the six sites increased the correlation coefficient ( $R^2$ ) or changed the direction of the relationship between the variables.

## Results

### *Sparrow Captures*

I banded 298 sparrows at nine sites from Waties Island, SC to Cape Romain, SC and Kiawah Wildlife Biologist Aaron Given banded 152 sparrows at nine sites on Kiawah Island, SC for a total of 450 sparrows used to investigate relationships with habitats. Capture totals at all 18 sites combined were as follows: 236 (52%) Seaside, 126 (28%) Saltmarsh, and 88 (20%) Nelson's Sparrows. The relative abundances of the three species differed drastically among sites: Seaside and Saltmarsh relative abundance at individual sites ranged from 0-100%, while Nelson's relative abundance ranged from 0-84%. Seasides were found at all but two sites, Nelson's were found at all but three sites, and Saltmarsh Sparrows were found at all but five sites. The number of individuals (not counting within season recaptures), capture rate, and relative abundances of each species recorded at each site for the entire season are presented in Table 2 and plotted in figures 2 and 3.

Relative abundances of all three species differed across marshes ( $\chi^2 = 122.3$ ,  $df = 8$ ,  $p < 0.0005$ ). A much higher proportion of Saltmarsh Sparrows were found at North Inlet and Cape Romain marshes than at Waties, Huntington, and Kiawah Island marshes. Seaside Sparrows made up a higher percentage of captures at Waties and Huntington marshes compared to other sites. Nelson's Sparrows had a much higher relative abundance at Kiawah Island marsh compared to the other four marshes.

I also compared relative abundance within sites located in the same marsh. Relative abundance of Seaside Sparrows did not differ between the two sites in Waties Marsh ( $\chi^2 = 0.11$ ,  $df = 1$ ,  $p > 0.3$ ). I did not test for differences in Saltmarsh or Nelson's Sparrows due to low expected counts. Likewise, I could not perform a chi-square test on the capture data on Huntington sites due to low expected values at Huntington South. Relative abundances of Seaside and Saltmarsh Sparrows differed among sites in North Inlet ( $\chi^2 = 31.6$ ,  $df = 3$ ,  $p < 0.0005$ ). Saltmarsh Sparrows had a much lower relative abundance at the North Boundary Road site. Saltmarsh Sparrow relative abundance was similar among the other three sites in North Inlet. Conversely, Seaside Sparrows had a higher relative abundance at the North Boundary Road

site. I did not perform a chi-square test comparing relative abundances at Kiawah due to low expected values of Seaside and Saltmarsh Sparrows at six out of the nine sites.

Many of the birds that I captured at four sites (Waties North, Seaside Island, Clam Far, and Island 1) were previously banded by Shaw (2012) during her 2010-2011 field seasons. During 2011-2012, I re-captured captured 28 Seaside, 18 Saltmarsh, and 4 Nelson's Sparrows from Shaw (2012). This yielded an across-season return rate (the proportion of Shaw's total number of birds captured again in this study) of 24% for Seaside, 32% for Saltmarsh, and 21% for Nelson's Sparrows.

### *Habitat Characteristics*

Banding locations were either patches of high marsh surrounded by low marsh (i.e., hummock) or located along the upland border of the marsh, except Captain Sam's River, where banding was performed in smooth cordgrass- (*Spartina alterniflora*) dominated low marsh at low tide. The average area of high marsh hummocks from which birds were flushed on banding visits was  $2634 \pm 1444 \text{ m}^2$ . Plant species most commonly found on these high marsh hummocks included bushy seaside tansy (*Borrchia frutescens*), needlegrass rush (*Juncus roemerianus*), sea lavender (*Limonium carolinianum*), glasswort (*Salicornia* sp.), marsh elder (*Iva frutescens*), saltgrass (*Distichlis spicata*), saltmeadow cordgrass (*Spartina patens*), *S. alterniflora* wrack, and turtleweed (*Batis maritima*) (Tables 3 and 4). Other plant species encountered infrequently included fimbry (*Fimbristylis* sp.), *Baccharis* spp., and prickly pear (*Opuntia* sp.).

At each site, I quantified habitat types within a 400-m radius circle (total area 50.25 ha) centered on the banding site. The composition of marsh landscapes at the 50-ha scale varied greatly among the 18 sites. The percentage of low marsh at banding sites ranged from 16-88%, high marsh 1-22%, open water 0-47%, upland 0-54%, and beach/shell gravel 0-18% (Table 5).

I also measured habitat within a 70-m radius circle (total area of 15,365 m<sup>2</sup> or 1.5 ha) centered on the banding site. Habitat at this scale also varied among sites, with low marsh ranging from 0-79%, high marsh 6%-98%, open water 0-21%, upland 0-39%, and beach/shell gravel 0-25% (Table 6).

### *GIS Accuracy*

I compared the composition of each vegetation plot to its classification in GIS to provide a measure of digitization accuracy. Because the locations of vegetation plots from four sites were lost from the GPS before they could be entered into the GIS, I was only able to compare ground and GIS classifications at 14 sites. I compared a total of 630 locations at these 14 sites. Ground classification at 536 (85%) of these sites matched my GIS classification. My GIS classification accuracy of 85% is comparable to other studies where GIS accuracy ranged from 60% to 94% (Stalmans et al. 2002; Petersen et al. 2005). The most common mismatch between ground and GIS classification occurred in *Salicornia*-dominated salt pannes where the GIS classified low marsh as high marsh (56%), and where the GIS classified high marsh as low marsh (32%). Other misclassifications occurred less frequently and included classifying high marsh as upland (7%) or low marsh as upland (5%). These later errors were most likely caused by shadows from trees on aerial photos overlapping with different land cover.

#### *Models to Predict Relative Abundance of Each Sparrow Species*

The REVS model building procedure produced regression models relating relative abundance of all three species (separately) to habitat variables. Because of ties in the model building process (Goodenough et al. 2012), different numbers of candidate models were produced for each species (25 for Saltmarsh, 16 for Seaside, and 8 for Nelson's Sparrows). I break the results down by species, starting with Saltmarsh Sparrows. Additionally, I include the direction of each relationship (+ or -) in parentheses in the model description.

The model building procedure generated three highly-supported ( $\Delta AIC_c < 2$ ) Saltmarsh Sparrow relative abundance habitat-driven models. The "best" model ( $AIC_c=112.0$ ,  $\Delta AIC_c = 0.0$ ), included (+) % *S. alterniflora* and (+) % low grass at the 50-ha scale and (-) % low grass at the 1.5-ha scale. A second model, which included only (+) % *S. alterniflora* and (+) % low grass at the 50-ha scale, had almost as much support ( $AIC_c=112.4$ ,  $\Delta AIC_c = 0.4$ ). The other top-ranked model consisted of (+) % *S. alterniflora*, (+) % low grass, and (+) % open water at the 50-ha scale, and (-) % low grass at the 1.5-ha scale ( $AIC_c=113.7$ ,  $\Delta AIC_c = 1.7$ ). All other habitat-driven models for Saltmarsh Sparrow relative abundance had moderate to poor levels of support ( $\Delta AIC_c > 2.0$ ) (Table 7).

All three Saltmarsh Sparrow relative abundance habitat driven models significantly reduced mean error when compared with the relative abundance null model at the 12 model-building sites (Table 10). However, the habitat-driven models were not able to predict Saltmarsh Sparrow occurrence at new sites. All three relative abundance habitat models failed to improve upon the relative abundance null model when they were applied to the six test sites (Table 11).

The model building procedure generated two habitat-driven models for Seaside Sparrow relative abundance that had a high-level of support. The first model included (+) % wrack at the 1.5-ha scale ( $AIC_c=112.6$ ,  $\Delta AIC_c = 0.0$ ), and the second (+) % wrack at the 1.5-ha scale and (-) % upland at the 50-ha scale ( $AIC_c=114.3$ ,  $\Delta AIC_c = 0.7$ ). All other habitat-driven models had moderate to poor levels of support (Table 8).

The Seaside Sparrow relative abundance habitat-driven model with % wrack within 1.5 ha as a predictor estimated Seaside Sparrow abundance significantly better than the relative abundance null model at the 12 model-building sites, while the model with % wrack within 1.5 ha and % upland within 50 ha did not differ significantly from the null model at those sites (Table 10). The habitat-driven models were not able to predict Seaside Sparrow occurrence at new sites. The habitat-driven model did not perform significantly better than the relative abundance null model when they were applied to data from the six test sites (Table 11).

The model building procedure generated only one habitat-driven model predicting Nelson's Sparrow relative abundance that met the criterion ( $\Delta AIC_c < 2$ ) for further consideration. That model included (+) % upland and (-) % high grass at the 50-ha scale as predictors of Nelson's Sparrow relative abundance. The other habitat-driven models that were produced had moderate to poor levels of support (Table 9).

The Nelson's Sparrow habitat-driven model did not perform significantly better than the relative abundance null model at the 12 model-building sites (Table 10). Additionally, the habitat-driven model was not able to predict Nelson's Sparrow relative occurrence at new sites. The habitat-driven model

predicting Nelson's Sparrow relative abundance did not improve upon the null model at the six test sites compared to the null model (Table 11).

### *Models To Predict Capture Rate*

The REVS procedure produced 5 models relating Saltmarsh Sparrow capture rates to habitat variables, 16 for Seaside Sparrows, and 6 for Nelson's Sparrows. There were three models with a high degree of support ( $\Delta AIC_c < 2$ ) for predicting Saltmarsh Sparrow capture rate. The "best" habitat-driven model ( $AIC_c=52.0$ ,  $\Delta AIC_c=0.0$ ) included (+) % low grass and (-) % upland within the 50-ha scale as predictors of Saltmarsh Sparrow capture rate. The 2<sup>nd</sup> best Saltmarsh model ( $AIC_c=52.9$ ,  $\Delta AIC_c=0.9$ ) included (+) % low grass and (-) % upland within the 50-ha scale, but also included (-) % low grass and (+) % *S. alterniflora* within the 1.5-ha scale. The 3<sup>rd</sup> best model ( $AIC_c=53.0$ ,  $\Delta AIC_c=1.0$ ) included (+) % low grass and (-) % upland within the 50-ha scale and (-) % low grass within the 1.5-ha scale. All other habitat-driven models generated had considerably less support ( $AIC_c > 60.0$ ,  $\Delta AIC_c > 8.0$ ) (Table 12).

All three top-ranked Saltmarsh Sparrow capture rate habitat-based models performed significantly better than the capture rate null model at the 12 model-building sites (Table 15). However, none of the top-ranked habitat-driven models were able to predict Saltmarsh Sparrow occurrence at new sites. All three top-ranked Saltmarsh Sparrow capture rate habitat-driven models failed to improve upon the capture rate null model at the six test sites (Table 16).

There was only one habitat-driven model with a high degree of support for predicting Seaside Sparrow capture rate. That model ( $AIC_c=70.9$ ,  $\Delta AIC_c=0.0$ ) contained (+) % high marsh within 50 ha as well as (+) % open water and (-) % upland within 1.5 ha as predictors. All other models were either moderately or poorly supported (Table 13).

The top-ranked Seaside Sparrow capture rate habitat-driven model did not perform significantly better than the null capture rate model at the 12 model-building sites (Table 15). Additionally, the habitat-driven model was not able to predict Seaside Sparrow occurrence at new sites. The Seaside Sparrow capture rate habitat-driven model performed worse than the capture rate null model at the six test sites (Table 16).

There was also a single model that had high support for predicting Nelson's Sparrow capture rate. That model ( $AIC_c = 85.3$ ,  $\Delta AIC_c = 0.7$ ) consisted of (+) % high marsh and (-) % high grass within 50-ha as predictors. All other models had less support ( $AIC_c > 87.0$ ,  $\Delta AIC_c > 2.0$ ) (Table 14).

The top-ranked Nelson's Sparrow capture rate habitat-driven model failed to perform better than the null capture rate model at the 12 model-building sites (Table 15). Additionally, the habitat-driven model was not able to predict Nelson's Sparrow occurrence at new sites; it performed significantly worse than the null model at the six test sites (Table 16).

#### *Relative Abundance Model Building from all 18 sites*

The best 18-site Saltmarsh Sparrow model maintained % open water within 50 ha from the 12-site model, but also added % high marsh within 1.5 ha as a predictor ( $AIC_c = 176.8$ ). This 18-site habitat model had a significantly lower mean error than the null model (Table 17). The addition of the six additional sites slightly increased the  $R^2$  value of the model, although the relationship was still weak and the scatter of the data was broad (Figure 4).

The best 18-site model for predicting Seaside Sparrow relative abundance kept % upland within 50 ha as a predictor, but not % wrack within 1.5 ha. Instead, the 18-site model included % upland, % wrack, and inter-tidal creek length within 50 ha as well as % upland within 1.5-ha as predictors ( $AIC_c = 171.7$ ). This habitat model did not perform significantly better than the null model. The addition of the six additional sites did not affect the direction or magnitude of the relationship and even lowered the  $R^2$  value upon visual exploration of the data plot (Figure 5).

The Nelson's Sparrow 18-site model was completely different from the 12-site model: the 18-site model had latitude, % open water and % woody shrubs within 50 ha and % low marsh within 1.5 ha ( $AIC_c = 161.3$ ) as predictors of relative abundance. This model had a significantly lower mean error and was more accurate than the null at 16 out of 18 sites. A second model, including the four variables listed above as well as % bare ground within 50 ha also fit the data significantly better than the null (Table 17).

#### *Capture Rate Model Building from all 18 sites*



All the habitat models for Saltmarsh Sparrow capture rate built using data from 18 sites retained % low grass and % upland at the 50-ha scale as important predictors (Table 18). Including six additional sites in model construction did not seem to affect the direction of the relationship with either % low grass or % upland within 50 ha, although it did reduce the  $R^2$  value of the model for both variables (Figs 6 and 7).

Both habitat models predicting Seaside Sparrow capture rate built from 18 sites kept % high marsh within 50 ha and % open water within 1.5 ha as predictors and fit the data significantly better than the null model (Table 18). The addition of six sites seemingly weakened the relationship between Seaside Sparrow capture rate and % high marsh within 50 ha. The addition of six sites did not greatly alter the relationship between Seaside Sparrow capture rate and % open water within 1.5 ha, although it did result in a slightly higher  $R^2$  value (Figs. 8 and 9).

The habitat model predicting Nelson's Sparrow capture rate built from 18 sites preserved % high grass within 50 ha as a predictor and did not differ from the null model in terms of model performance (Table 18). The addition of six sites slightly increased the  $R^2$  value of the relationship between % high grass within 50 ha and Nelson's capture rate (Fig. 10).

## **Discussion**

The main findings of this study were: 1) *Ammodramus* marsh sparrow occurrence differed among 18 wintering sites in South Carolina, 2) Habitat composition differed among the 18 sites, and 3) models built from habitat measured at two different scales failed to predict occurrence of *Ammodramus* marsh sparrows.

Sparrow relative abundance differed by both marsh and site within the same marsh, sometimes dramatically. One of the most interesting patterns was the low relative abundance of Nelson's Sparrows at all of the northern marshes, yet the dominance of the species on Kiawah Island. A likely reason for this pattern is the winter range of Nelson's Sparrows. Northern South Carolina is the northern portion of Nelson's winter range, and the proportion of wintering Nelson's along the Atlantic coast increases southward to northeast Florida (Greenlaw and Woolfenden 2007). Conversely, Seaside Sparrow

abundance was higher in the more northerly sites in this study, although there is no evidence this is due to this species' winter range: Seaside Sparrows are found in the winter from North Carolina to the tip of Florida and along the Gulf Coast to Texas (Post and Greenlaw 2009).

Four of my banding locations (Waties North, Seaside Island, Clam Far, and Island 1) were also used by Shaw (2012) in which she found differences in sparrow relative abundance among marshes and sites. More specifically, Shaw found a higher proportion of Seaside Sparrows at Waties Island and a relatively higher proportion of Saltmarsh Sparrows at North Inlet. I also found that Seaside Sparrows were more abundant at Waties and Saltmarsh Sparrows were more abundant at North Inlet (compared to Waties). This pattern is still observed even after excluding year-to-year returners that may have been included in Shaw's study. I found similar patterns of abundance to Shaw (2012) at the Waties island sites. However, I banded a slightly higher proportion of Saltmarsh Sparrows at Clam Far and a higher proportion of Seaside Sparrows at Island 1 than Shaw (2012). The patterns of relative abundance between the two studies supports the idea that these patterns of abundance are stable within a marsh, with slightly more variation of sparrow assemblage occurring from year to year at individual banding sites. Furthermore, the exclusion of birds first banded by Shaw (2012) from my data when comparing the relative abundances between our studies indicates that the stability of the patterns observed is not due to strong winter site fidelity alone. Other factors, such as habitat, social attraction, dominance behaviors, or arrival times of different species on the wintering grounds may be factors that contribute to the consistent patterns of relative abundance.

My use of four of Shaw's sites also gave me the opportunity to examine across-season fidelity at those four sites. My results on across-season return rates of 24% for Seaside, 32% for Saltmarsh, and 21% for Nelson's Sparrows were much different from those found by Shaw who found return rates of 43% for Seaside, 63% for Saltmarsh, and 14% for Nelson's Sparrows (Shaw 2012). My results for both Seaside and Saltmarsh Sparrow return rates were lower than Shaw's yet higher than those found by another study on site fidelity in North Carolina, which found return rates of 11% for Seaside Sparrows

and 10% for Saltmarsh Sparrows (Winder et al. 2012). However, my return rate of 21% for Nelson's Sparrows is much higher than that found in either study (Winder et al. 2012; Shaw 2012).

The intriguing result of this study is that even though both habitat composition and sparrow abundance differed among sites, habitat-driven models failed to predict sparrow abundance. Several possible explanations exist as to why habitat could not be used to predict sparrow abundance. One explanation is that habitat measurements that were not used in this study could be more reliable predictors of *Ammodramus* sparrow abundance and could improve model performance. McClure et al. (2012) compared the performances of models built using only macrohabitat data (% cover of different landcover classes), models built using only microhabitat data (including basal area of trees, leaf litter depth, shrub layer thickness, and ground layer thickness), and models built from both macro- and micro- habitat data in predicting abundances of wintering passerines. The authors found that the best models included both macro- and micro- habitat data as birds selected habitat patches based on both landscape-scale cues and small-scale characteristics including vegetation structure (McClure 2012). There is evidence that, during the breeding season, both Saltmarsh and Seaside Sparrows select nest sites based on vegetation structure and composition. Saltmarsh Sparrows nested in patches of marsh dominated by *S. patens* in which the vegetation was taller and denser than random plots (DiQuinzio et al. 2002; Gjerdrum et al. 2005). Seaside Sparrows selected vegetation that was taller than either random plots or Saltmarsh Sparrow nesting plots, but was less dense than random plots. There is additional evidence that during the post-fledgling stage, Saltmarsh Sparrows use patches of marsh with taller *S. alterniflora*, presumably for the increased cover this habitat provides during foraging (Hill 2008). Even though I quantified vegetation composition at each site, I did not include measurements of vegetation height or density in this study. It is possible that marsh sparrows may be selecting habitat based on height and density, especially in high marsh roost sites: taller vegetation may help sparrows escape from rising waters during especially high tides, while denser vegetation could offer concealment from predators.

I hypothesized that the largest scale at which marsh sparrows select habitat would be the largest recorded home range size for any of the three species, or 50 ha (Shriver et al. 2010). However, it is

possible that broad-scale factors, such as marsh size and isolation, could have an effect on the distributions of *Ammodramus* marsh sparrows. Positive associations to habitat area have been demonstrated in many species of marsh and grassland birds (Johnson and Igl 2001; Shriver et al. 2004; Craig 2008). Both Seaside and Saltmarsh Sparrows are more abundant in larger marshes in the breeding range, with Seaside Sparrows being limited to larger marshes. However, the minimum marsh size in which Seaside Sparrows have been detected during the breeding season is 67 ha, while the minimum marsh size in which Saltmarsh Sparrows have been detected during the breeding season is 10 ha (Benoit and Askins 2002). All the marshes in the present study were larger than 67 ha (470 ha-12,110 ha), so all marshes theoretically met the minimum size requirements of both Seaside and Saltmarsh Sparrows. Additionally, none of the sparrow species had a relationship to distance of the banding site to nearest tree, which was used as a proxy for marsh size. In this study, Seaside Sparrows were more abundant in the smaller marshes (Waties Island and Huntington Beach) while Saltmarsh Sparrows were more abundant in the two largest marshes (North Inlet and Cape Romain). It may be possible that relationships between sparrow abundance and marsh size in the winter differ from those found in the breeding season and that marsh size affects patterns of sparrow relative abundance.

Another possible explanation of the poor performance of the habitat-driven models is that marsh sparrow winter habitat selection could be dependent upon each site's landscape context, and that predictors of sparrow occurrence could be different in different marshes. Shriver et al. (2004) examined patterns of marsh bird occurrence in two separate landscapes: the Gulf of Maine and the more developed Long-Island sound. The study found that predictors of Seaside and Saltmarsh Sparrow occurrence were different in each landscape. Marsh size was a reliable predictor of both Seaside and Saltmarsh occurrence at study sites in the Gulf of Maine. However, in Long Island sound, % cover of native vegetation was the most important predictor for Saltmarsh Sparrow occurrence, and there were no predictors of Seaside Sparrow occurrence (Shriver et al. 2004). Alternatively, sparrows could have the same predictors between marshes, but the slope or direction of the relationship could be different among landscapes. Johnson and Igl (2001) studied the relationship between grassland bird species occurrence and patch size

in 9 different counties and found positive relationships between area and occurrence for some species in some counties but negative relationships between area and occurrence for those same species in different counties. Flather and Sauer (1996) found that the relationship between neotropical migrants and degree of forest fragmentation differed between regions.

Within my study, landscape context differed among marshes. Kiawah Island was most notably different from the other sites; there are several golf courses and heavy residential development in close proximity to the marsh habitat. Several banding sites, including Cinder Creek, River Course, and Marsh Island were less than 150 m from the nearest house. There is a moderate degree of development surrounding Huntington Marsh (although nowhere near the degree at Kiawah): the marsh is part of a state park that is within 2 km of a major highway and the community of Murrell's Inlet. Waties Island is less developed, although it is still close (2 km) to the town of Cherry Grove. Cape Romain and North Inlet were the least developed marshes included in the study and were relatively isolated from human development. It is possible that within each of these landscapes, there are different predictors of abundance, as has been found in other studies of avian habitat use (Flather and Sauer 1996; Donovan et al. 1997; Johnson and Igl 2001; Shriver et al. 2004). I used sites from different marshes when building models, so it is possible that differences in habitat selection based on different landscape context resulted in poor predictive ability. It is possible that information from the six northern sites could have skewed the model so that it performed poorly at Kiawah sites, and vice versa. The random selection of model building and testing sites resulted in no sites from Huntington Marsh being used to build the model, so lack of information from that marsh in the model could have led to poor predictions at those sites. If landscape context does influence habitat selection in sparrows, it may be possible to predict occurrences of sparrows at different sites in the same marsh if the influence is at the marsh level. The limitation of this study in investigating such a question is that I sampled few sites (<5) in each marsh (with the exception of Kiawah) and so it would be difficult to build and test a marsh-specific predictive model. However, even if marsh-specific models were successful in predicting sparrow occurrence, they would be

too narrow for their application to be useful to the conservation and management of *Ammodramus* sparrows.

In addition to the habitat factors not measured in this study, patterns of sparrow abundance may also be driven by factors such as arrival time on the wintering grounds, social dominance by one species, or colonization history of a site. Arrival time on wintering grounds may affect patterns of abundance if one species arrives on the wintering grounds before another, allowing it to select the best habitat and leaving other patches for species arriving later. However, all three species of *Ammodramus* sparrows are similar in the timing of their fall migrations, with peak numbers of individuals arriving on wintering grounds in early-mid October (Greenlaw and Rising 1994; Post and Greenlaw 2009; Shriver et al. 2011). Since all three species arrive on the winter grounds around the same time, it is unlikely that one of the three species could fill a habitat before the arrival of the others. Social dominance could also play a role; Seaside Sparrows are larger than Saltmarsh or Nelson's sparrows and so it is possible Seaside sparrows could drive the other two species out of desirable habitat. However, I visited some sites like Clam Far and Cape Romain where there were similar numbers of both Seaside and Saltmarsh Sparrows, indicating that neither Seaside nor Saltmarsh Sparrows were able to establish complete dominance. Another site, Bass Creek 2, had similar numbers of Seaside and Nelson's Sparrows. It may also be possible that marsh sparrows colonized sites based on past conditions and that the current patterns of relative abundance result from a combination of this colonization history and winter site fidelity.

The differences in wintering *Ammodramus* marsh sparrow assemblage among 18 sites in South Carolina indicate that sparrows are selecting habitat patches based on some factor. However, the inability of habitat-driven models in this study to accurately predict sparrow occurrence, even though habitat differed among sites, indicates that the factors at the two scales measured in this study are not the sole factors influencing sparrow assemblage at winter sites. The results of this study are still important, as they provide information on the sparrow assemblage and habitat composition around winter high tide roost sites: two subjects that have not been studied extensively. However, it is still important to determine what factors, if any, are responsible for the differences in relative abundance observed among

sites. Factors such as marsh size and isolation, landscape context, or sparrow behavior, which could affect wintering sparrow site selection, are likely to change as a result of continued coastal development and sea level rise. Additional studies investigating these factors' relationships to wintering *Ammodramus* sparrow assemblages will help provide additional information as to how changes to these factors as a result of development and sea level rise will affect wintering populations of sparrows.

## Literature Cited

- Bayard, T.S. and C. Elphick. 2011. Planning for sea-level rise: quantifying patterns of Saltmarsh Sparrow (*Ammodramus caudacutus*) nest flooding under current sea-level conditions. *Auk*, **128**: 393-403.
- Benoit, L. and R. Askins. 1999. Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *Wetlands*, **19**: 194-208.
- Benoit, L. and R. Askins. 2002. Relationship between habitat area and the distribution of tidal marsh birds. *Wilson Bulletin*, **114**: 314-323.
- Bernstein, L., R. Pachauri and A. Reisinger. 2007. Climate Change 2007: Synthesis report. *Intergovernmental Panel on Climate Change*.
- Bolger, D.T., Scott, T.A., and J.T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology*, **11**: 406-421.
- Craig, R. and K. Beal. 1992. The influence of habitat-variables on marsh bird communities of the Connecticut River Estuary. *Wilson Bulletin*, **104**: 295-311.
- Craig, R. J. 2008. Determinants of species-area relationships for marsh-nesting birds. *Journal of Field Ornithology*, **79**: 269-279.
- Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H. and M. Machmuller. 2008. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, **7**: 73-78.
- Cristol, D.A., Smith, F.M., Varian-Ramos, C.W., and B.D. Watts. 2011. Mercury levels of Nelson's and saltmarsh sparrows at wintering grounds in Virginia, USA. *Ecotoxicology*, **20**: 1773-1779.
- Donovan, T.M., Jones, P.W., Annand, E.M., and F. R. Thompson III. 1997. Variation in local-scale edge effects : mechanisms and landscape context. *Ecology*, **78**: 2064-2075.
- Erwin, R., G. Sanders, D. Prosser and D. Cahoon . 2006. High tides and rising seas: potential effects on estuarine waterbirds. *Studies in Avian Biology*, **32**: 214-228.
- Flather, C.H. and J.R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology*, **77**: 28-35.
- Gjerdrum, C., C. Elphick and M. Rubega. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: the importance of nest habitat, timing, and study site differences. *Condor*, **107**: 849-862.
- Goodenough, A.E., Hart, A.G., and R. Stafford. 2012. Regression with empirical variable selection: description of a new method and application to ecological datasets. *PLoSOne*, **7**:1-10.
- Greenberg, R., Maldonado, J., Droege, S., and M. McDonald. 2006. Tidal marshes: A global perspective on the evolution and conservation of their terrestrial vertebrates. *BioScience*, **56**: 675-685.



- Greenlaw, J. and J. Rising. 1994. Saltmarsh Sparrow (*Ammodramus caudacutus*). Birds of North America [Online.] Available at <http://bna.birds.cornell.edu>.
- Greenlaw, J. and G. Woolfenden. 2007. Wintering distributions and migration of Saltmarsh and Nelson's Sharp-tailed Sparrows. *Wilson Journal of Ornithology*, **119**: 361-377.
- Higanbotham, C., M. Alber, and A. Chalmers. 2004. Analysis of tidal marsh vegetation patterns in two Georgia estuaries using aerial photography and GIS. *Estuaries*, **27**: 670-683.
- Hill, J. 2008. Postfledging habitat use by adult female Saltmarsh Sharp-tailed Sparrows. M.S. Thesis, University of Connecticut, Storrs, CT.
- Johnson, D.H. and L.D. Igl. 2001. Area requirements of grassland birds: a regional perspective. *Auk*, **118**: 24-34.
- Kennish, M.J. 2001. Coastal salt marsh systems in the U.S.: A review of anthropogenic impacts. *Journal of Coastal Research*, **17**: 731-748.
- Meiman, S. 2011. Modeling Saltmarsh Sparrow distribution in Connecticut. M.S. Thesis, University of Connecticut, Storrs, CT.
- Marshall, R.M. and S.E. Reinert. 1990. Breeding ecology of Seaside Sparrows in a Massachusetts salt marsh. *Wilson Journal of Ornithology*, **102**: 501-513.
- McClure, C. J.W., Rolek, B.W. and G.E. Hill. 2012. Predicting occupancy of wintering migratory birds: is microhabitat information necessary? *Condor*, **114**: 482-490.
- NOAA . 2010. Mean sea level trends for stations in South Carolina. National Oceanographic and Atmospheric Administration.
- Orson, R., W. Panageotou, S. Leatherman. 1985. Response of tidal salt marshes of the U.S. Atlantic and Gulf coasts to rising sea levels. *Journal of Coastal Research*, **1**: 29-37.
- Pepper, M. and W. Shriver. 2010. Effects of Open marsh water management on the reproductive success and nesting ecology of seaside sparrows in tidal marshes. *Waterbirds*, **33**: 381-388.
- Petersen, S.L., Stringham, T.K. and A.S. Laliberte. 2005. Classification of willow species using large-scale aerial photography. *Rangeland Ecology and Management*, **58**: 582-587.
- Plentovich, S., N. Holler, and G. Hill. 1998. Site fidelity of wintering Henslow's Sparrows. *Journal of Field Ornithology*, **69**, 486-490.
- Post, W. and J. Greenlaw. 2006. Nestling diets of coexisting salt marsh sparrows: opportunism in a food-rich environment. *Estuaries and Coasts*, **29**: 765-775.
- Post, W. and J. Greenlaw. 2009. Seaside Sparrow (*Ammodramus maritimus*). The Birds of North America [Online.] Available at <http://bna.birds.cornell.edu>.
- Rosenzweig, C., G. Casassa, D.J. Karoly, A. Imeson, C. Liu, A. Menzel, S. Rawlins, T.L. Root, B. Seguin, P. Tryjanowski, 2007: Assessment of observed changes and responses in natural and managed systems. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of*

*Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, UK, 79-131.

- Sillett, T. and R. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, **71**: 296-308.
- Shaw, S. 2012. Winter site fidelity in secretive marsh sparrows along the coast of South Carolina. M.S. Thesis. Coastal Carolina University. Conway, SC.
- Shriver, W., T. Hodgman, J. Gibbs, and P. Vickery. 2004. Landscape context influences salt marsh bird diversity and area requirements in New England. *Biological Conservation*, **119**: 545-553.
- Shriver, W., P. Vickery, T. Hodgman, and J. Gibbs. 2007. Flood tides affect breeding ecology of two sympatric Sharp-tailed Sparrows. *Auk*, **124**: 552-560.
- Shriver, W., T. Hodgman, J. Gibbs and P. Vickery. 2010. Home range sizes and habitat use of Nelson's and Saltmarsh Sparrows. *Wilson Journal of Ornithology*, **122**: 340-345.
- Shriver, W., T. Hodgman, and A. Hanson. 2011. Nelson's Sparrow (*Ammodramus nelsoni*). The Birds of North America [Online]. Available at: <http://bna.birds.cornell.edu>.
- Stalmans, M.E., Witkowski, E.T.F and K. Balkwill. 2002. Evaluating the ecological relevance of habitat maps for wild herbivores. *Journal of Range Management*, **55**: 127-134.
- Titus J.G. ed. 1988. Greenhouse Effect, Sea Level Rise, and Coastal Wetlands. Washington (DC): US Environmental Protection Agency. EPA 230-05-86-013.
- U.S. Fish and Wildlife Service. 2008. Birds of Conservation Concern 2008. Division of Migratory Bird Management, Arlington, VA.
- Wilson, M.D., B. Watts and D. Brinker. 2007. Status review of Chesapeake Bay marsh lands and breeding marsh birds. *Waterbirds*, **30**: 122-137.
- Winder, V. L., Michaelis, A.K. and S.D. Emslie. 2012. Winter survivorship and site fidelity of Nelson's, Saltmarsh, and Seaside Sparrows in North Carolina. *Condor*, **114**: 421-429.

Table 1: List of sites (listed north to south), including abbreviations, the marsh where each site was located, and geographic coordinates (listed in decimal degrees). The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

<b>Site Abbreviation</b>	<b>Site Name</b>	<b>Marsh</b>	<b>Latitude</b>	<b>Longitude</b>
SSISLD (M)	Seaside Island	Waties Island	33.853	-78.572
WATIESN (T)	Waties North	Waties Island	33.849	-78.588
HBSPJ (T)	Huntington Beach Jetty	Huntington Marsh	33.518	-79.049
HBSPS (T)	Huntington Beach South	Huntington Marsh	33.513	-79.057
NBRD (M)	North Boundary Road	North Inlet	33.365	-79.171
ISLD2 (M)	Island 2	North Inlet	33.343	-79.167
CLAMFR (M)	Clam Far	North Inlet	33.340	-79.183
ISLD1 (M)	Island 1	North Inlet	33.335	-79.173
CRNWR (M)	Cape Romain	Cape Romain	33.054	-79.373
MNTIDE1 (M)	Moon Tide 1	Kiawah Marsh	32.632	-80.034
MRSHISLD (T)	Marsh Island	Kiawah Marsh	32.625	-80.056
CNDRCRK (M)	Cinder Creek	Kiawah Marsh	32.624	-80.042
MRSHEDGE (M)	Marsh Edge	Kiawah Marsh	32.620	-80.069
BASSCRK2 (M)	Bass Creek 2	Kiawah Marsh	32.617	-80.029
RIVCRSE (T)	River Course	Kiawah Marsh	32.615	-80.096
INDPRK (M)	Indigo Park	Kiawah Marsh	32.614	-80.086
KRBS (M)	Kiawah River Bridge South	Kiawah Marsh	32.603	-80.131
CAPSAMSR (T)	Captain Sam's River	Kiawah Marsh	32.583	-80.143

Table 2: Total numbers of individuals captured, relative abundances by site (listed north to south), and CPUE for each of three species of sparrow captured at 18 South Carolina salt marsh sites (listed from North to South) from October 2011 through April 2012. The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

SITE NAME	Species									
	Site Totals	Seaside Sparrow			Saltmarsh Sparrow			Nelson's Sparrow		
		Total	Abundance	Capture rate	Total	Abundance	Capture rate	Total	Abundance	Capture rate
SSISLD (M)	24	23	96%	7.7	0	0%	0.0	1	4%	0.3
WATIESN (T)	26	24	92%	4.0	0	0%	0.0	2	8%	0.3
HBSPJ (T)	34	26	76%	4.3	4	12%	0.7	4	12%	0.7
HBSPS (T)	4	0	0%	0.0	4	100%	1.0	0	0%	0.0
NBRD (M)	27	27	100%	5.4	0	0%	0.0	0	0%	0.0
ISLD2 (M)	14	8	57%	2.7	6	43%	2.0	0	0%	0.0
CLAMFR (M)	96	38	40%	9.5	46	48%	11.5	12	13%	3.0
ISLD1 (M)	36	21	58%	7.0	13	36%	4.3	2	6%	0.7
CRNWR (M)	37	20	54%	6.7	16	43%	5.3	1	3%	0.3
MNTIDE1 (M)	25	4	16%	4.0	0	0%	0.0	21	84%	21.0
MRSHISLD (T)	10	6	60%	6.0	0	0%	0.0	4	40%	4.0
CNDRCRK (M)	13	3	23%	3.0	1	8%	1.0	9	69%	9.0
MRSHEDGE (M)	8	2	25%	2.0	3	38%	3.0	3	38%	3.0
BASSCRK2 (M)	40	17	43%	17.0	7	18%	7.0	16	40%	16.0
RIVCRSE (T)	14	1	7%	1.0	12	86%	12.0	1	7%	1.0
INDPRK (M)	7	0	0%	0.0	5	71%	5.0	2	29%	2.0
KRBS (M)	14	11	79%	11.0	2	14%	2.0	1	7%	1.0
CAPSMSR (T)	21	5	24%	5.0	7	33%	7.0	9	43%	9.0

Table 3: Visually-estimated percent cover of vegetation at each site (listed north to south) within a 400-m radius of the banding site or 50.25ha. The “woody shrubs” category is a combination of *Borrchia frutescens* and *Iva frutescens*, “high grass” is a combination of *Juncus roemerianus* and *Spartina patens* and “low grass” is a combination of *Salicornia* spp., *Distichlis spicata*, *Limonium carolinianum*, and *Batis maritima*. The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

Site	% Vegetation Cover at 50 ha Scale					
	<i>Spartina alterniflora</i>	Bare Ground	Wrack	Woody Shrubs	High Grass	Low Grass
SSISLD (M)	48%	35%	12%	4%	2%	0%
WATIESN (T)	36%	28%	0%	4%	6%	24%
HBSPJ (T)	31%	20%	7%	16%	11%	15%
HBSPS (T)	28%	28%	6%	11%	6%	19%
NBRD (M)	40%	27%	6%	4%	16%	8%
ISLD2 (M)	51%	29%	0%	4%	11%	4%
CLAMFR (M)	32%	28%	1%	5%	8%	24%
ISLD1 (M)	53%	37%	4%	4%	0%	2%
CRNWR (M)	43%	43%	1%	5%	0%	8%
MNTIDE1 (M)	46%	43%	1%	2%	1%	8%
MRSHISLD (T)	36%	31%	4%	8%	6%	15%
CNDRCRK (M)	28%	16%	1%	38%	4%	13%
MRSHEDGE (M)	49%	30%	2%	7%	3%	8%
BASSCRK2 (M)	34%	27%	1%	20%	3%	15%
RIVCRSE (T)	35%	35%	1%	9%	6%	15%
INDPRK (M)	38%	24%	4%	9%	9%	17%
KRBS (M)	46%	40%	3%	3%	5%	4%
CAPSMSR (T)	16%	18%	1%	26%	1%	37%

Table 4: Visually-estimated percent cover of vegetation at each site (listed north to south) within a 70-m radius of the banding site or 1.54ha. The “woody shrubs” category is a combination of *Borrichia frutescens* and *Iva frutescens*, “high grass” is a combination of *Juncus roemerianus* and *Spartina patens* and “low grass” is a combination of *Salicornia* spp., *Distichlis spicata*, *Limonium carolinianum*, and *Batis maritima*. The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

Site	% Vegetation Cover at 1.5 ha Scale					
	<i>Spartina alterniflora</i>	Bare Ground	Wrack	Woody Shrubs	High Grass	Low Grass
SSISLD (M)	34%	33%	16%	11%	5%	0%
WATIESN (T)	19%	25%	0%	4%	10%	41%
HBSPJ (T)	18%	14%	9%	30%	5%	24%
HBSPS (T)	0%	19%	10%	21%	13%	34%
NBRD (M)	24%	22%	15%	11%	21%	7%
ISLD2 (M)	16%	32%	0%	12%	27%	13%
CLAMFR (M)	5%	17%	4%	16%	25%	34%
ISLD1 (M)	38%	34%	11%	11%	0%	6%
CRNWR (M)	24%	51%	4%	9%	0%	13%
MNTIDE1 (M)	36%	35%	2%	1%	2%	24%
MRSHISLD (T)	4%	38%	5%	12%	11%	30%
CNDRCRK (M)	6%	18%	0%	60%	10%	7%
MRSHEDGE (M)	42%	31%	2%	12%	0%	13%
BASSCRK2 (M)	13%	26%	1%	46%	0%	14%
RIVCRSE (T)	12%	26%	1%	22%	13%	26%
INDPRK (M)	31%	25%	3%	18%	15%	8%
KRBS (M)	40%	32%	8%	4%	6%	10%
CAPSAMSR (T)	31%	30%	0%	19%	1%	20%

Table 5: Area of habitat cover types recorded at each site (listed north to south) within a 400-m radius of the banding site or 50.25 ha. The unit of area is 1000m<sup>2</sup> and percent cover of each habitat type is included in parentheses. The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

Site	% Habitat Cover at 50 ha Scale				
	Low Marsh	High Marsh	Open Water	Upland	Beach
<b>SSISLD (M)</b>	321 (64%)	13 (3%)	89 (18%)	75 (15%)	4 (1%)
<b>WATIESN (T)</b>	249 (50%)	72 (14%)	26 (5%)	155 (31%)	0 (0%)
<b>HBSPJ (T)</b>	184 (37%)	76 (15%)	21 (4%)	132 (26%)	89 (18%)
<b>HBSPS (T)</b>	177 (35%)	68 (14%)	27 (5%)	206 (41%)	25 (5%)
<b>NBRD (M)</b>	167 (33%)	103 (20%)	25 (5%)	207 (41%)	0 (0%)
<b>ISLD2 (M)</b>	279 (55%)	38 (8%)	175 (35%)	10 (2%)	0 (0%)
<b>CLAMFR (M)</b>	441 (88%)	62 (12%)	0 (0%)	0.09 (0%)	0 (0%)
<b>ISLD1 (M)</b>	261 (52%)	4 (1%)	237 (47%)	0.21 (0%)	0 (0%)
<b>CRNWR (M)</b>	261 (52%)	6 (1%)	205 (41%)	0 (0%)	30 (6%)
<b>MNTIDE1 (M)</b>	289 (57%)	47 (9%)	28 (6%)	139 (28%)	0 (0%)
<b>MRSHISLD (T)</b>	256 (51%)	37 (7%)	24 (5%)	185 (37%)	0 (0%)
<b>CNDRCRK (M)</b>	120 (24%)	51 (10%)	61 (12%)	270 (54%)	0 (0%)
<b>MRSHEDGE (M)</b>	281 (56%)	28 (6%)	18 (4%)	175 (35%)	0 (0%)
<b>BASSCRK2 (M)</b>	220 (44%)	70 (14%)	95 (19%)	118 (24%)	0 (0%)
<b>RIVCRSE (T)</b>	128 (25%)	78 (16%)	158 (31%)	139 (28%)	0 (0%)
<b>INDPRK (M)</b>	182 (36%)	29 (6%)	30 (6%)	261 (52%)	0 (0%)
<b>KRBS (M)</b>	292 (58%)	68 (14%)	89 (18%)	53 (11%)	0 (0%)
<b>CAPSAMSR (T)</b>	827 (16%)	110 (22%)	151 (30%)	100 (20%)	60 (12%)

Table 6: Areas of habitat cover types recorded at each site (listed north to south) within a 70-m radius of the banding site or 1.54 ha. The unit of area is 100m<sup>2</sup> and percent cover of each habitat type is included in parentheses. The abbreviations of model building sites are followed by a (M) and the names of test sites are followed by a (T).

Site	% Habitat Cover at 1.5 ha Scale				
	Low Marsh	High Marsh	Open Water	Upland	Beach
<b>SSISLD (M)</b>	121 (79%)	11 (7%)	20 (13%)	1 (1%)	0 (0%)
<b>WATIESN (T)</b>	11 (70%)	22 (15%)	0 (0%)	24 (16%)	0 (0%)
<b>HBSPJ (T)</b>	44 (29%)	89 (58%)	0 (0%)	21 (13%)	0 (0%)
<b>HBSPS (T)</b>	0 (0%)	150 (98%)	0 (0%)	3 (2%)	0 (0%)
<b>NBRD (M)</b>	48 (32%)	45 (29%)	0 (0%)	60 (39%)	0 (0%)
<b>ISLD2 (M)</b>	100 (65%)	45 (29%)	0 (0%)	8 (5%)	0 (0%)
<b>CLAMFR (M)</b>	35 (23%)	119 (77%)	0 (0%)	0 (0%)	0 (0%)
<b>ISLD1 (M)</b>	111 (72%)	9 (6%)	32 (21%)	1 (1%)	0 (0%)
<b>CRNWR (M)</b>	94 (61%)	13 (8%)	8 (5%)	0 (0%)	38 (25%)
<b>MNTIDE1 (M)</b>	118 (77%)	33 (22%)	0 (0%)	3 (2%)	0 (0%)
<b>MRSHISLD (T)</b>	58 (38%)	89 (58%)	0 (0%)	7 (4%)	0 (0%)
<b>CNDRCRK (M)</b>	48 (31%)	56 (36%)	12 (8%)	38 (25%)	0 (0%)
<b>MRSHEDEGE (M)</b>	110 (72%)	21 (14%)	0 (0%)	22 (14%)	0 (0%)
<b>BASSCRK2 (M)</b>	67 (44%)	71 (47%)	15 (10%)	0 (0%)	0 (0%)
<b>RIVCRSE (T)</b>	50 (32%)	94 (61%)	0 (0%)	9 (6%)	0 (0%)
<b>INDPRK (M)</b>	112 (73%)	38 (25%)	0 (0%)	4 (2%)	0 (0%)
<b>KRBS (M)</b>	66 (43%)	61 (40%)	12 (8%)	14 (9%)	0 (0%)
<b>CAPSAMSR (T)</b>	57 (37%)	77 (51%)	19 (13%)	0 (0%)	0 (0%)



Table 7: List of candidate habitat-driven predictive models for Saltmarsh Sparrow relative abundance and their corrected Akaike's Information Criterion and  $\Delta$  corrected Akaike's Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. 25 candidate models were produced. The large number of candidate models reflects “ties” in the variable-ranking process. %Low Grass-50ha and % *S. alterniflora* were both ranked highly and had to be entered into separate 1-variable candidate models. % Open Water 50-ha, % High Marsh 50-ha, % Wrack 50-ha, % Upland 1.5-ha, % High Grass 1.5-ha and 50-ha, were all given the same ranking, so all permutations of the variables had to be entered in separate candidate models.

Saltmarsh Sparrow relative abundance habitat-driven models	$AIC_c$	$\Delta AIC_c$
<b>%<i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha</b>	<b>112.0</b>	<b>0.0</b>
<b>%<i>S. alterniflora</i> 50-ha + %Low Grass 50-ha</b>	<b>112.4</b>	<b>0.4</b>
<b>%<i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Open Water 50-ha</b>	<b>113.7</b>	<b>1.7</b>
%Low Grass 50-ha	115.3	3.3
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %High Marsh 50-ha	117.0	5.0
% <i>S. alterniflora</i> 50-ha	117.5	5.5
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Wrack 50-ha	118.3	6.3
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha	119.9	7.9
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %High Grass 1.5-ha	120.4	8.4
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %High Grass 50-ha	120.7	8.7
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Open Water 50-ha + %High Marsh 50-ha	125.5	13.5
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Open Water 50-ha + %High Grass 1.5-ha	125.5	13.5
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %High Marsh 50-ha + %High Grass 50-ha	126.5	14.5
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Open Water 50-ha + %Wrack 50-ha	126.6	14.6
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Open Water 50-ha + %High Grass 50-ha	126.6	14.6

<b>Saltmarsh Sparrow relative abundance habitat-driven models (Cont'd)</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + % High Marsh 50-ha + %High Grass1.5-ha	126.7	14.7
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha + %Open Water 50-ha	126.8	14.8
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + % High Marsh 50-ha + %Wrack 50-ha	126.9	14.9
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + % High Grass 50-ha + %High Grass1.5-ha	129.6	17.6
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha + %High Marsh 50-ha	130.0	18.0
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha + %Wrack 50-ha	130.2	18.2
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + % Wrack 50-ha + %High Grass1.5-ha	130.6	18.6
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + % Wrack 50-ha + %High Grass 50-ha	131.4	19.4
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha + %High Grass1.5-ha	131.8	19.8
% <i>S. alterniflora</i> 50-ha + %Low Grass 50-ha + %Low Grass 1.5-ha + %Upland 1.5-ha + %High Grass 50-ha	133.0	21.0

Table 8: List of candidate habitat-driven predictive models for Seaside Sparrow relative abundance and their corrected Akaike’s Information Criterion and  $\Delta$  corrected Akaike’s Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. The large number of candidate models (n=16) reflects “ties” in the variable-ranking process. % Wrack 1.5-ha and % Upland 50-ha were given the same ranking; % Low Marsh 1.5-ha, % *S. alterniflora* 50-ha, and Creek Length 1.5-ha also tied with a separate ranking. Therefore, all combinations of the variables were used for model building.

Seaside Sparrow relative abundance habitat-driven models	$AIC_c$	$\Delta AIC_c$
<b>%Wrack 1.5-ha</b>	<b>112.6</b>	<b>0.0</b>
<b>%Wrack 1.5-ha + %Upland 50-ha</b>	<b>114.3</b>	<b>1.7</b>
%Upland 50-ha + %Wrack 1.5-ha + %Low Marsh 1.5-ha	118.0	5.4
%Upland 50-ha + % <i>S. alterniflora</i> 50-ha + %Low Marsh 1.5-ha + Creek Length 1.5-ha	118.2	5.6
%Upland 50-ha + %Wrack 1.5-ha + % <i>S. alterniflora</i> 50-ha	120.3	7.7
%Upland 50-ha + %Wrack 1.5-ha + Creek Length 1.5-ha	120.6	8.0
%Upland 50-ha + Creek Length 1.5-ha	121.3	8.7
%Upland 50-ha	122.5	9.9
%Upland 50-ha + %Wrack 1.5-ha + % <i>S. alterniflora</i> 50-ha + % Low Marsh 1.5-ha	124.4	11.8
%Upland 50-ha + %Low Marsh 1.5-ha + Creek Length 1.5-ha	124.5	11.9
%Upland 50-ha + %Low Marsh 1.5-ha	126.7	14.1
%Upland 50-ha + % <i>S. alterniflora</i> 50-ha	127.0	14.4
%Upland 50-ha + % <i>S. alterniflora</i> 50-ha + Creek Length 1.5-ha	127.5	14.9
%Upland 50-ha + % <i>S. alterniflora</i> 50-ha + %Low Marsh 1.5-ha	128.5	15.9
%Upland 50-ha + %Wrack 1.5-ha + % <i>S. alterniflora</i> 50-ha + Creek Length 1.5-ha	129.1	16.5
%Upland 50-ha + %Wrack1.5ha + % <i>S. alterniflora</i> 50-ha + %Low Marsh 1.5-ha + Creek Length 1.5-ha	130.9	18.3

Table 9: List of candidate habitat-driven predictive models for Nelson’s Sparrow relative abundance and their corrected Akaike’s Information Criterion and  $\Delta$  corrected Akaike’s Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. Both % Low Grass 1.5-ha and % High Grass 50-ha were given the same ranking. % Woody Shrub 50-ha, Latitude, and % Upland 1.5-ha were tied with a separate ranking, so all combinations of the variables were used for model building.

<b>Nelson’s Sparrow relative abundance habitat-driven models</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>
<b>%Upland 50-ha + %High Grass 50-ha + %Low Grass 1.5-ha</b>	<b>112.3</b>	<b>0.0</b>
%Upland 50-ha + %High Grass 50-ha	116.9	4.6
%Upland 50-ha	117.6	5.3
%Upland 50-ha + %High Grass 50-ha + %Low Grass 1.5-ha + %Low Grass 50-ha	117.9	5.6
%Upland 50-ha + %Low Grass 1.5-ha	118.6	6.3
%Upland 50-ha + %High Grass 50-ha + %Low Grass 1.5-ha + %Low Grass 50-ha + %Woody Shrub 50-ha	121.4	9.1
%Upland 50-ha + %High Grass 50-ha + %Low Grass 1.5-ha + %Low Grass 50-ha + Latitude	131.0	18.7
%Upland 50-ha + %High Grass 50-ha + %Low Grass 1.5-ha + %Low Grass 50-ha + %Upland 1.5-ha	131.0	18.7

Table 10: Comparison of habitat model performance vs. null model performance for predicting species' relative abundances when back-fitted to the 12 model building sites.

Model	Total error of habitat-driven model	Total error of null model	Mean error of habitat-driven model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Relative Abundance Habitat Model</b>						
<i>%S. alterniflora 50ha + %Low Grass 50ha + % Low Grass 1.5ha</i>	29.6	63.0	2.5 $\pm$ 0.7	5.3 $\pm$ 1.4	-2.0	0.04
<i>%S. alterniflora 50ha + %Low Grass 50 ha</i>	40.1	63.0	3.3 $\pm$ 0.9	5.3 $\pm$ 1.4	-2.1	0.03
<i>%S. alterniflora 50ha + %Low Grass 50ha + % Open Water 50ha + % Low Grass 1.5ha</i>	23.6	63.0	2.0 $\pm$ 0.6	5.3 $\pm$ 1.4	-2.2	0.02
<b>Seaside Sparrow Relative Abundance Habitat Model</b>						
<i>%Wrack 1.5ha</i>	36.8	64.9	3.1 $\pm$ 0.6	5.4 $\pm$ 1.2	-1.6	0.05
<i>%Wrack 1.5ha + %Upland 50ha</i>	45.7	64.9	3.8 $\pm$ 1.5	5.4 $\pm$ 1.2	-1.2	0.12
<b>Nelson's Sparrow Relative Abundance Habitat Model</b>						
<i>%Upland 50ha + %High Grass 50ha</i>	56.5	64.9	4.7 $\pm$ 1.5	5.4 $\pm$ 1.2	-0.5	0.30

Table 11: Comparison of habitat-driven model performance vs. null model performance in predicting relative abundances of all three species at six test sites.

Model	Total error of habitat-driven model	Total error of null model	Mean error of habitat-driven model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Relative Abundance Habitat Model</b>						
<i>%S. alterniflora 50ha + %Low Grass 50ha + % Low Grass 1.5ha</i>	45.2	28.0	7.5 $\pm$ 2.0	5.4 $\pm$ 1.2	1.5	0.10
<i>%S. alterniflora 50ha + %Low Grass 50 ha</i>	40.1	28.0	6.7 $\pm$ 2.5	5.4 $\pm$ 1.2	1.0	0.19
<i>%S. alterniflora 50ha + %Low Grass 50ha + % Open Water 50ha + % Low Grass 1.5ha</i>	49.5	28.0	8.2 $\pm$ 2.6	5.4 $\pm$ 1.2	1.2	0.13
<b>Seaside Sparrow Relative Abundance Habitat Model</b>						
<i>%Wrack 1.5ha</i>	28.9	34.2	4.8 $\pm$ 2.6	5.7 $\pm$ 1.5	-0.5	0.33
<i>%Wrack 1.5ha + %Upland 50ha</i>	31.0	34.2	5.2 $\pm$ 2.7	5.7 $\pm$ 1.5	-0.3	0.4
<b>Nelson's Sparrow Relative Abundance Habitat Model</b>						
<i>%Upland 50ha + %High Grass 50ha</i>	12.6	15.4	2.1 $\pm$ 0.9	2.6 $\pm$ 0.6	-0.5	0.33

Table 12: List of candidate habitat-driven predictive models for Saltmarsh Sparrow Capture Rate and their corrected Akaike’s Information Criterion and  $\Delta$  corrected Akaike’s Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. Only five candidate models were produced because no variables were given the same ranking so no different combinations of the variables needed to be included during model building.

<b>Saltmarsh Sparrow Capture Rate habitat-driven models</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>
<b>%Low Grass 50-ha + %Upland 50-ha</b>	<b>52.0</b>	<b>0.0</b>
<b>%Low Grass 50-ha + %Upland 50-ha + %Low Grass 1.5-ha + %<i>S. alterniflora</i> 1.5-ha</b>	<b>52.9</b>	<b>0.9</b>
<b>%Low Grass 50-ha + %Upland 50-ha + %Low Grass 1.5-ha</b>	<b>53.1</b>	<b>1.1</b>
%Low Grass 50-ha	60.9	8.9
%Low Grass 50-ha + %Upland 50-ha + %Low Grass 1.5-ha + % <i>S. alterniflora</i> 1.5-ha + % <i>S. alterniflora</i> 50-ha	63.7	11.7

Table 13: List of candidate habitat-driven predictive models for Seaside Sparrow capture rate and their corrected Akaike's Information Criterion and  $\Delta$  corrected Akaike's Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. % Upland 1.5-ha, % High Marsh 1.5-ha, % Low Marsh 1.5-ha, and % Open Water 1.5-ha all had the same ranking, so all combinations of those variables was included in the model building process.

<b>Seaside Sparrow Capture Rate habitat-driven models</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>
<b>%High Marsh 50-ha + %Open Water 1.5-ha + %Upland 1.5-ha</b>	<b>70.9</b>	<b>0.0</b>
%High Marsh 1.5-ha + %High Marsh 50-ha + %Open Water 1.5-ha + %Upland 1.5-ha + %Low Marsh 1.5-ha	74.0	3.1
%High Marsh 1.5-ha + %Open Water 1.5-ha	74.6	3.7
%High Marsh 1.5-ha + %Open Water 1.5-ha + %Upland 1.5-ha + %Low Marsh 1.5-ha	76.2	5.3
%High Marsh 1.5-ha	76.3	5.4
%High Marsh 1.5-ha + %High Marsh 50-ha + %Open Water 1.5-ha	79.6	8.7
%High Marsh 1.5-ha + %High Marsh 50-ha + %Open Water 1.5-ha + %Upland 1.5-ha	79.6	8.7
%High Marsh 1.5-ha + %Upland 1.5-ha	79.9	9.0
%High Marsh 1.5-ha + %Open Water 1.5-ha + %Upland 1.5-ha	80.4	9.5
%High Marsh 1.5-ha + %Open Water 1.5-ha + %Low Marsh 1.5-ha	80.8	9.9
%High Marsh 1.5-ha + %High Marsh 50-ha	81.0	10.1
%High Marsh 1.5-ha + %Low Marsh 1.5-ha	81.0	10.1
%High Marsh 1.5-ha + %Upland 1.5-ha + %Low Marsh 1.5-ha	81.7	10.9
%High Marsh 1.5-ha + %High Marsh 50-ha + %Upland 1.5-ha	83.0	12.1
%High Marsh 1.5-ha + %High Marsh 50-ha + %Low Marsh 1.5-ha	87.2	16.3
%High Marsh 1.5-ha + %High Marsh 50-ha + %Open Water 1.5-ha + %Low Marsh 1.5-ha	87.9	17.0



Table 14: List of candidate habitat-driven predictive models for Nelson’s Sparrow capture rate and their corrected Akaike’s Information Criterion and  $\Delta$  corrected Akaike’s Information Criterion ( $AIC_c$  – lowest  $AIC_c$ ). Top models (in bold) had a  $\Delta AIC_c < 2$  and were tested against null models. % Low Marsh 1.5-ha and % Low Grass 1.5-ha were given the same rating and so all combinations of the two variables was included in the model building process.

<b>Nelson’s Sparrow Capture Rate habitat-driven models</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>
<b>%High Grass 50-ha + %High Marsh 50-ha</b>	<b>85.3</b>	<b>0.0</b>
%High Grass 50-ha	87.1	2.5
%High Grass 50-ha + %High Marsh 50-ha + %Low Marsh 1.5-ha	89.3	4.7
%High Grass 50-ha + %High Marsh 50-ha + % Low Grass 1.5-ha	90.2	5.6
%High Grass 50-ha + %High Marsh 50-ha + %Low Marsh 1.5-ha + %Low Grass 1.5-ha + % <i>S. alterniflora</i> 1.5-ha	93.0	8.4
%High Grass 50-ha + %High Marsh 50-ha + %Low Marsh 1.5-ha + %Low Grass 1.5-ha	94.9	10.4

Table 15: Comparison of habitat model performance vs. null model performance for predicting species' capture rates when back-fitted to the 12 model building sites.

Model	Total error of habitat-driven model	Total error of null model	Mean error of habitat-driven model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Capture Rate Habitat Model</b>						
<i>%Low Grass 50ha + %Upland 50ha</i>	23.8	86.0	2.0 $\pm$ 0.5	7.2 $\pm$ 2.6	-1.9	0.04
<i>%Low Grass 50ha + %Upland 50ha + %Low Grass 1.5ha + %S. alterniflora1.5ha</i>	10.3	86.0	0.9 $\pm$ 0.2	7.2 $\pm$ 2.6	-2.4	0.02
<i>%Low Grass 50ha + %Upland 50ha + %Low Grass 1.5ha</i>	18.8	86.0	1.6 $\pm$ 0.4	7.2 $\pm$ 2.6	-2.1	0.03
<b>Seaside Sparrow Capture Rate Habitat Model</b>						
<i>%High Marsh 50ha + %Open Water 1.5ha + %Upland 1.5ha</i>	38.9	66.7	3.2 $\pm$ 0.91	5.6 $\pm$ 1.1	-1.4	0.10
<b>Nelson's Sparrow Capture Rate Habitat Model</b>						
<i>%High Marsh 50ha + %High Grass 50ha</i>	102.2	81.7	7.3 $\pm$ 1.2	6.8 $\pm$ 1.6	0.3	0.40

Table 16: Comparison of habitat model performance vs. null model performance in predicting capture rates of all three species at six test sites.

Model	Total error of habitat-driven model	Total error of null model	Mean error of habitat-driven model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Capture Rate Habitat Model</b>						
<i>%Low Grass 50ha + %Upland 50ha</i>	123.6	66.1	20.6 $\pm$ 7.8	11.0 $\pm$ 3.1	1.9	0.06
<i>%Low Grass 50ha + %Upland 50ha + %Low Grass 1.5ha + %S. alterniflora 1.5ha</i>	96.7	66.1	16.1 $\pm$ 6.5	11.0 $\pm$ 3.1	1.2	0.15
<i>%Low Grass 50ha + %Upland 50ha + %Low Grass 1.5ha</i>	99.7	66.1	16.6 $\pm$ 5.9	11.0 $\pm$ 3.1	1.7	0.08
<b>Seaside Sparrow Capture Rate Habitat Model</b>						
<i>%High Marsh 50ha + %Open Water 1.5ha + %Upland 1.5ha</i>	101.4	60.4	16.9 $\pm$ 5.0	10.1 $\pm$ 3.9	2.7	0.02
<b>Nelson's Sparrow Capture Rate Habitat Model</b>						
<i>%High Marsh 50ha + %High Grass 50ha</i>	126.5	43.8	21.1 $\pm$ 7.3	7.3 $\pm$ 2.0	2.4	0.03

Table 17: Comparison of habitat model performance vs. null model performance for predicting species' relative abundances when all 18 sites were used to build the predictive model.

Model	Total error of predictive model	Total error of null model	Mean error of predictive model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Relative Abundance Habitat Model</b>						
<i>%High Marsh 1.5ha + %Open Water 50ha</i>	59.4	91.3	3.3 $\pm$ 0.5	5.1 $\pm$ 1.0	-1.7	0.05
<b>Seaside Sparrow Relative Abundance Habitat Model</b>						
<i>%Upland 50ha + %Upland 1.5ha + %Wrack 50ha</i>	101.3	99.1	5.6 $\pm$ 1.7	5.5 $\pm$ 1.0	0.1	0.47
<i>%Upland 50ha + %Upland 1.5ha + %Wrack 50ha + Creek length 50ha</i>	78.6	99.1	4.4 $\pm$ 1.7	5.5 $\pm$ 1.0	-0.7	0.25
<b>Nelson's Sparrow Relative Abundance Habitat Model</b>						
<i>Latitude + %Open Water 50ha + %Wood Shrub 50ha + %Low Marsh 1.5ha</i>	34.1	78.4	1.9 $\pm$ 0.6	4.4 $\pm$ 0.9	-3.9	0.0005
<i>Latitude + %Open Water 50ha + %Wood Shrub 50ha + %Low Marsh 1.5ha + %Bare Ground 50ha</i>	39.4	78.4	2.2 $\pm$ 0.6	4.4 $\pm$ 0.9	-3.2	0.003

Table 18: Comparison of habitat model performance vs. null model performance for predicting species' capture rates when all 18 sites were used to build the predictive model.

Model	Total error of predictive model	Total error of null model	Mean error of predictive model $\pm$ SE	Mean error of null model $\pm$ SE	t-value	p
<b>Saltmarsh Sparrow Capture Rate Habitat Model</b>						
<i>%Low Grass 50ha + %Upland 50ha + Latitude + %Woody Shrub 50ha + % Woody Shrub 1.5ha</i>	66.0	135.8	3.7 $\pm$ 0.7	7.5 $\pm$ 2.0	-2.2	0.02
<i>%Low Grass 50ha + %Upland 50ha + Latitude</i>	75.1	135.8	4.2 $\pm$ 1.0	7.5 $\pm$ 2.0	-2.7	0.007
<i>%Low Grass 50ha + %Upland 50ha</i>	112.8	135.8	6.3 $\pm$ 1.8	7.5 $\pm$ 2.0	-0.8	0.23
<b>Seaside Sparrow Capture Rate Habitat Model</b>						
<i>%Low Marsh 50ha + %Open Water 1.5ha + %High Marsh 50ha</i>	77.8	110.5	4.3 $\pm$ 0.8	6.1 $\pm$ 1.3	-1.8	0.05
<i>%Low Marsh 50ha + %Open Water 1.5ha + %High Marsh 50ha + %Wrack 1.5ha</i>	76.0	110.5	4.2 $\pm$ 0.9	6.1 $\pm$ 1.3	-1.9	0.04
<b>Nelson's Sparrow Capture Rate Habitat Model</b>						
<i>Latitude + %High Grass 50ha</i>	111.3	109.0	6.2 $\pm$ 1.1	6.1 $\pm$ 1.2	0.1	0.56

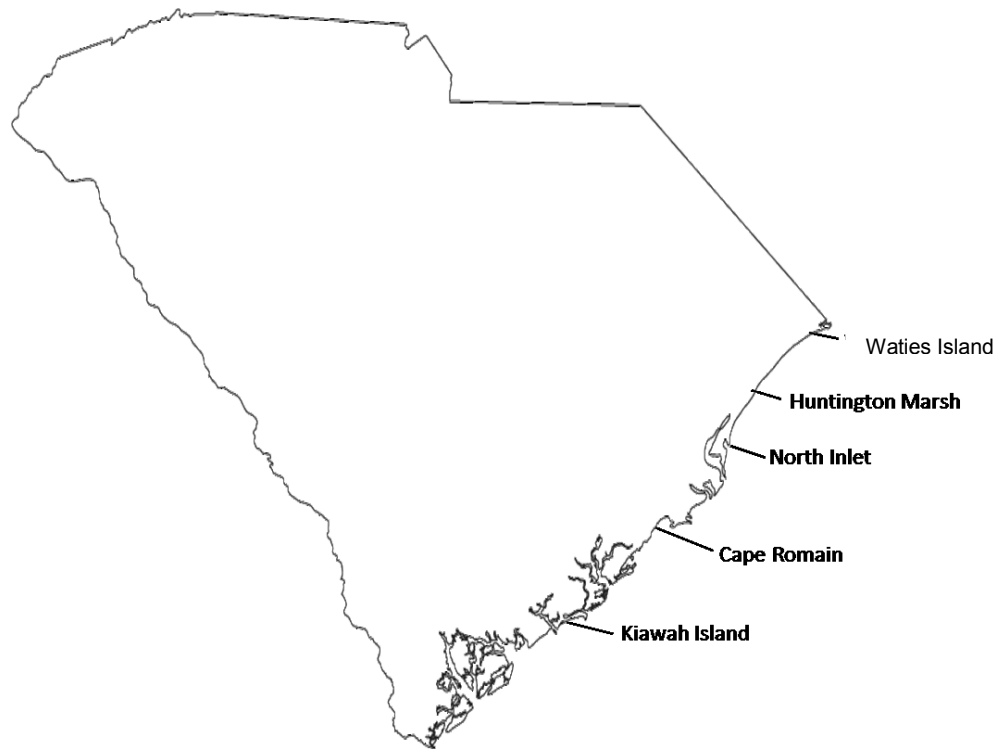


Figure 1: Map of South Carolina showing the approximate locations and distribution of marshes used in this study.

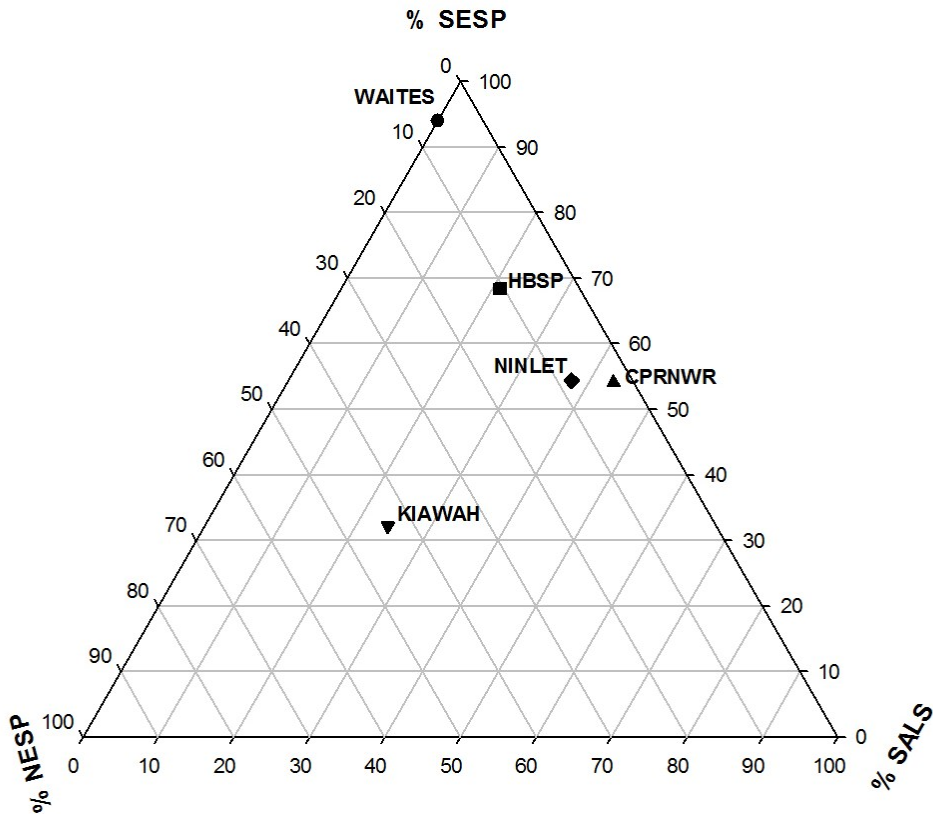


Figure 2: Ternary plot comparing the relative abundances (%) of Seaside (SESP), Saltmarsh (SALS), and Nelson's (NESP) sparrows at the five study marshes. The relative abundance of Seaside Sparrows decreases from top to bottom along the right axis. The relative abundance of Saltmarsh Sparrows decreases from right to left along the bottom axis, and the relative abundance of Nelson's Sparrows decreases from bottom to top along the left axis.

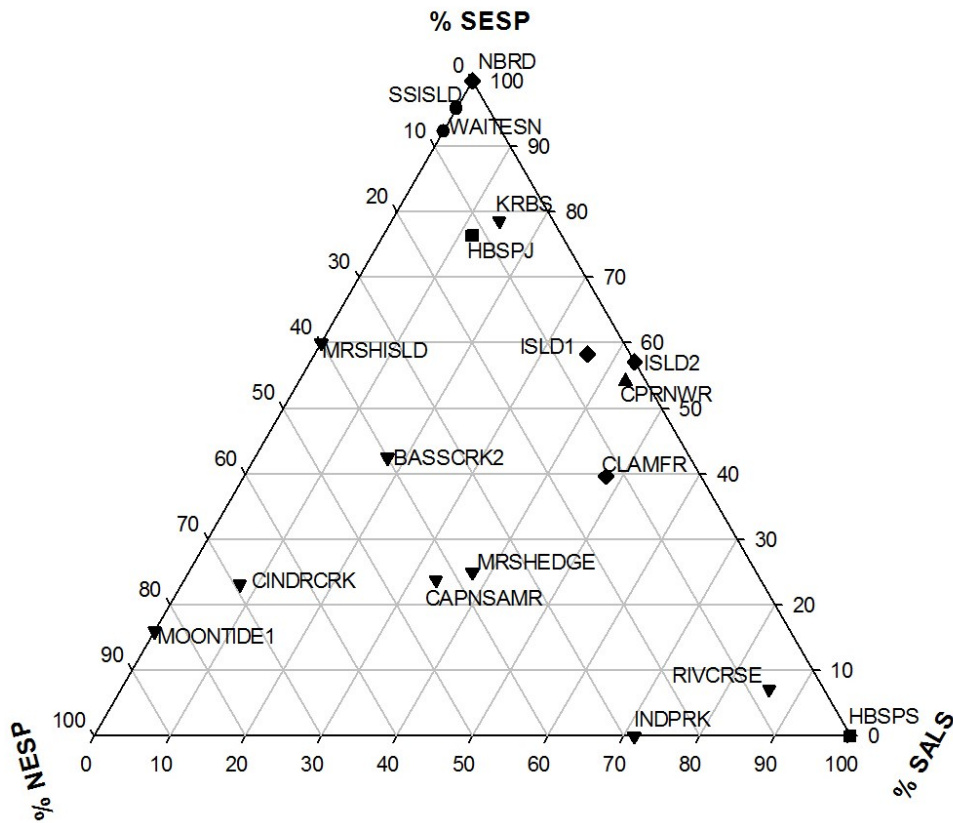


Figure 3: Ternary plot comparing the relative abundances (%) of Seaside (SESP), Saltmarsh (SALS), and Nelson’s (NESP) sparrows among all 18 sites. All sites are labeled with their abbreviation. Waties Sites are represented by circles, Huntington by squares, North Inlet by diamonds, Cape Romain by a triangle, and Kiawah by upside down triangles. The relative abundance of Seaside Sparrows decreases from top to bottom along the right axis. The relative abundance of Saltmarsh Sparrows decreases from right to left along the bottom axis, and the relative abundance of Nelson’s Sparrows decreases from bottom to top along the left axis.



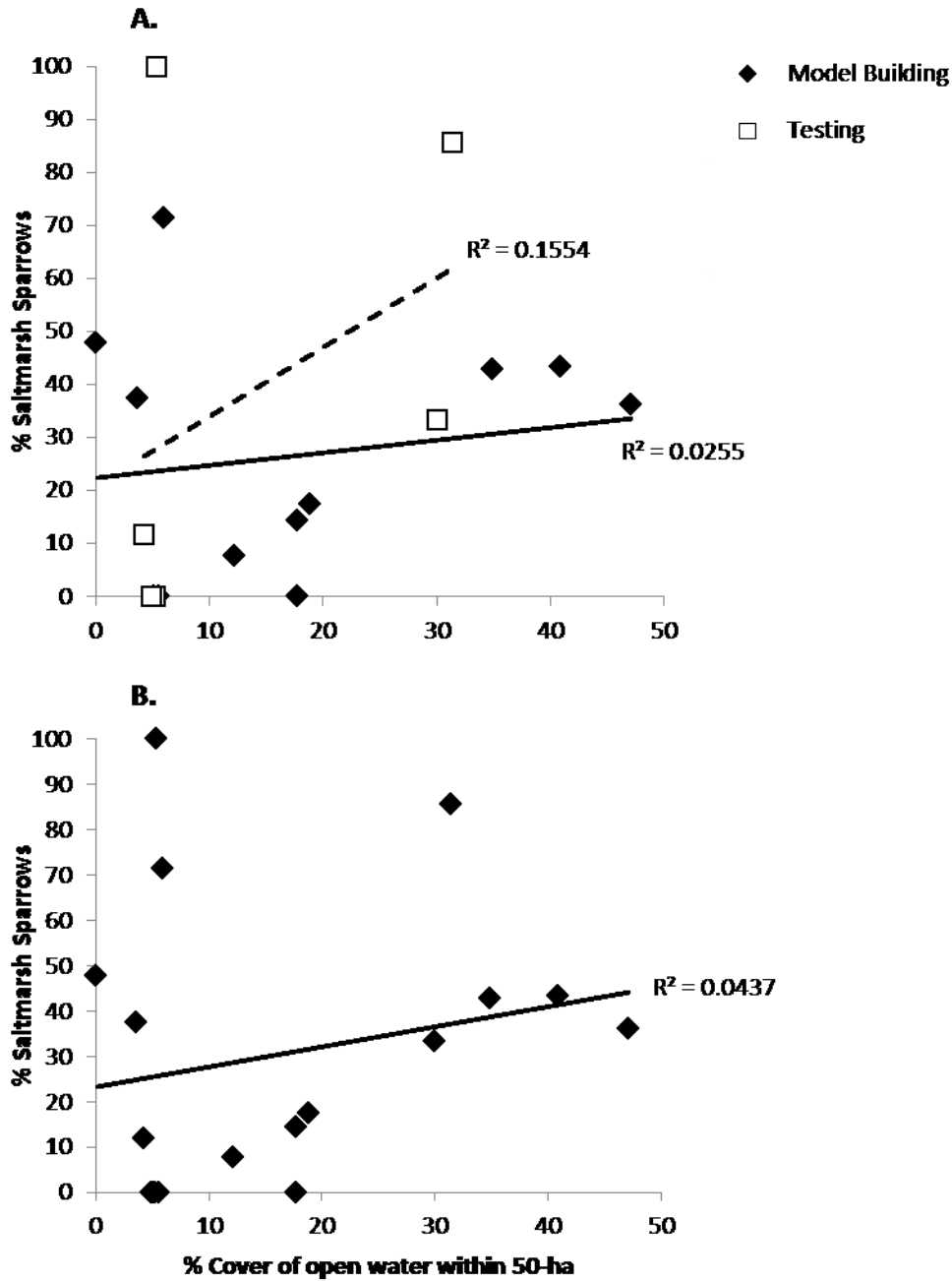


Figure 4: Comparison the relationship between Saltmarsh Sparrow relative abundance and % cover of open water within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

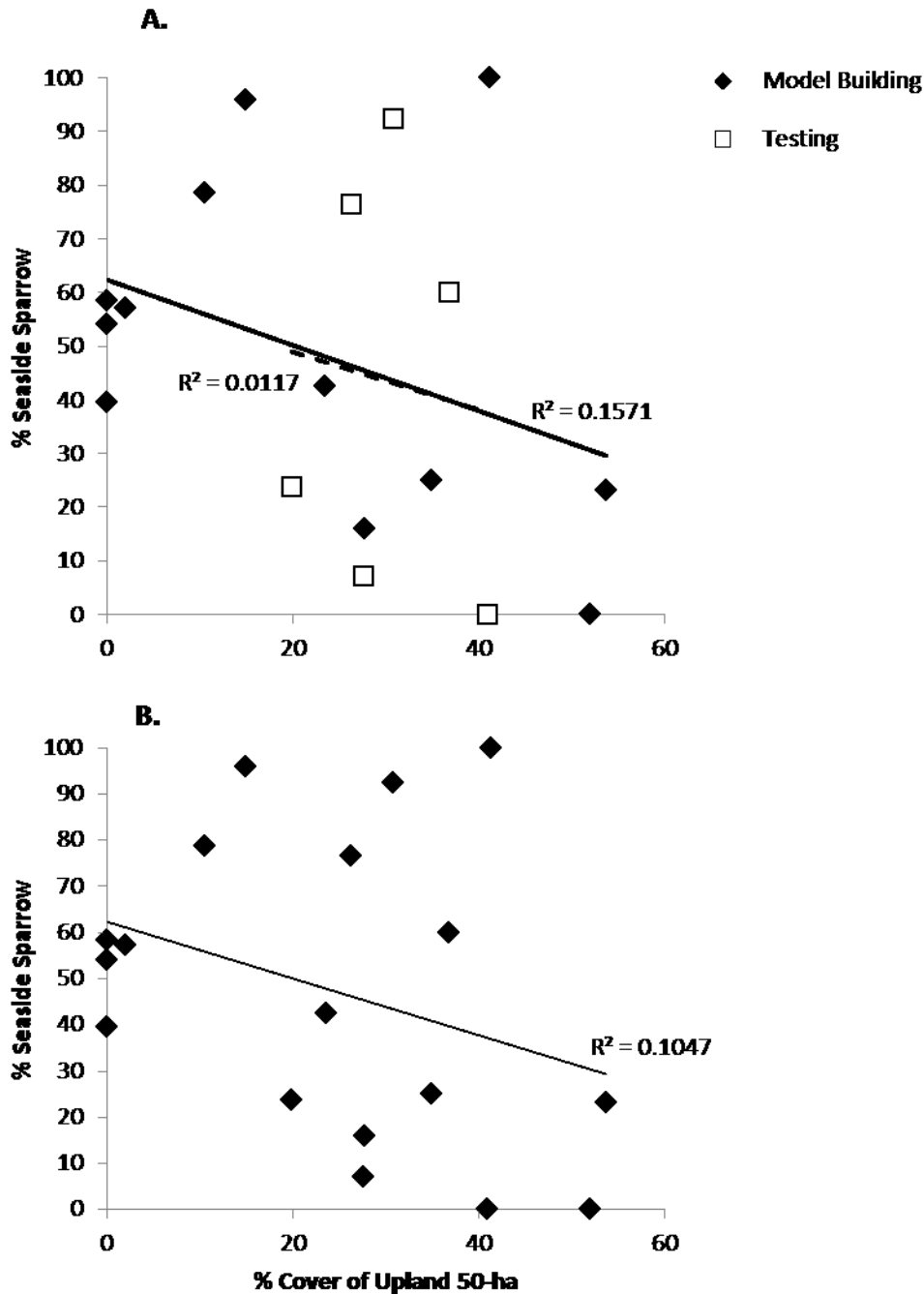


Figure 5: Comparison of the relationship between Seaside Sparrow relative abundance and % cover of upland within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

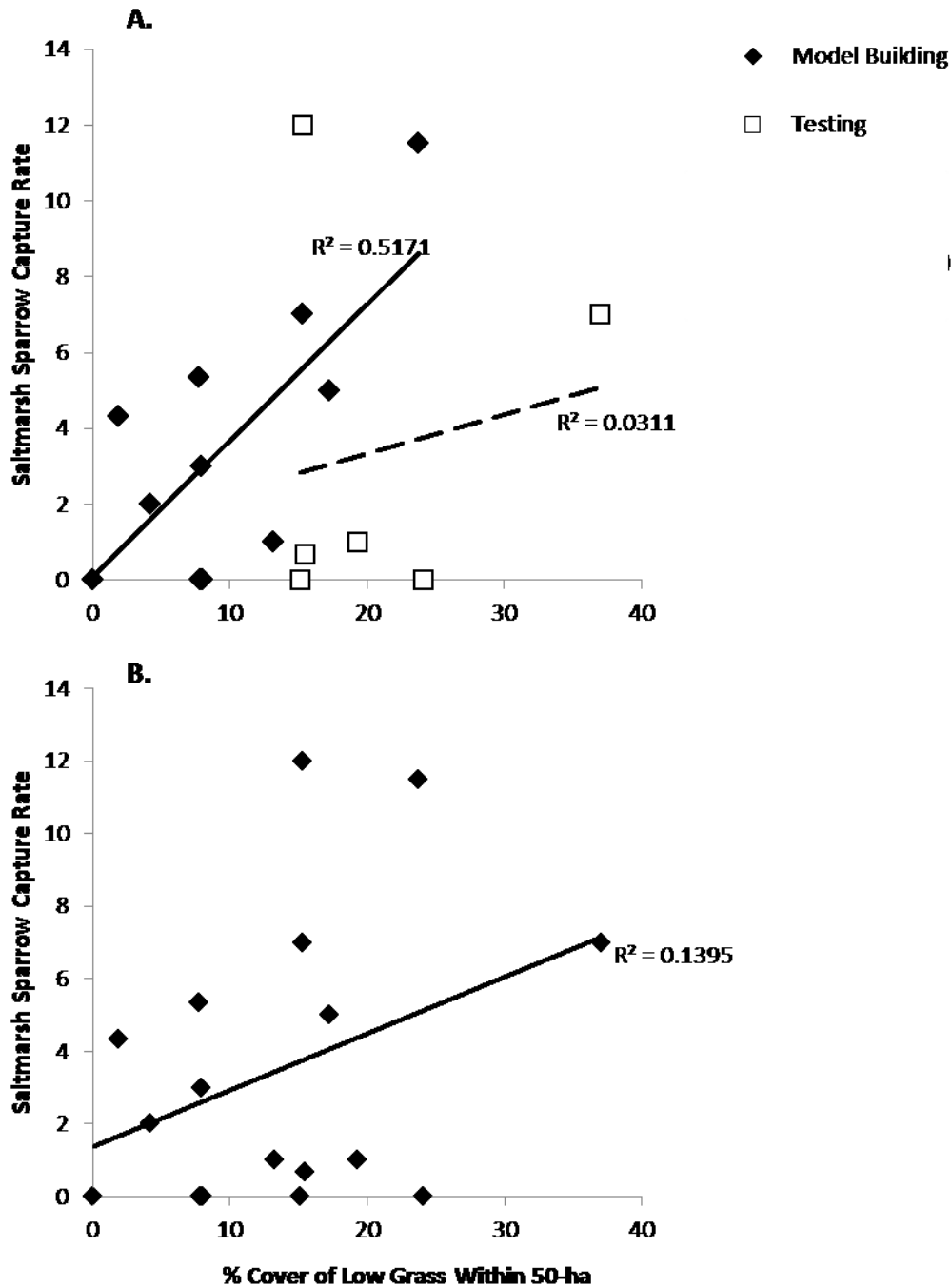


Figure 6: Comparison of the relationship between Saltmarsh Sparrow capture rate and % cover of low grass within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

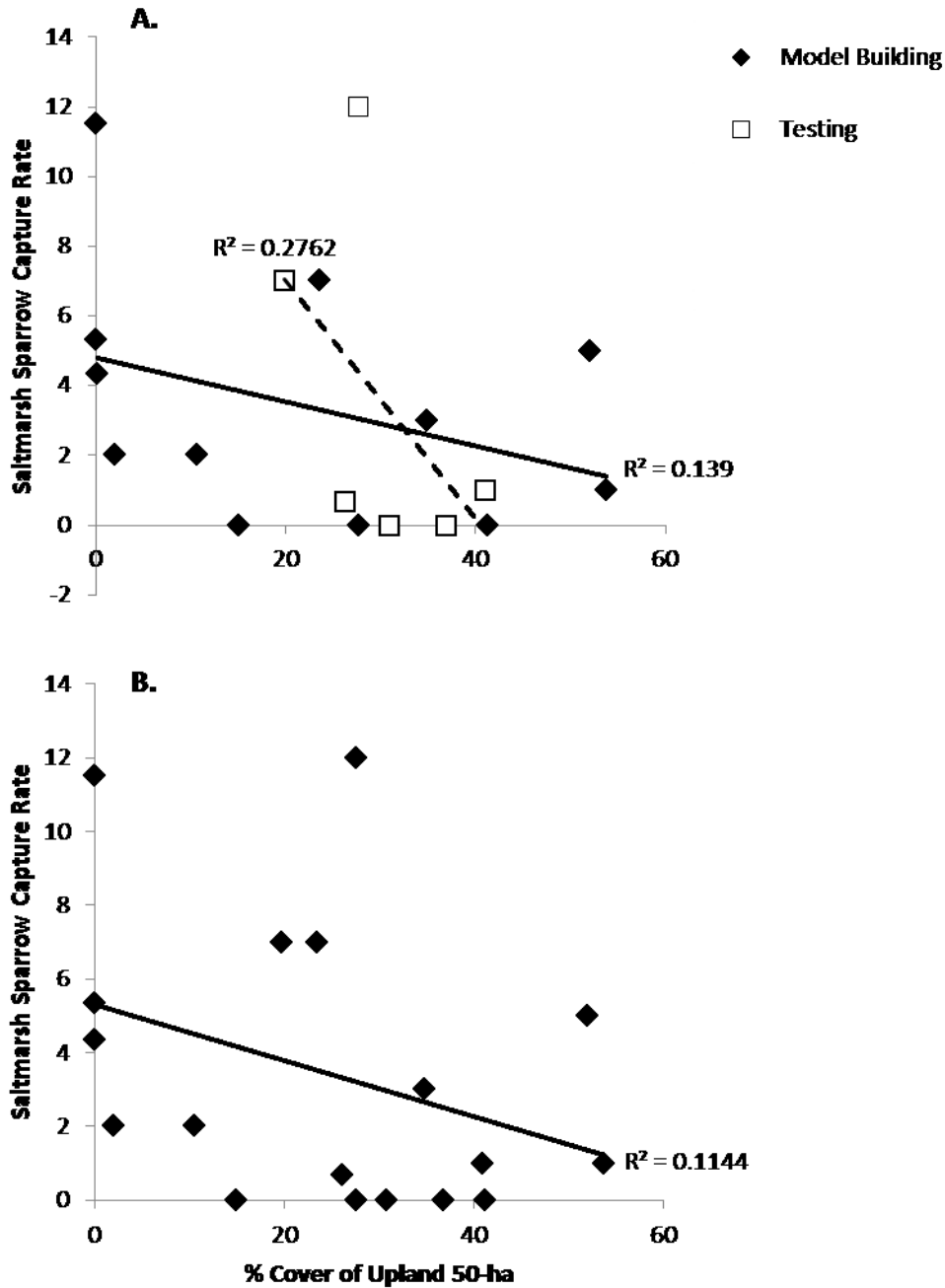


Figure 7: Comparison of the relationship between Saltmarsh Sparrow capture rate and % cover of upland within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

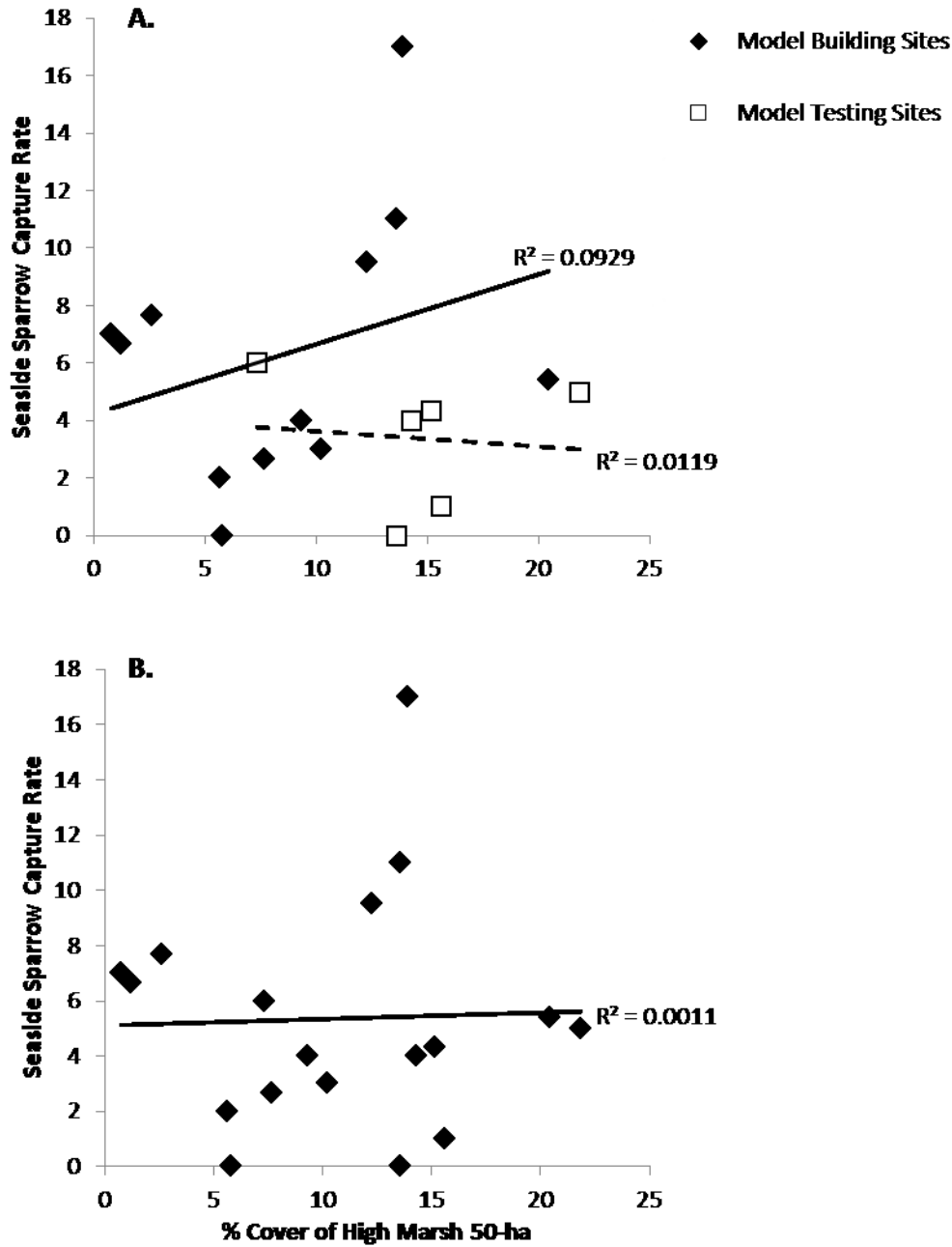


Figure 8: Comparison of the relationship between Seaside Sparrow capture rate and % cover of high marsh within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

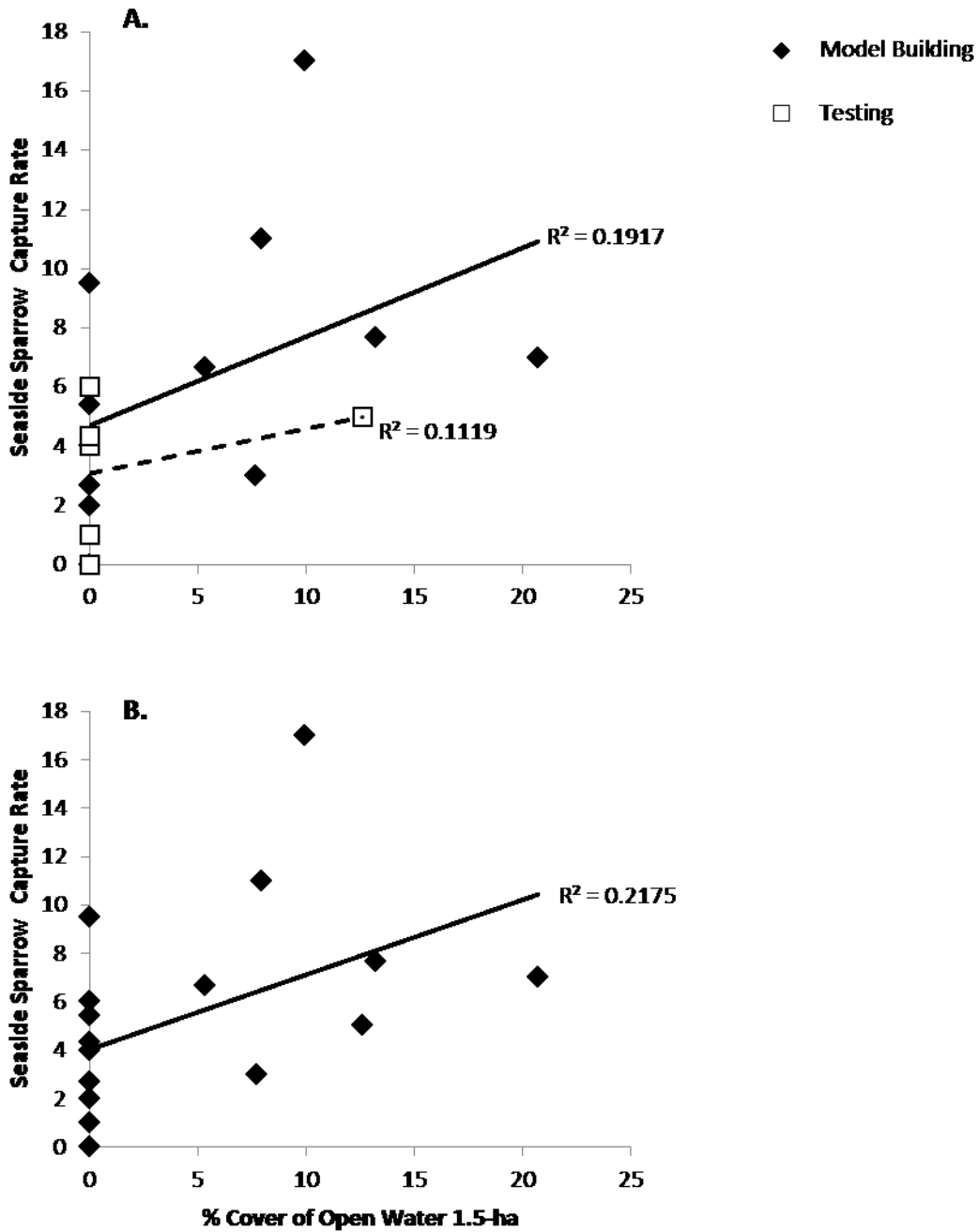


Figure 9: Comparison the relationship between Seaside Sparrow capture rate and % cover of open water within 1.5-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

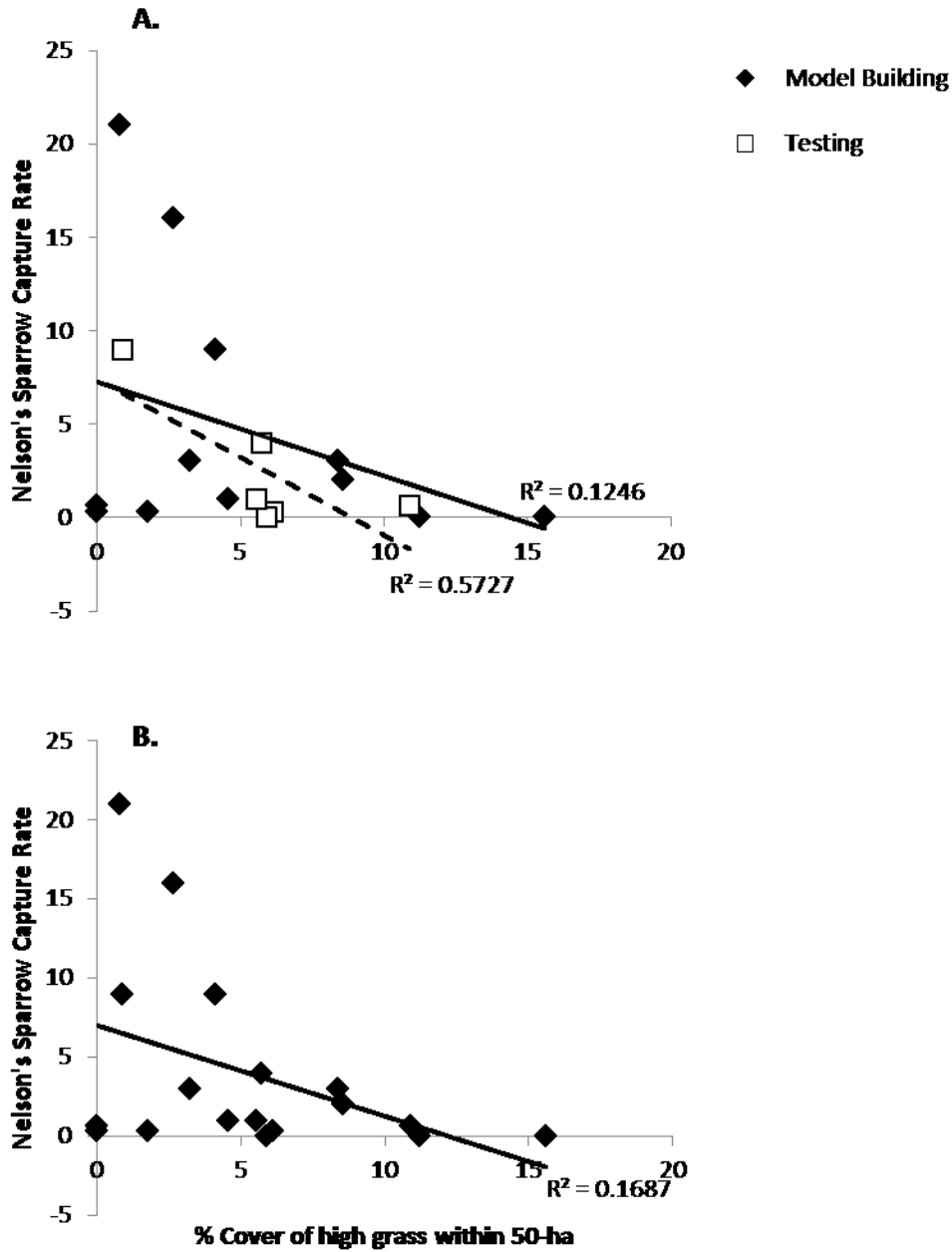


Figure 10: Comparison of the relationship between Nelson's Sparrow capture rate and % cover of high grass within 50-ha at A) the 12 model building sites and the six testing sites, and B) all 18 sites. The solid line indicates the line of best fit for model building sites while the dashed line is the line of best fit for testing sites. Best fit lines are meant to show relationships, but do not indicate significance. The  $R^2$  of each relationship is also shown.

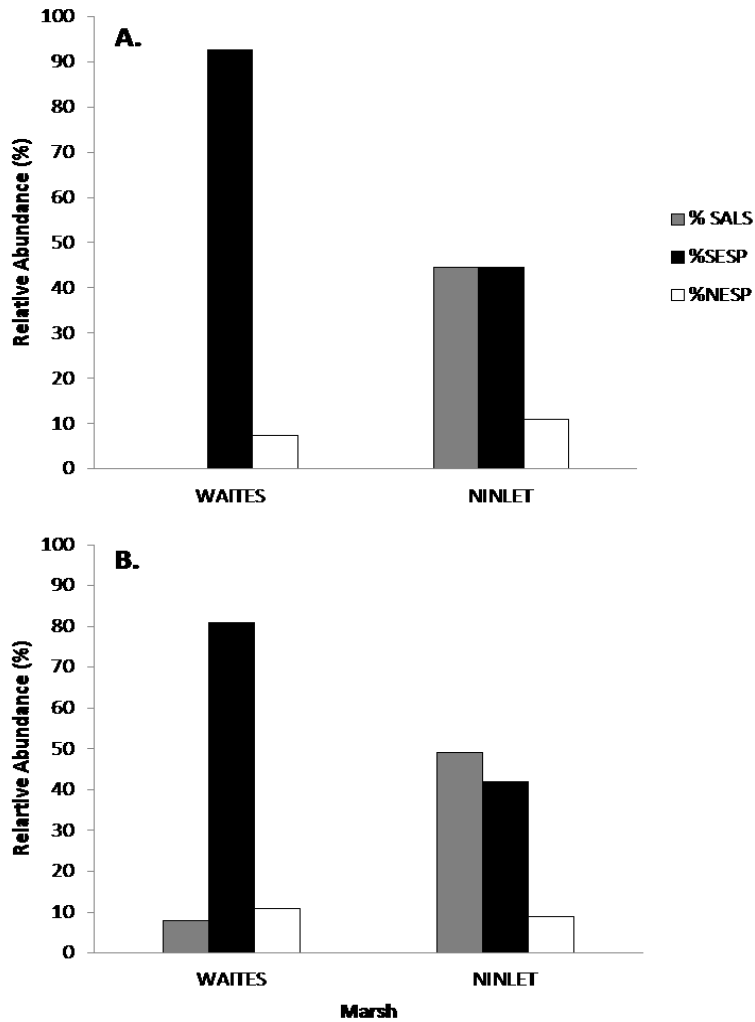


Figure 11: Visual comparison of relative abundances of newly banded birds (excluding year-to-year returns) found in A) the present study, and B) Shaw 2012, which occurred from 2010-2011 at shared study marsh.



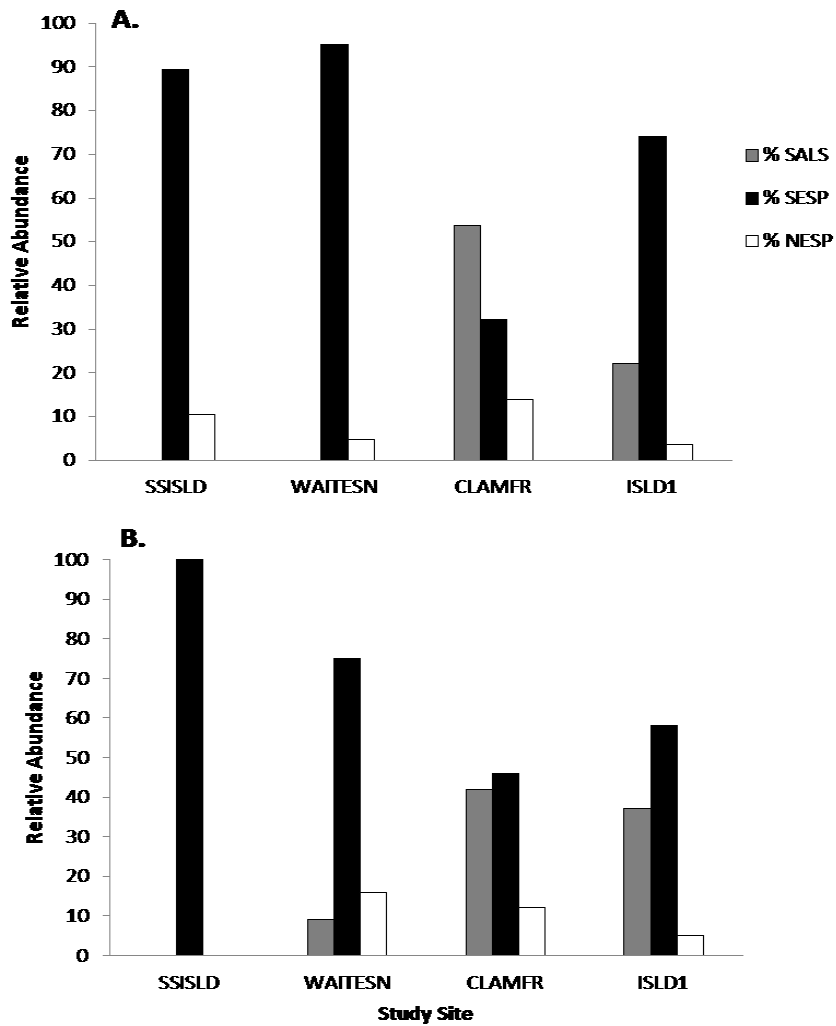


Figure 12: Comparison of relative abundances of newly banded birds (excluding year-to-year returns) found in A) the present study, and B) Shaw 2012, which occurred from 2010-2011 at shared study sites.

