

**Testing habitat model assumptions for Seaside Sparrows (*Ammodramus maritimus*) in
northern Gulf Coast tidal marsh: final report**

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Table of Contents

Executive Summary	1
Chapter 1: Introduction	3
Chapter 2: Habitat Quality	8
Introduction	
Methods	
Results	
Discussion	
Chapter 3: Population Viability Analysis	56
Introduction	
Methods	
Results	
Discussion	
Chapter 4: Conclusions and Recommendations	65
Literature Cited	67

Executive Summary

Tidal salt marshes are critically important habitats that have experienced serious declines in the United States and still face current and future threats. Due to both its conservation status and year-round reliance on coastal marsh habitat, the Seaside Sparrow (SESP; *Ammodramu maritimus*) has been chosen as a priority species by the Landbird Monitoring, Evaluation, and Research Team (MERT) of the Gulf Coast Joint Venture (GCJV), representing salt and brackish marshes. However, a lack of data from the Gulf Coast population made it necessary to use data collected primarily from Atlantic Coast SESP to inform habitat models for Gulf Coast SESP. Here, we present the results of research intended to provide Gulf-specific data to better inform the species-habitat relationships of SESP along the Gulf Coast.

In order to gain a better understanding of what constitutes high-quality habitat for SESP, we examined factors affecting nest site selection, nest success, and overall SESP density. Nest placement and survival both appear to be strongly influenced by predation. Nests were built in areas with more ground cover than random points and better-concealed nests were more likely to fledge young. These results contrast with those from Atlantic coast tidal marshes, where nest placement and nest survival are both mainly driven by tidal flooding. Survival was higher for nests that had closer active neighbors and successful nests were spatially clustered, while unsuccessful nests were not. More research is needed to determine if Seaside Sparrows are clustering in areas of low predator potential or if higher densities of birds can more effectively drive off or warn one another of predators.

The mean density of sparrows in our study marsh was 4.58 birds/ha, with individual point ranges from 0.68 to 13.58 birds/ha. This average is likely high relative to other marshes along the

Gulf Coast, because almost the entire marsh is occupied by SESP. Seaside Sparrow density and elevation were positively related in our study marsh, a result that contrasts with patterns of occupancy at a broader scale. We suggest that because broad- and fine-scale habitat relationships do not always agree, both must be considered when predicting species-level responses to potential future habitat alterations.

A preliminary population viability analysis (PVA) using the data that we collected highlighted the need for more robust data on female and juvenile survival. The results suggested that if survival is high enough, the population may be robust to fluctuating rates of reproductive success and to more frequent environmental catastrophes. More data are also needed on how environmental events such as hurricanes affect SESP survival.

While research across a broader area of the northern Gulf of Mexico is still needed, the results of this study will contribute to a better understanding of the demography and habitat relationships of the Seaside Sparrow and will increase its usefulness as an indicator for tidal marsh integrity.

Chapter 1

Introduction

Globally, tidal salt marsh covers about 45,000 km² (Greenberg et al. 2006b), an area slightly larger than the state of Maryland. The United States has more of this habitat than any other country, totaling 16,500 km², over 95% of which is along the Atlantic and Gulf coasts. Tidal salt marshes are highly productive ecosystems (Adam 1990) and are important both ecologically and economically. Ecologically, they play an important role in filtering pollutants from water (Gersberg et al. 1986), are an essential part of estuarine nutrient cycles (Welsh 1980), and help protect coastlines from erosion (Broome et al. 1988). Economically, they act as nurseries for many commercially important species of fish and shellfish (Knieb 1997), and provide numerous opportunities for those seeking outdoor recreation (Niering and Warren 1980).

For centuries, this ecosystem has been threatened in the United States by human activities. Over the 200-year period from 1780 to 1980, the contiguous United States lost 53% of its original wetlands (Dahl 1990). These threats continue even today, with an estimated 1% loss in tidal salt marsh area between 1998 and 2004 (Stedman and Dahl 2008). In the near future, one of the greatest threats to tidal salt marsh is predicted to be sea level rise (McFadden et al. 2007).

Because of its limited extent, high economic and ecological importance, and continued threats, tidal salt marsh health must be closely monitored. Since it is often difficult to monitor the overall health of an entire ecosystem, managers and researchers may rely on one or a suite of indicator species as proxies for ecosystem health. For tidal marsh in the United States, the Seaside Sparrow (SESP; *Ammodramus maritimus*) is perhaps the strongest candidate for this

role. It is one of only five species of terrestrial vertebrates worldwide that is completely restricted to coastal marsh (instead of having only a subspecies so completely restricted; (Greenberg and Maldonado 2006). Unlike the Saltmarsh Sparrow (*Ammodramus caudacutus*), another such endemic, SESP breeding range includes most of the marsh on the Atlantic and Gulf coasts. They are highly active and visible, making them easy to monitor compared to other marsh endemics, such as diamondback terrapins (*Malaclemys terrapin*) or salt marsh harvest mice (*Reithrodontomys raviventris*).

SEASIDE SPARROW LIFE HISTORY AND CONSERVATION STATUS

Seaside Sparrows are obligate coastal marsh-dwelling passerines that occur in scattered populations from southern Maine to the northwestern coast of the Gulf of Mexico in Texas (Post and Greenlaw 2009). They spend their entire life cycle in coastal marshes, staying in the marsh for both the breeding season and the winter. They are socially monogamous breeders, building nests predominately in marsh grass and rushes. They lay between two and five eggs per nest, with the average varying by location, but generally slightly over three (Post and Greenlaw 2009). The populations on the northern end of the range are migratory, wintering in marshes along the southeastern Atlantic coast. Southern populations are presumed to be non-migratory. The species is split into seven extant subspecies across its range; two on the Atlantic coast, one in the Everglades, and four on the Gulf coast.

Although many populations of SESP are currently stable, a naturally limited population size (estimated at slightly more than 100,000) and threats to their coastal wetland habitat raise concerns for their future conservation status (National Audubon Society 2007). They have already proven sensitive to habitat alteration, with two subspecies extinct (*A. m. pelonata*, *A. m. nigrescens*) and one endangered (Cape Sable Seaside Sparrow; *A. m. mirabilis*). They are on the

Audubon WatchList of species in need of conservation action due to their highly specialized habitat needs and continuing habitat loss (National Audubon Society 2007) and are categorized as a species of conservation concern throughout their range by the U.S. Fish and Wildlife Service (2008).

The life history of SESP has been relatively well-studied in Atlantic coastal marshes (Post 1974, Marshall and Reinert 1990, Gjerdrum et al. 2005, Greenberg et al. 2006c), but similar research is lacking for Gulf coast SESP populations. The Gulf coast has almost 40% more tidal marsh than the Atlantic coast (2.4 and 1.7 million acres, respectively; (Stedman and Dahl 2008) and has important differences in vegetation makeup and tidal regime (Bertness et al. 1992, Odum 1995). Therefore, it is important that the basic life history and breeding ecology of SESP be studied in Gulf coast marshes in addition to those on the Atlantic coast to inform habitat management and better predict the effects of future threats to the tidal marsh ecosystem.

GULF COAST JOINT VENTURE HABITAT MODEL

Due to both its conservation status and year-round reliance on coastal marsh habitat, the SESP has been chosen as a priority species by the Landbird Monitoring, Evaluation, and Research Team (MERT) of the Gulf Coast Joint Venture (GCJV; Vermillion et al. 2008), representing salt and brackish marshes. A habitat model has been created to determine population goals, habitat targets, and promote suitable habitat management. However, very little data is available on Gulf Coast SESP populations, so many of the assumptions of the model are based on data from research conducted in Atlantic coast marshes. Distinct differences distinguish Gulf coast from Atlantic coast marshes, including different tidal regimes and dominant plant species (Stout 1984).

According to the Joint Venture plan, a better understanding of what constitutes suitable and high quality marsh habitat would help improve estimates of SESP area and habitat requirements. Determining whether a habitat can be considered “high-quality” requires information about both abundance and demographic parameters (Van Horne 1983, Johnson 2007).

In the Northeast, where most Seaside Sparrow research has been conducted, breeding densities vary widely among marshes (Post and Greenlaw 2009). Several studies have examined the factors driving density differences among marshes. Benoit and Askins (2002) found that larger marshes generally have higher breeding densities, a factor which also has a strong positive effect on marsh occupancy by SESP (Shriver et al. 2004). Past and present marsh management practices can also affect occupancy and/or density of SESP. Marsh plots in Delaware that had experienced extensive open marsh water management (OMWM) had half the territory and nest density of plots that had no or limited OMWM (Pepper and Shriver 2010).

Where marshes are generally small, as in the Northeast, it may be reasonable to treat each marsh as a cohesive unit and consider marsh-level factors, such as size and management history, when attempting to determine what drives marsh bird occupancy or density. However, in large marshes such as those found along the Gulf coast, SESP density can vary widely within a single marsh and marsh-level characteristics will not provide any information on what is driving patterns of density within a marsh.

While optimum SESP nesting habitat has been studied and described in Atlantic Coast marshes, this information may not be transferrable to Gulf Coast marshes. In Atlantic Coast populations, SESP nest predominately in saltmarsh cordgrass (*Spartina alterniflora*; (Post et al. 1983, Marshall and Reinert 1990, Gjerdrum et al. 2005), which is usually the dominant plant

species. Based on these findings, the GCJV recommended the creation and/or restoration of marsh which areas of medium-height cordgrass. However, in many Gulf Coast marshes the dominant plant species is black needlerush (*Juncus roemerianus*) and while *S. alterniflora* is present, it is in lower density and may not be as important as a nesting substrate. Seaside Sparrows are year-round residents in Gulf Coast marshes, while those in Atlantic marshes are migratory (Post and Greenlaw 2009), which could affect territory and breeding dynamics and introduces the possibility of different habitat needs during the summer and winter. These important differences between Atlantic and Gulf coast tidal marshes highlight the need to revise the GCJV habitat plan by using data collected from Gulf Coast SESP population.

Chapter 2

Habitat Quality

A critical component of any species conservation or management plan is a clear understanding of what defines high-quality habitat for that species (Van Horne 1983, Block and Brennan 1993, Johnson 2007). Limited resources compel managers to focus attention on areas that are most valuable from a population standpoint. This raises the obvious question: how should high-quality habitat be defined? Quality can be considered from both an individual and a population-level perspective (Van Horne 1983, Pidgeon et al. 2006, Johnson 2007) – habitat is high-quality for an individual if nesting there leads to successful reproduction, whereas areas that are high-quality at a population level allow for long-term population growth or persistence (Block and Brennan 1993).

Understanding demographic factors is a crucial element when attempting to describe high-quality habitat for a particular species (Pidgeon et al. 2006, Johnson 2007). Adult occupancy or density alone may not reflect the true quality of an area for several reasons (Van Horne 1983, Maurer 1986). Dominant adults could push young birds into marginal areas, thus inflating abundance in low quality habitats (Oro 2008). Birds may also fall into ecological traps (Dwernychuk 1972), where individuals preferentially nest in areas where breeding success is too low to maintain population viability (Boal and Mannan 1999, Battin 2004). Population-level productivity of an area is a combination of both individual breeding success and density of breeding adults, and both components must be considered when deciding what constitutes habitat quality for a species.

When determining what environmental components contribute to breeding success for birds, it is necessary to consider both nest-site selection and nest success (Clark and Shutler 1999). Comparing locations used for nests with sites that are available but not used can provide information on what females perceive as components of a high-quality nest site. However, relying solely on nest-site selection can be misleading if individuals nest in sub-optimal locations either because they are young birds that have not yet learned what a good nesting site comprises (Hatchwell et al. 1999) or if they are excluded from optimal nesting sites by intra- or interspecific competition (Post 1981). Therefore, it is also necessary to compare successful and unsuccessful nest sites and see if patterns of nest survival match or contradict those of nest site selection.

For a species that is completely restricted to one habitat, such as SESP, it can be incorrectly assumed that its habitat relationships are already fully understood and no finer-scale studies are necessary. However, even within a seemingly well-defined habitat type, variation in local-level environmental factors can lead to large differences in quality for species that breed there. Therefore, fine-scale habitat characteristics may be an important consideration when attempting to reach management goals.

Several studies have examined SESP nest site selection and nest survival in Atlantic coast marshes, with most study sites north of Maryland. In these marshes, SESP build their nests in vegetation that is either taller than the average height of vegetation at random points (Gjerdrum et al. 2005) or not different from the vegetation surrounding the nest site (Post et al. 1983). Nests that are higher off the ground have a higher probability of survival which suggests that nest site selection is driven by the need to avoid flooding-induced nest failure caused by high spring tides (Marshall and Reinert 1990, Gjerdrum et al. 2005). Nests are built primarily in *Spartina*

alterniflora, particularly on the banks of tidal creeks where the vegetation is taller (Post et al. 1983, Gjerdrum et al. 2005).

Due to drastic differences in vegetation communities (Wiegert and Freeman 1990), tidal regime (Odum 1995), and SESP genetics (Awise and Nelson 1989) between Atlantic and Gulf coast marshes, it is probably inappropriate to use data collected from Atlantic Coast SESP populations to inform management decisions for Gulf Coast SESP. Unlike Atlantic Coast populations, SESP populations on the Mississippi Gulf Coast do not face regular flood tides, although strong storms or the combination of a high tide and strong winds can push water to higher than normal levels (Odum 1995). These extra-high tide events are infrequent and unpredictable, and the majority of nest failures are caused by predation rather than flooding (Post et al. 1983). Thus, nest location may be optimized to minimize predation risk rather than to avoid flooding.

Only two published papers exist on nest site characteristics of a Gulf Coast SESP population, both based on the same field study (Post 1981, Post et al. 1983). The authors found that the vegetation at nest sites is shorter than the vegetation at random points and is slightly less dense. Seaside Sparrow nests were built most often in glasswort (*Salicornia virginica*), yet nests built in this substrate had a very low probability of survival (0.003 – 0.004 over the nesting interval). Nests built in taller, denser *Juncus roemerianus* had a much higher survival probability (0.012 – 0.139), but SESP infrequently built nests in this vegetation type possibly due to competitive exclusion by marsh rice rats (*Oryzomys palustris*; (Post 1981).

Seaside Sparrows also provide a unique opportunity to examine the relationship between population density and breeding success. Throughout their range, SESP nest at a variety of densities, ranging from areas with large, clearly-defined territories to semi-colonial areas where

territories are small, ill-defined, and frequently overlapping (Post 1974). This range of variation can occur within a single marsh and was seen in both of our focal marshes. Previous research on SESP in New York has found either no relationship between nesting density and nest success (Post 1974) or a negative relationship, suggesting that nest predation in those marshes may be density-dependent (Post et al. 1983).

Examining landscape factors that correlate with SESP density on the Gulf coast will help refine our understanding of how SESP interact with, and may respond to change in, their coastal marsh habitat. Increased understanding of species-habitat relationships of potential indicator species makes it easier to interpret how changes in population dynamics may reflect changes in the underlying ecosystem. While the general habitat requirements of SESP are well understood, there is much less understanding of what drives patterns of density and abundance within marshes, information that is essential when trying to predict how small-scale changes to tidal marshes will affect SESP populations.

Information on the relationship between density and landscape variables can also be used to inform decisions on how to manage existing marsh to increase habitat quality for SESP. While density of individuals may not always correlate with habitat quality (Van Horne 1983), SESP do not possess any of the suggested attributes of bird species that are most likely to experience this disconnect, such as high territoriality and a habitat with a high degree of anthropogenic disturbance (Bock and Jones 2004).

The only published study concerning spatial patterns of SESP along the Gulf coast examined factors affecting SESP occupancy at 227 survey points spread among six marshes in Mississippi and Alabama (Rush et al. 2009). Seaside Sparrow occupancy at a point was positively related to salinity and the amount of emergent marsh within 200 m of a point, and was

negatively related to the percent of developed land within 500 m of a point. These results generally agree with the marsh-level studies done in the Northeast – more marsh and less human disturbance may increase SESP occupancy and/or density. While studies of local occupancy can provide useful information over broad scales such as those covered by Rush et al. (2009), they fail to detect relationships between landscape factors and abundance, especially in marsh complexes where occupancy of surveyed points approaches 100%.

We sought to determine factors associated with high-quality nesting habitat for Seaside Sparrows in two northern Gulf Coast tidal marshes. Our first objective was to examine nest-site selection by female SESP at a within-territory scale. Because production of young directly affects adult fitness, individuals are expected to choose nest sites that will maximize the probability of reproductive success (Clark and Shutler 1999).

Our second objective was to determine what factors were associated with nest survival. If a landscape factor appeared to be important both for nest site selection and nest survival, we would interpret this as evidence that females were correctly assessing the reproductive potential of nest sites. Because the majority of failed nests in our study area were depredated, we hypothesized that both nest site selection and nest survival would be determined by factors that would minimize predation risk.

Finally, we examined landscape factors that were associated with SESP density in a marsh complex on the Gulf coast of Mississippi. We believed that SESP density was related to the ability of individual birds to carry out necessary activities related to survival and created the following biological hypotheses to reflect various underlying processes:

- 1. SESP density is influenced by the probability of nest success.**

Risk of nest predation, which is directly related to reproductive success, can influence choice of habitat by adult birds (Eggers et al. 2006, Fontaine and Martin 2006, Peluc et al. 2008). In our study population, a concurrent demography study (Chapter 2) showed that most nest failures were caused by predation, which led us to hypothesize that landscape factors related to predator presence might influence SESP density. A small proportion of nest failures are flooding-induced, so we also included elevation as a potential factor influencing habitat selection.

2. SESP density increases with availability of foraging sites.

Resource availability can also be a major factor influencing species distributions (Orians and Wittenberger 1991, McCollin 1998, Johnson and Sherry 2001), so availability of foraging areas such as beach and salt panne may directly affect SESP density.

3. SESP density is positively influenced by the availability of nest sites.

For many bird species, nest site availability is a limiting factor (Brawn and Balda 1988, Burke and Nol 1998). We therefore hypothesized that SESP density would be positively related to the two marsh types (intermediate and high) used almost exclusively for nest sites in our study.

4. SESP density is positively related to the diversity of cover types.

Because SESP often use disparate areas of the marsh for foraging and nesting (Post 1974), we hypothesized that SESP may be choosing areas with a high number or diversity of available cover types.

5. SESP density is influenced by the same factors that predict occupancy at a larger scale.

Finally, we hypothesized that factors previously found to influence SESP occupancy in Gulf Coast marshes (Rush et al. 2009) would similarly influence SESP density.

We used data from ongoing marsh bird surveys to test the above hypotheses and determine which habitat variables may be affecting Seaside Sparrow density in a large tidal salt marsh in coastal Mississippi. Understanding the potential effects of local-level variables on SESP nest success and density will make SESP a more useful indicator species and will help better inform future management practices and land acquisition decisions.

METHODS

Nest-site Selection and Nest Success

Study Site

Our demographic work was conducted in two marsh complexes: Grand Bay National Wildlife Refuge/National Estuarine Research Reserve (GBNERR) and Pascagoula River Marsh Coastal Preserve. Both marshes are located on the Mississippi coast in Jackson County, approximately 20 km apart. Both sites are protected and include large areas of relatively pristine tidal marsh. The Grand Bay NERR is composed of about 7,300 hectares of wetlands, pine savannas, and terrestrial habitats. The tidal marsh areas are predominately polyhaline (salinity 18-35 ppt, (Cowardin 1979) and are dominated by *Juncus roemerianus*, interspersed with narrow bands of *Spartina alterniflora*. The Pascagoula River Marsh Coastal Preserve is a 4,700 hectare site of mostly oligohaline and mesohaline (0.5-5 ppt and 5-18 ppt, (Cowardin 1979) marsh, dominated by *J. roemerianus*, *S. patens*, and *S. cynosuroides*. Both sites were fully open to public use and did not require special permission for access.

Focal plot selection

At the beginning of our first field season (2010), we conducted marsh bird surveys at established points in each marsh complex as part of a long-running monitoring program, following standard survey protocols (Conway 2011). Prior to plot selection, each marsh was divided into quadrats to avoid spatial clumping of sites. We then identified the three or four survey points in each quadrat that had the highest number of SESP detections in the early round of surveys. This ensured that we did not randomly select a point that was not occupied. From these points, we randomly selected one per quadrat for a total of eight points (four in each marsh complex). These eight points served as the centers of our focal plots. The size of the plots was not strictly controlled, but we limited them to 2-4 ha for practical purposes. One plot at GBNERR was dropped early in the season due to low sparrow density, giving a total of 7 sites for analysis.

Field Methods

Nest monitoring

From late March to mid-July 2011 and 2012, we intensively searched for nests on each plot. Nests were found almost exclusively through behavioral observations of adults, though occasionally a nest would be found by accidentally flushing an incubating female. Once a nest was located, it was marked with a single flag at least five meters away. Nests were checked every two to four days and the contents and status were recorded. If a nest failed, we attempted to determine the cause (predation, flooding, or abandonment). If a nest had some shell fragments or was empty and dry we considered it predated and if a nest was empty and wet we considered it flooded. Since tides high enough (or storms strong enough) to flood a nest were rare, we were generally confident about attributing nest failure to flooding. If a nest retained all of its eggs but

had no evidence of adult activity we considered it abandoned. After a nest had fledged or failed, we attempted to find re-nest attempts by the same pair, identified either by the presence of uniquely color-banded adults or by proximity to the previous nest.

Vegetation measurements

After each nest was complete (failed or fledged), we took a series of measurements both at the nest and at a random point near the nest, based on vegetation measurements suggested for grassland breeding birds (Wiens 1969). Random points were determined by selecting a random compass bearing and a random distance between 8 and 25 m. If this landed in open water we adjusted the compass bearing by 90°. Restricting the maximum distance to 25 m ensured that the point was likely within the territory of the male and represented a potential nest site that the female had not chosen (i.e., the random site was available for use; Jones 2001). At the nest, we measured nest height (from the ground to the rim of the nest cup) and the height from the rim of the nest cup to the top of the vegetation above the nest. At the random site we measured the height of the vegetation at the center of the point.

At both the nest and random sites, we centered a 1-m² plot either on the nest or on the center of the random point. At each corner, we placed a dowel marked in two decimeter increments and counted the number of stems touching the dowel in each decimeter. We then estimated the cover of all plant species within the 1-m² plot and a 5-m² plot with the same center. Using a GPS point taken at the nest or random point, we later used ArcGIS (ESRI 2013) to calculate the elevation, distance to upland, and distance to water of each nest or random point, and both the minimum and average distance of each nest to other concurrently active nests.

Statistical Methods

All statistical analyses were performed in Program R (R Core Team 2013)

Nest site selection

Since nest sites were not independent from their paired random sites, we used paired logistic regression (1-1 matched case-control; Hosmer and Lemeshow 2000, Compton et al. 2002) to model differences between nest sites and paired random sites. We created a data frame that contained the difference in covariate measurements between nest and random sites (nest minus random) and used program R to fit a logistic regression model, using a vector of all 1s as the response and a no-intercept model. Using this method, coefficients are interpreted as the effect of a one-unit increase in the difference in habitat measurements between nest sites and random sites rather than as a one-unit increase in the absolute value of the habitat measurement.

We created four variable sets: vegetation measurements, 1-m² ground cover, and 5-m² ground cover (Table 2.1). Elevation was included as a lone variable rather than being included in a variable set. We then ran models with different combinations of these sets and compared the models using an information-theoretic approach (Burnham and Anderson 2011) which determined the support for each candidate model given our data. We ranked models based on AIC score with a small-sample correction (AIC_c; Akaike 1973, Hurvich and Tsai 1989). We did not run any models that combined the 1-m² set and 5-m² set as each ground cover type was highly correlated ($r > 0.6$) between the two scales. In order to incorporate model selection uncertainty into the parameter estimates, we computed model-averaged coefficients using all models with $\Delta AIC_c \leq 2$. We scaled these estimates by factors that we determined to be biologically meaningful (e.g., a 10% change in ground cover) and computed odds ratios for each parameter to make the results more interpretable.

Daily nest survival

We modeled daily nest survival using a logistic exposure model (Shaffer 2004) in program R using a custom logistic exposure link function (Bolker 2013, Herzog 2013). This method allowed us to model explanatory variables that remained constant over the duration of a nest attempt (e.g., nest height) and those that remained constant within but varied among nest check intervals (e.g., nest age). This method also allowed for varying nest check frequencies, as we checked nests at inconsistent intervals throughout the two field seasons.

We created five covariate groups at different scales that we thought may affect nest survival: nest site measurements, 1-m² ground cover, 5-m² ground cover, landscape factors, and social factors. (See Table 2.2 for a complete list of covariates in each group). For both 1- and 5-m² ground cover, we only included vegetation types that were present around at least 20% of nests to prevent uncommon vegetation types from having an inflated influence. Many of our nest site measurements were highly correlated; in these cases, we compared single-variable model and eliminated the variable with the higher AIC_c score. Since we had no a priori hypotheses for which covariates within the first three groups were most important, we found the best model from each of those groups of covariates (Table 2.3) and used that to represent the group. Temporal factors (date and nest age) frequently affect nest survival in birds (Grant et al. 2005) so we also created a temporal covariate group (Table 2.2).

We then created models using all combinations of the best model from each scale and evaluated the set of models using information-theoretic approaches, using AIC score with small-sample size correction (AIC_c) to rank models. We created a confidence set with all models where $\Delta AIC_c \leq 2$ and used this set to develop model-averaged predictions of daily survival rate. We generated model-specific predictions across a range of values for covariates of interest and

calculated 95% confidence intervals. We also computed model-averaged estimates and unconditional standard errors (Burnham and Anderson 2011) for a range of covariate values. We then used a logit-link function to transform these estimates into daily survival rates (restricted between zero and one) and plotted the trends and confidence intervals.

After we determined the top model in the set, we created four new mixed-effect models by adding a random effect of plot, year, marsh, or individual female to this top model. We only retained random effects if they noticeably affected the parameter estimates of the fixed effects in the model.

Factors Affecting Density

Study Area

The density analysis was restricted to the Grand Bay National Estuarine reserve because suitably detailed land cover maps were not available for the Pascagoula River Marsh Coastal Preserve. While the marshes of the GBNERR were originally formed by deposits from the Escatawpa River (Otvos 2007), there is currently no riverine input to the GBNERR. While SESP are widely distributed throughout the marshes of the GBNERR, there are areas that are not occupied.

Bird Surveys

Seaside Sparrows were surveyed as part of a larger marsh bird monitoring program from 2010-2012. We followed the survey methods outlined in the North American Marsh Bird Monitoring protocol (Conway 2011). We surveyed 40 sampling points throughout the GBNERR, each separated by at least 400m to reduce the chance of double-counting an individual bird (Fig. 2.1). The same points have been used annually since 2005, but the initial placement of the first

point was random. Each point was visited three times per year between late March and mid-June. Points were grouped into four routes of ten points each, and points within routes were always surveyed in the same order. During each survey we estimated the distance to each individual SESP that was seen or heard during a 13-minute unlimited radius point count. Each bird was tracked throughout the survey, but only its initial distance was recorded. One observer was exclusively focused on passerines (primarily SESP and Red-winged Blackbirds [*Agelaius phoeniceus*]) while a second concentrated on secretive marsh birds. This made it much easier for each observer to detect and keep track of individual birds. At each point we also recorded wind speed, temperature, sky condition, salinity, and background noise to use as detection and availability covariates in our modeling efforts.

Developing Covariates

We used ArcGIS (ESRI 2013) to extract landcover variables from a highly detailed (2.8-m cell size) land-cover map of the GBNERR (Fig. 2.1). While vegetation cover estimated on the ground can add explanatory power to models, covariates extracted from satellite imagery can be reliable predictors of abundance for birds (Stralberg et al. 2010). The land-cover map included seven different cover types within the surveyed area. Inundated/low marsh included areas that flooded almost on a daily basis, intermediate marsh only flooded during especially high tides or storm, and high marsh almost never flooded. The map also distinguished salt panne, shrub, tree, and beach/sand within the marsh. We overlaid the marsh bird survey points on the map and created a 200-m buffer around each point to correspond to our observation truncation value. To determine the amount of each cover type around each point, we calculated the percentage of cells within the buffer representing each land-cover category. We then considered the number and proportion of cover types within each 200-m buffer and calculated a reciprocal Simpson's

diversity index for cover type at each point. We thought that a measure of diversity would be important because SESP use diverse areas for nesting and foraging (Post 1974). We then increased the buffer size to 1000 m and calculated the percentage of cells within the buffer representing upland cover types (industrial, roads, trees, and upland grasses). We used the same land cover map to calculate the distance to upland and distance to development for each point by creating Euclidean distance rasters and extracting the values to each individual survey point.

For elevation we used a digital elevation map (DEM) from the National Elevation Dataset with a 1/9 arc-second resolution (~3-meter cell size; Gesch et al. 2002). We clipped the DEM to the non-water portions of our land-cover map and calculated the average elevation of the land within the same 200 m buffer. This left us with 13 predictor variables (Table 4). Based on the hypotheses outlined at the end of the introduction, we used these variables to create a set of ten a priori models regarding what specific landscape factors we thought might affect SESP density (Table 2.5).

To avoid potential problems due to multicollinearity, we calculated Pearson correlation coefficients for all pairs of density predictor variables. If two variables were strongly correlated ($r > 0.6$), we did not include both variables in the same model. All covariates were mean-centered and scaled prior to analysis to improve model performance.

Statistical Analysis

We used the “gdistsamp” function (Chandler et al. 2011) in package “unmarked” (Fiske and Chandler 2011) in program R (R Core Team, 2013) to simultaneously model density, availability, and detection probability of SESP throughout the GBNERR. This function allows multiple visits to each point (as opposed to the related “distsamp” which is based on a single visit to each point), and allows the modeling of availability based on survey-specific covariates.

While the stated purpose of the availability component of the `gdistsamp` model is to account for temporary emigration (Chandler et al. 2011), it also allows the possibility that a bird is present at a point but is not “available” to be detected during a specific survey because it is not visible or does not vocalize during the survey period.

Prior to any analysis, we truncated observations at 200 m in an attempt to avoid double-counting individual birds at neighboring points. While this may seem like a high truncation value, the marsh habitat is flat and open and many SESP observations were by sight. Therefore, we believe that we could accurately identify birds up to 200 m away. Because the R function “`unmarked`” does not yet have a function to allow for multiple visits per year over multiple years, we analyzed all nine visits together. We felt that this was appropriate because SESP at our sites had very high site fidelity, so patterns of density remained consistent over the three years of our surveys. We were also not interested in annual variations in density, but rather in spatial patterns.

We began by running null models using each of three key functions (half-normal, hazard-rate, and uniform). We chose not to include the exponential key function because Buckland et al. suggest that it should only be used with “...poorly collected data where there is strong reason to believe that the distance data are truly spiked” (2001; p. 24). We did not believe that this described our data so we excluded the exponential key function. We modeled each key function using both Poisson and negative binomial latent abundance distributions. While the Poisson distribution constrains the mean and standard deviation to be equal, negative binomial distributions allow for data that are overdispersed; that is, data for which the standard deviation is greater than the mean. In all models, we included an offset for the proportion of the count area that was marsh, since SESP do not utilize open water and the proportion of marsh differed widely among our survey points (from 0.23 to 0.83). Adding an offset also greatly decreased the

AIC_c score of our initial null models (from 1890.97 to 1867.38). We evaluated all models using an information-theoretic approach (Burnham and Anderson 2011) which determined the support for each candidate model given our data. We ranked models based on AIC score with a small-sample correction (AIC_c; Akaike 1973, Hurvich and Tsai 1989). This model-selection process was used for all subsequent modeling. Once we determined the key function/abundance distribution combination with the most support, we used the same combination in all further models.

After we selected the best-supported key function model, we fit several detection models while still keeping the availability and abundance components null. We used wind speed, noise, and observer as detection covariates. Wind speed was a continuous variable and noise and observer were treated as factors. We fit all possible detection models excluding higher-order terms and interactions (seven total) and ranked the models using AIC_c scores. The top detection model was then held constant through the rest of the modeling process.

We then fit availability models, a capability unique to the `gdistsamp` function. We included temperature, Julian date, and minutes past sunrise as covariates that we felt may affect availability by influencing movement or male singing rates. As with our detection models, we fit all possible models but also included a quadratic term for temperature, since it is reasonable that both extreme low and extreme high temperatures could negatively affect singing or movement rate.

Once we had determined the best key function, detection model and availability model we began building abundance models, using the same key function, detection model, and availability model for all. The models in the set, including a global and a null model, were ranked based on AIC_c score. We then took the final top model and re-ran it with any other

detection probability or availability models that had been within two AIC_c units of the top model in its respective set.

We created a confidence set of models that included all models where $\Delta AIC_c \leq 2$ (including those with modified detection and/or availability models), and, if necessary, created a composite model using averaged parameter estimates from all models in the confidence set. All inferences were based on model-averaged parameters. We evaluated the fit of the top model with a Freeman–Tukey test based on a parametric bootstrap (Fiske and Chandler 2011). We created 100 simulated data sets from our top model and calculated a fit statistic for each simulated data set. We then compared a fit statistic for our observed data to those computed from the simulated data. The model was considered to fit if the observed data were not too extreme when compared to the simulated data. Finally, using the top model or composite model, we plotted the estimated densities and 95% confidence intervals over the observed range of each of the covariates in the top or composite model.

RESULTS

Nest-site Selection

The top model for nest site selection included vegetation measurements and 1-m² ground cover (Table 2.6). This model was 2.85 times more likely than the second-ranked model, which added elevation. No models were within 2 AIC_c units of the top model, so we did not perform model averaging. The amount of bare ground within 1-m² was negatively correlated with nest presence. When bare ground increased by 10%, the probability of being a nest site decreased by 2.33 times (Table 2.7). The percentage of *S. patens* and *D. spicata* in a 1-m² around the point were

positively associated with nest presence. A 10% increase in each corresponded to a nest being 1.19 and 1.23 times more likely, respectively.

As vegetation height in the center of the point increased, the probability of nest presence also increased. A 10-cm increase in height made a nest 1.54 times more likely. A more positive difference between vegetation height in the center and edge of the 1-m² plot was also positively correlated with nest presence. A 10-cm increase in the difference (i.e., when the center vegetation was an extra 10 cm taller relative to the vegetation on the edge of the 1-m² plot) made a nest 1.20 times more likely. The odds-ratio confidence intervals for woody vegetation cover, *J. roemerianus* cover, and total stems broadly overlapped zero and so the direction of the relationship was not clear (Table 2.7).

Daily Nest Survival

Under the constant-survival model, the daily survival rate (DSR) for nests was 0.922 (95% CI: 0.909 – 0.933) for 2011 and 2012 combined and did not differ between the two years (2011: 0.920, 95% CI 0.901 – 0.936; 2012: 0.923, 95% CI 0.906 – 0.938). Assuming a modal 24-day nesting period (from first egg to fledge), this leads to an overall success rate of 14.26% (95% CI: 10.24 – 18.95).

The top model of daily nest survival included nest measurements, 1-m² measurements, landscape factors, and nearest-neighbor distance (Table 2.8). Three other models were within 1 AICc unit and received almost as much support as the top model. The confidence set contained eight models. We averaged the parameter estimates of these models and used the model-averaged estimates for further predictions (Table 2.9). None of the random effects we included had any influence on model parameters when added to the top model. This is supported by the

extremely small variance estimates associated with each random factor (female = 5.04×10^{-13} ; year = 7.82×10^{-12} ; marsh = 2.80×10^{-14} ; plot = 1.30×10^{-11}).

Daily survival rate increased with the age of a nest ($\beta = 0.043$, SE = 0.014), from 0.895 on day one (first egg) to 0.961 on day twenty-four (generally fledge day; lower 95% CI 0.861 – 0.940, upper 95% CI 0.922 – 0.974, Figure 2.2). The number of stems around the nest in the same two-dm height class as the nest was positively related to survival ($\beta = 0.011$, SE = 0.005). Model-averaged predicted DSR across the natural range of stem densities we observed (5 – 120) ranged from 0.913 to 0.977 (lower CI 0.886 - 0.941; upper CI 0.934 – 0.991, Figure 2.3). Nearest-neighbor distance was negatively correlated with DSR ($\beta = -0.009$, SE = 0.003); that is, as a nest was farther from another active nest, its DSR declined. Predicted across our observed range of nearest-neighbor distances (excluding several high outliers; 8 – 100), DSR ranged from 0.946 – 0.889 (lower 95% CI 0.932 – 0.844; upper 95% CI 0.958 – 0.922, Figure 2.4).

The percent of bare ground within a 1-m² around the nest and the laying date of a nest's first egg appeared to have a negative effect on nest success, though both confidence intervals narrowly included zero (ground: $\beta = -0.026$, SE = 0.013; first egg date: $\beta = -0.007$, SE = 0.004; Figures 2.5 and 2.6). For all other covariates in the confidence set, the 95% confidence interval of the beta estimate broadly overlapped zero (Table 2.9).

After finding that nest survival increased with decreasing nearest-neighbor distance, we performed a chi-square test to see if nearest neighbors shared the same fate more often than would be expected, based on the overall proportion of successful and unsuccessful nests. We found that successful nests were much more likely to have a successful nearest neighbor than expected – about 50/50 successful/unsuccessful instead of the overall ratio of about 25/75 ($\chi^2 =$

18.646, $df = 1$, $P > 0.0001$) while failed nests were not more likely to have a failed nearest neighbor ($\chi^2 = 0.065$, $df = 1$, $P = 0.798$, Table 2.10).

Density

Our observed patterns of SESP density were best described by our “nest success” a priori model, with no other models within two AIC_c units (Table 2.11). The predicted per-point densities based on the top model ranged from 0.68 to 13.58 birds/ha, averaging 4.58 birds/ha with a mean standard error of 1.33. The top a priori model, “nest success”, included elevation, distance to upland, percent trees, and percent upland within one km. Average elevation within 200 m of a point had a positive relationship with density ($\beta = 0.472$, 95% CI 0.285 – 0.659; Fig. 2.7). Distance to upland had a negative relationship with density — that is, sites farther from upland had a lower density of SESP ($\beta = -0.255$, 95% CI -0.471 – -0.129; Fig. 2.8). Percent tree cover within 200 m had a negative relationship with density ($\beta = -0.155$, 95% CI -0.302 – -0.008; Fig. 2.9). Percentage of upland within one km had a mostly negative relationship with density, but the confidence interval slightly overlapped zero ($\beta = -0.121$, 95% CI -0.271 – 0.029, Fig. 2.10). Based on the results of a Freeman-Tukey test on our bootstrap simulations, there was no evidence that our top model did not sufficiently fit our data ($P = 0.257$).

DISCUSSION

Nest-site Selection

On our study sites, nest sites had more vegetation cover at the 1-m² scale than random points, demonstrated by nest sites having both less open ground and more cover of two common grass species. Increased vegetation cover around nest sites is common in grassland-nesting bird species (e.g., (Dieni and Jones 2003, Lusk et al. 2003, Aguilar et al. 2008, Schill and Yahner

2009) and likely contributes to nest concealment. This supports our hypothesis that female SESP choose nest sites that will decrease predation risk by increasing nest concealment.

Seaside Sparrows built nests in vegetation that was taller than at random points. This relationship remained even when we excluded random points (and their associated nests) where the vegetation was clearly too low to support a nest. This result agrees with studies of SESP and Sharp-tailed Sparrow (*Ammodramus caudacutus*, a closely related congener that breeds in the same habitat on the Atlantic Coast) nest placement from the Atlantic coast (Marshall and Reinert 1990, DiQuinzio et al. 2002, Gjerdrum et al. 2005) but disagrees with the one study conducted on the Gulf coast (Post et al. 1983). On the Atlantic coast, where flooding is the most common cause of nest failure, it is clear why SESP should nest in vegetation that is taller than average. In our system, where flooding is much less common, it is not as apparent why SESP should nest in taller vegetation. One possibility is that SESP are still responding to the threat of flooding, even though it is rarer and less predictable than in Atlantic marshes. Females could also be attempting to raise their nests above the reach of ground predators such as marsh rice rats and saltmarsh snakes (*Nerodia clarkia*), which are more common at our study sites than aerial predators.

The vegetation in which nests were built was also taller than the vegetation immediately surrounding the nest, while the vegetation at the center of random points was the same height as the surrounding vegetation. This finding reflects the search image we developed for finding nests – females tended to nest in discrete clumps of taller vegetation. This is most likely an artifact of how taller vegetation is distributed throughout the landscape – as compact clumps of grass rather than as uniform areas of tall vegetation.

Nest Success

At the habitat level, there was a clear positive relationship between nest stems and nest survival, suggesting that nests placed in denser vegetation had higher daily survival rates. Nest concealment is generally assumed to be related to nest survival in birds (Lima 2009), an assertion that is supported by some studies (e.g. (Martin and Roper 1988) but not supported by many others (e.g., (Holway 1991, Howlett and Stutchbury 1996, Burhans and Thompson 1998). In systems with a varied suite of predators with diverse search methods, there may not be optimal nest sites that protect nests from all predation (Filliater et al. 1994, Liebezeit and George 2002). Tidal salt marsh systems have a low diversity of potential nest predators, so increasing nest concealment may be a viable strategy for minimizing all predation.

Our results that nest success increased with vegetation density directly contradict results from Atlantic coast marshes which found that successful nests were associated with less dense vegetation than unsuccessful nests (Gjerdrum et al. 2005). This is not surprising given that dense vegetation does not offer any protection against nest flooding, which is the major cause of nest failure in North Atlantic marshes. While Post (1981) did not explicitly measure vegetation density or nest concealment, he did find that nests built in grass species that are generally more dense (*Juncus roemerianus* and *Distichlis spicata*) were far more successful than nests built in sparse vegetation (*Salicornia virginica*).

Nest success increased with decreasing bare ground cover, a result that is frequently seen in studies of ground and near ground-nesting birds (Lusk et al. 2003). Since bare ground is necessarily directly inverse to ground cover, this result could also be interpreted as increasing nest success with increasing vegetation cover. This gives more support to our conclusion that nests built in areas of generally higher vegetation density were more successful. Bare ground was

also negatively associated with nest presence, suggesting that female SESP are choosing sites with characteristics that are associated with nest success.

Our findings on the relationship between breeding density and nest success directly contradict previous research on both SESP and many other bird species. When attempting to define high-quality habitat, density is generally easier to measure than breeding success, but may be a misleading indicator if density and breeding success are not positively related (Van Horne 1983). Research examining the connection between nest density and nest survival has had varying results. Early hypotheses (Tinbergen et al. 1967) predicted that predation pressure on camouflaged nests should be greater at higher nesting densities because predators will develop a search image as a density-dependent response. While many studies have supported this prediction (Larivière and Messier 1998, Barber et al. 2001) others have found no relationship (Vickery et al. 1992, Clotfelter and Yasukawa 1999) or the opposite – that nests in higher-density areas were more successful (Cairns 1980, Ackerman et al. 2004).

Seaside Sparrows offer a unique opportunity to examine the connection between density and demographic parameters because they naturally breed at a wide range of densities that varies both within and among marshes (Post and Greenlaw 2009). Post (1974) monitored SESP nests in New York marshes with both dense and dispersed breeding birds and found no difference in predation rates between the nesting patterns. He also tested for an interaction between nearest-neighbor distance and predation (i.e., is a nest more likely to share its fate with its nearest neighbor than with a random nest?) and did not find an effect for either predated or successful nests. He attributed the lack of an interaction to the paucity of ground predators and generally low predation rates in the study marshes. However, later research in the same marshes found that nests with closer neighbors were more likely to be predated (Post et al. 1983), hypothetically due

to the tendency of crows (*Corvus sp.*), a major predator in the system, to increase hunting efforts in areas where they have previously found prey (Sugden and Beyersbergen 1986).

Contrary to previous research on SESP, our results support a positive relationship between nest density and nest survival in two ways. First, decreasing nearest-neighbor distance was positively related to daily nest survival. The contrary – that having a closer nearest neighbor increases predation risk – is more commonly seen in studies of nest predation (Cresswell 1997, Aguilar et al. 2008), though some studies have found no effect of nearest-neighbor distance (Rendell and Robertson 1989, Ackerman et al. 2004). Much less common are situations where nest survival increases as nearest-neighbor distance decreases (Ringelman et al. 2012, Ringelman et al. 2014).

Second, successful nests were much more likely to have a successful nearest neighbor than would be expected based on the overall ratio of successful to unsuccessful nests. Conversely, unsuccessful nests were not more likely to have an unsuccessful nearest neighbor – their nearest neighbors instead matched the expected success/failure ratio almost exactly. So while successful nests tended to be clustered together, unsuccessful nests were not. This suggests that predation events were not spatially related, which does not support density-dependent predation in our system. This is likely due to a lack of avian predators in our study marshes (AJL and MSW, pers. obs.), as birds are generally more visual hunters and have been shown to form search images for specific prey items (Tinbergen 1960, Sugden and Beyersbergen 1986, Reid and Shettleworth 1992).

Spatial clustering of successful nests in a system where predation is the dominant cause of nest failure suggests two possibilities: higher densities of birds are better able to drive off, distract, or warn one another of nest predators, or birds are preferentially settling in areas with

lower predator density. Birds living in colonies or clustered territories may have a greater ability to warn one another of potential predators (Beletsky et al. 1986, Brown and Brown 1987, Perry and Andersen 2003), decreasing the time it takes for an individual bird to detect a predator, and nests near the interior of such clusters may have higher survival (Brown and Brown 1987, Perry et al. 2008). Some birds have been shown to preferentially nest in areas of low predator density (Forstmeier et al. 2001, Morosinotto et al. 2010, Trnka et al. 2011), suggesting an ability to assess predation potential before choosing a territory. These hypotheses could be distinguished by observing and comparing adult anti-predator behavior at low- and high-nest density sites and by estimating predator density at each site. In either case, whether density is a cause or an effect of low predation rates, adult density is likely a good indicator of high-quality breeding habitat and landscape factors that predict high SESP density could also serve as indicators of highly productive habitat.

Density

The strongest relationship to emerge from our modeling was between SESP density and elevation. The average elevation within 200 meters of a point (excluding water) was positively related to density. This supports our hypothesis that birds would preferentially nest in areas of higher elevation to lessen the risk of nest failure through flooding. Saltmarsh and Nelson's Sparrows, also marsh-obligate passerines and congeneric with SESP, chose nest sites whose elevation was higher than random points (Shriver et al. 2007), presumably to avoid flooding by high tides. Even though the majority of nest failures that we observed were caused by predation, 11% of failures were a result of flooding (Chapter 2). This is not an insignificant proportion of nests, so it is possible that SESP are still responding to the threat of flooding even though it is not the primary cause of nest failure on our study sites.

In salt marshes, where both predation and flooding threaten nests, nest-site selection is constrained by the need to minimize both of these risks (Storey et al. 1988, Greenberg et al. 2006a, Reinert 2006). Rather than females balancing these two competing threats at the individual nest-site level (Reinert 2006, Ricketts 2011), SESP may be initially choosing broader areas of higher elevation as a strategy to avoid nest loss by flooding. This would allow females to then choose specific nest sites that minimize risk of predation.

The apparent importance of elevation could also be due to correlations with other landscape variables. Elevation was significantly correlated with intermediate marsh ($r = 0.476$, $P = 0.002$), which was used almost exclusively for nesting in our study areas. When modeled alone, the percent of intermediate marsh has a clear positive effect on density, so it is possible that the positive effect of intermediate marsh is having some influence on the estimated effect of elevation. At most of our points the intermediate marsh is dominated by black needlerush, which Rush et al. (2009) found was positively correlated with SESP occupancy, and saltmeadow cordgrass (*Spartina patens*). Over 60% of the SESP nests we found at the GBNERR were built in one of those two grass species, showing the importance of intermediate marsh for SESP reproduction.

In salt marshes, the plant community is determined by a combination of elevation and salinity (Chapman 1960, Pennings et al. 2005) so rather than responding to elevation directly, SESP may instead be choosing the plant community that is associated with higher elevation marsh within the GBNERR because it represents preferred nesting habitat. The range of average elevation of our survey points was fairly small (0.092 – 0.680 meters) and certainly does not represent the full range of elevations at which SESP are found along the northern Gulf Coast. It is likely that there is an optimal elevation within a marsh that is associated with preferred

vegetation types, and SESP may exhibit a quadratic relationship with elevation in marshes with a wider elevational range.

Our finding that SESP density increased with elevation is very important from a management perspective. Marsh elevation is one factor that is likely to be affected by future sea-level rise (SLR; Rybczyk and Cahoon 2002, Erwin et al. 2006, Kirwan et al. 2010, Glick et al. 2013), particularly in a marsh such as the GBNERR that does not have regular sediment input from an associated riverine system (Morris et al. 2002, FitzGerald et al. 2008). Decreasing marsh elevation can lead to increased tidal flooding (Erwin et al. 2006), which would likely convert black needlerush-dominated intermediate marsh to smooth cordgrass-dominated tidally inundated marsh, as smooth cordgrass is generally confined to areas of low elevation and high salinity (Pennings et al. 2005). Seaside Sparrows along the Atlantic Coast preferentially use smooth cordgrass as nesting substrate (Marshall and Reinert 1990, Gjerdrum et al. 2005), which led Rush et al. (2009) to hypothesize that SLR could lead to an increase in SESP occupancy if coverage of smooth cordgrass increased. However, the birds on our study sites very rarely nested in smooth cordgrass, preferring intermediate marsh plants such as black needlerush and saltmeadow cordgrass. Areas of smooth cordgrass on the GBNERR were flooded almost daily and so likely would not be suitable nesting habitat for SESP. The plants also grew sparsely and likely would not provide suitable protection from nest predators. If areas of black needlerush and saltmeadow cordgrass were converted to smooth cordgrass, it is possible that SESP density and/or occupancy would actually decrease because of a decrease in suitable nesting sites.

The relationship between elevation and salinity in the GBNERR also has implications for future SESP density. Previous research on the northern Gulf Coast (Rush et al. 2009) found that SESP occupancy was positively associated with cover of black needlerush. In the study, black

needlerush was used as a proxy for salinity, with increasing cover associated with increasing salinity on a landscape scale. This led the authors to conclude that SLR-induced salinity increases may have a positive effect on SESP occupancy in northern Gulf Coast marshes. Our finding that density increases with elevation could lead to the exact opposite conclusion, as elevation and salinity were strongly negatively correlated in our system ($r = -0.793$, $P > 0.001$). When a study area includes large portions of fresh or nearly-fresh marsh, which are already known to be unsuitable for SESP (as did that surveyed by Rush et al. 2009), then it will appear that salinity positively influences SESP presence. However, our study was restricted to areas where SESP occupancy is nearly 100%. Within this narrower habitat band, SESP displayed a trend that was the opposite of that seen at a broader scale.

We further examined the relationships between density and elevation and salinity by analyzing another set of data collected from points in the Pascagoula River Marsh Coastal Preserve, also in Jackson County, MS. We did not include these points in the full analysis because we did not have a detailed land-cover map like we did for the GBNERR. We did have salinity data for each point and we were able to calculate average elevation from the same DEM used for the GBNERR analysis. The marshes along the Pascagoula extend far upriver and transition from brackish to fresh marsh about 10 km inland from the mouth of the river. Interstate 10 is a fairly clear dividing line between where SESP occur and where they do not (AJL and MSW, pers. obs.). North of Interstate 10, the marsh becomes essentially fresh and is not suitable for SESP. When we ran single-factor density models for elevation and salinity that included all of the Pascagoula survey points, elevation had a significant negative effect on SESP density ($\beta = -1.43$, 95% CI $-2.16 - -0.70$) and salinity had a significant positive effect ($\beta = 3.29$, 95% CI $1.77 - 4.81$). However, when we excluded the points north of I-10, both relationships became non-

significant (elevation: $\beta = -0.63$, 95% CI $-1.72 - 0.46$; salinity: $\beta = -0.13$, 95% CI $-0.99 - 0.73$).

This shows that relationships inferred from an examination of landscape-scale data may not hold at a finer scale, especially when the landscape analysis includes areas of habitat that are already known to be unsuitable. It also demonstrates that relationships may vary among marshes, and managers should be cautious in applying results garnered from a large-scale study to a single smaller system.

With different relationships between density, elevation, and salinity at different scales, it is difficult to predict how SESP may respond to changes brought about by future SLR. The broader positive relationship between salinity and SESP presence does suggest that SESP may be able to shift their range in large marsh systems that extend far inland and contain a wide salinity gradient, as their current habitat becomes too saline and formerly fresh marshes become suitably saline. However, in marshes such as the GBNERR that are not contiguous with fresh riverine marsh, it is possible that decreases in elevation and/or increases in salinity will make all habitat unsuitable for SESP. Even in marsh systems where SESP are able to migrate inland, generally narrowing marshes will be in closer proximity to both trees and upland habitat, which may make the new habitat less suitable due to increasing predator populations.

Contrary to our hypotheses, distance to upland was negatively related to SESP density. Upland habitat likely serves as a source of predators of both nests and adults such as raccoons and corvids. Marsh rice rats (*Oryzomys palustris*), another potentially important nest predator (Post 1981), nest in the marsh but use upland habitat, particularly during the winter and spring months and during high tides (Kruchek 2004). Therefore, we believed that SESP would avoid areas close to upland habitat because of potentially higher concentrations of predators. Previous research on SESP occupancy (Rush et al. 2009) found that occupancy was negatively associated

with the amount of development within 500 m of a point. While development and upland habitat are not equivalent, we thought that SESP density may exhibit a similar negative relationship with non-marsh habitat. However, two studies on nest survival of Red-winged Blackbirds (*Agelaius phoeniceus*) in freshwater marshes did not find a relationship between nest survival and proximity to the marsh/upland interface (Picman et al. 1993, Grandmaison and Niemi 2007) so our initial assumption of higher predator density nearer to the edge may be incorrect.

We do not believe that correlations with other variables were driving the relationship between density and distance to upland. While it may seem that elevation would increase with proximity to upland habitat, the mean elevation within 200 m of a point was not correlated with distance to upland ($r = -0.011$, $P = 0.945$), nor was the maximum elevation within the same radius ($r = -0.205$, $P = 0.204$). Therefore, we do not believe that the strong positive effect of elevation was confounding the true effect of distance to upland. Salt panne was the only cover type that was significantly correlated with distance to upland, with more salt panne occurring closer to upland ($r = -0.526$, $P = 0.0005$). Salt panne by itself does have a slight positive effect on density ($\beta = 0.294$, 95% CI: 0.043 – 0.545), so the effect of distance to upland may be slightly confounded with the effect of salt panne. It also may benefit SESP to be closer to upland habitat that could be used as a refuge during storms or extreme high tides.

Another possible explanation for the observed relationship is that SESP are using upland habitat as a visual proxy for the minute elevation changes (often less than one meter) found in tidal marshes, even though there may not be a true relationship between the two. Sites that are closer to upland are also generally farther from open water and may be better protected from storm surges and wind-generated high tides. The relationship could also be an artifact of our point locations. There are several areas of the GBNERR that have high densities of SESP and are

far from any upland habitat (> 2 km), but could not be sampled effectively because of regular rough water and strong winds. It is possible that if these high-density sites were included, the negative relationship between density and distance to upland would become non-significant.

Percent cover of trees within 200 m of a point had the expected negative relationship with density, but the confidence interval slightly overlapped zero. However, the bulk of the interval was below zero, suggesting that the true relationship is negative. While we did not collect information on the identity of nest predators, raccoons (*Procyon lotor*) are common nest predators in wetlands (Post 1981, Jobin and Picman 1997, Ricketts 2011) and it is likely that they were at least occasional nest predators on our study sites. Even when raccoons forage in wetlands, they will often still use trees as den sites (Ivey 1948) so the percentage of trees within 200 meters of a point could be influencing the density or likelihood of raccoons. Other upland predators species, such as the short-tailed weasel (*Mustela frenata*), have also been observed foraging in marshes (Picman et al. 1993).

Our results highlight the importance of using locally-collected data to inform habitat or species management plans. While SESP along the Atlantic coast preferentially nest in smooth cordgrass, in our study area the low-elevation areas occupied by this grass species had lower SESP density than higher elevation areas with different dominant plant species. If only information from Atlantic coast SESP were considered, managers may incorrectly target areas dominated by smooth cordgrass as preferential SESP habitat. Likewise, the positive relationship inferred between SESP and salinity from surveys at a regional scale may not hold at a more local level and may in fact be contradictory.

The conclusions drawn from this research suggest that SESP may be strong indicators for the presence of healthy intermediate (irregularly flooded) marsh in northern Gulf coast marshes.

These areas are generally safe from flooding-induced nest failure and also provide suitable nesting substrate. Higher detected densities of SESP may indicate an elevation threshold or the presence of a specific plant community, and bird surveys are likely easier and cheaper to carry out than intensive elevation or vegetation surveys. The development of highly detailed land-cover maps for more marsh complexes would allow for similarly detailed analyses at a broader spatial scale. Broader data may show important differences among marshes and could also help to highlight factors that affect SESP density similarly across a wider geographic range.

TABLES AND FIGURES

Table 2.1. Explanatory variables used to model nest site selection of Seaside Sparrows (*Ammodramus maritimus*). The top models for each scale were combined to find the top overall model.

Group	Variable Name	Variable Description
Vegetation measurements	center height	height of vegetation containing nest or in center of random point
	max 1m	maximum height of vegetation on edge of 1-m ² around nest or random point
	totstems	total stems counted at corners of 1-m ² centered on nest or random point
1-m ² and 5-m ²	ground	percent bare ground in a 1-m ² and 5-m ² around the nest or random point
	juncus	percent cover of <i>Juncus roemerianus</i> in a 1-m ² and 5-m ² around nest or random point
	patens	percent cover of <i>Spartina patens</i> in a 1-m ² and 5-m ² around nest or random point
	dist	percent cover of <i>Distichlis spicata</i> in a 1-m ² and 5-m ² around nest or random point
	woody	percent cover of woody vegetation in a 1-m ² and 5-m ² around nest or random point
Elevation	elev	elevation of nest site or random point

Table 2.2. Explanatory variables used to model nest success of Seaside Sparrows (*Ammodramus maritimus*). The top models for each scale were combined to find the top overall model.

Scale	Variable Name	Description
Nest-level	nestht	distance from ground to nest rim
	nesttop	distance from nest rim to top of vegetation above nest
	nestht	distance from ground to top of vegetation above nest
	nestprop	relative height of nest in vegetation (0-1)
	neststems	stems around nest in same dm as nest
	max1m	maximum height of vegetation within 1-m ² around nest
	htdiff	difference between max1m and toht
	totstems	all stems around nest
1-m ² and 5-m ²	ground	% bare ground in a 1-m ² and 5-m ² around the nest
	juncus	% cover of <i>Juncus roemerianus</i> in a 1-m ² and 5-m ² around nest
	patens	% cover of <i>Spartina patens</i> in a 1-m ² and 5-m ² around nest
	dist	% cover of <i>Distichlis spicata</i> in a 1-m ² and 5-m ² around nest
	woody	% cover of woody vegetation in a 1-m ² and 5-m ² around nest
Landscape-level	disth2o	distance from nest to water
	DistUp	distance from nest to upland
	elev	elevation of nest site
Social	MinDist	minimum distance to another active nest
	AvgDist	average distance to another active nest
Temporal	AvDayRd	average julian date of interval*, rounded to nearest whole number
	FirstEgg	julian date of nest's first egg
	AvgAge	average age of nest during interval*

* *interval* = time between two consecutive nest checks

Table 2.3. Top models from each scale used in subsequent multi-scale models of nest success

Scale	Best Model
Nest-Level	survival ~ NestStems + NestProp
1-m ²	survival ~ ground1
5-m ²	survival ~ juncus5
Landscape	survival ~ DistH2O + DistUp
Social	survival ~ MinDist
Temporal	survival ~ FirstEgg + AvgAge

Table 2.4. Landscape variables, with mean and range, used to model the density of Seaside Sparrows (*Ammodramus maritimus*) in the Grand Bay National Estuarine Research Reserve, Jackson Co., MS, USA. All percentages are cover within 200m of a survey point.

Variable	Mean (range)
% Low marsh	63.50 (0 - 97.75)
% Intermediate marsh	25.99 (0 - 94.01)
% High marsh	1.39 (0 - 15.76)
% Shrub	0.29 (0 - 5.82)
% Beach / sand	1.82 (0 - 40.59)
% Salt pan	4.59 (0 - 22.50)
% Tree	2.07 (0 - 22.52)
# Classes	4.2 (2 - 8)
Simpson's Reciprocal Diversity Index	0.41 (0.11 - 0.75)
Upland within 1km	5.20 (0 - 47.23)
Average elevation (m)	0.42 (0.09 - 0.68)
Distance to upland (m)	629 (35 - 1542)
Distance to development (m)	1494 (109 - 3398)

Table 2.5. Set of a priori candidate models to assess relationships between habitat and density of Seaside Sparrows in GBNERR, Jackson Co, MS

Model	Covariates
<i>Nest Success</i> : trees and upland serve as nest predator sources, while elevation affects nest flooding risk	%tree + distance to upland + % upland within 1 km + elevation
<i>Nest Site</i> : SESP nest preferentially in intermediate and high marsh	% intermediate marsh + % high marsh
<i>Predation</i> : sparrows are choosing sites based on nest predation risk, but not flooding risk	% tree + distance to upland + % upland within 1 km
<i>Diversity</i> : SESP require a diversity of habitats for nesting and foraging	diversity + # of cover classes
<i>Foraging</i> : SESP require open ground and mud for foraging	% beach + % saltpan + % low marsh
<i>Previous Research</i> : SESP density is affected by the same variables found previously to affect occupancy.	% intermediate marsh + % upland within 1 km + distance to development
<i>Nest Success + Nest Site</i>	% tree + distance to upland + % upland within 1 km + elevation + % intermediate marsh + % high marsh
<i>Nest Success + Foraging</i>	% tree + distance to upland + % upland within 1 km + elevation + % beach + % saltpan + % low marsh
<i>Nest Site + Predation</i>	% intermediate marsh + % high marsh + % tree + distance to upland + % upland within 1 km
<i>Diversity + Foraging</i>	diversity + # of classes + % beach + % saltpan + % low marsh

Table 2.6. Nest-site selection models for Seaside Sparrow (*Ammodramus maritimus*). Models did not include an intercept. Minimum AIC_c was 214.69.

Model	<i>K</i>	Δ AIC _c	<i>w_i</i>	Log likelihood
1-m ² + veg	8	0	0.74	-99.09
1-m ² + veg + elev	9	2.06	0.26	-99.06
5-m ² + veg	8	11.98	0	-105.08
1-m ²	9	14.10	0	-105.07
5-m ² + elev + veg	5	43.96	0	-124.22
1-m ² + elev	6	45.94	0	-124.17
veg	3	47.82	0	-128.21
veg + elev	4	49.22	0	-127.89
5-m ²	5	129.86	0	-167.17
5-m ² + elev	6	131.66	0	-167.03
elev	1	184.93	0	-198.81

Table 2.7. Parameter estimates, scaled odds-ratios (OR), and lower and upper 95% confidence limits (LCL, UCL) for nest site selection by Seaside Sparrows based on the top model. An asterisk (*) denotes an odds-ratio confidence interval that does not include 1.

Parameter	Estimate (SE)	Scalar	Scaled OR	OR 95% LCL	OR 95% UCL
Ground1	-0.083 (0.021)	10	0.43*	0.29	0.66
Juncus1	0.005 (0.007)	10	0.95	0.82	1.10
Patens1	0.017 (0.008)	10	1.19*	1.02	1.38
Dist1	0.021 (0.008)	10	1.23*	1.05	1.45
Woody1	0.023 (0.014)	10	1.25	0.95	1.65
toht	0.043 (0.007)	10	1.54*	1.33	1.78
totstems	0.006 (0.004)	20	1.08	0.90	1.28
totminmax	0.018 (0.008)	10	1.20*	1.03	1.40

Table 2.8. Daily nest survival models for Seaside Sparrow (*Ammodramus maritimus*). We ran a total of 33 models with a minimum AIC_c of 763.37. Only models with $w_i \geq 0.05$ are shown.

Model	K	ΔAIC_c	w_i	Log likelihood
1- m^2 + nest site + landscape + social	9	0	0.15	-372.58
1- m^2 + landscape + social	7	0.3	0.13	-374.77
1- m^2 + nest site + social	7	0.4	0.12	-374.82
1- m^2 + 5- m^2 + landscape + social	8	0.93	0.09	-374.07
nest site + landscape + social	8	1.11	0.09	-374.15
1- m^2 + 5- m^2 + nest site + social	8	1.4	0.07	-374.30
1- m^2 + 5- m^2 + nest site + landscape + social	10	1.42	0.07	-372.27
nest site + social	6	1.79	0.06	-376.53
landscape + social	6	2.37	0.05	-376.82

Table 2.9. Model-averaged coefficient estimates used to predict daily survival of Seaside Sparrows (*Ammodramus maritimus*) across a range of covariate values. Asterisks indicate confidence intervals that do not include zero.

	β Estimate (SE)	95% CI
(Intercept)	3.19 (0.670)	(1.875, 4.521)
Ground1	-0.026 (0.013)	(-0.052, 0.0006)
Juncus5	-0.004 (0.004)	(-0.012, 0.004)
NestStems	0.011 (0.005)	(0.001, 0.022)*
NstProp	-0.417 (0.772)	(-1.931, 1.097)
DistH2O	0.004 (0.003)	(-0.0006, 0.009)
DistUp	-0.0004 (0.0003)	(-0.001, 0.0002)
MinDist	-0.009 (0.003)	(-0.014, -0.003)*
FirstEgg	-0.007 (0.004)	(-0.015, 0.0002)
AvgAge	0.043 (0.014)	(0.015, 0.072)*

Table 2.10. Nearest-active neighbor fate for all nests with known fate. Successful nests were more likely than expected to have a successful nearest neighbor, while the fates of unsuccessful nests' nearest-neighbors almost exactly fit the expected ratio (28.7% successful and 71.3% failed). Nests with no concurrently active nest at the same site were excluded from the analysis.

	Successful Nearest Neighbor	Unsuccessful Nearest Neighbor
Successful Nests ($n = 77$)	38 (49%)	39 (51%)
Unsuccessful Nests ($n = 203$)	54 (26%)	149 (74%)

Table 2.11. A priori models for Seaside Sparrow (*Ammodramus maritimus*) density in GBNERR, Jackson Co, MS. All models include an offset for proportion of marsh. Minimum AIC_c was 1841.92.

Model	K	ΔAIC_c	w_i	Log Likelihood
nest success	15	0	0.98	-895.96
null	11	9.98	0.01	-910.24
nest site	13	10.84	0	-906.38
nest site+success	16	11.27	0	-898.77
forage+nestsuccess	17	16.29	0	-898.2
diversity	13	17.12	0	-909.52
foraging	14	18.15	0	-907.63
predators	14	19.2	0	-908.16
prev research	14	21.6	0	-909.36
preds+site	17	23.88	0	-901.99
div+forage	16	25.93	0	-906.1

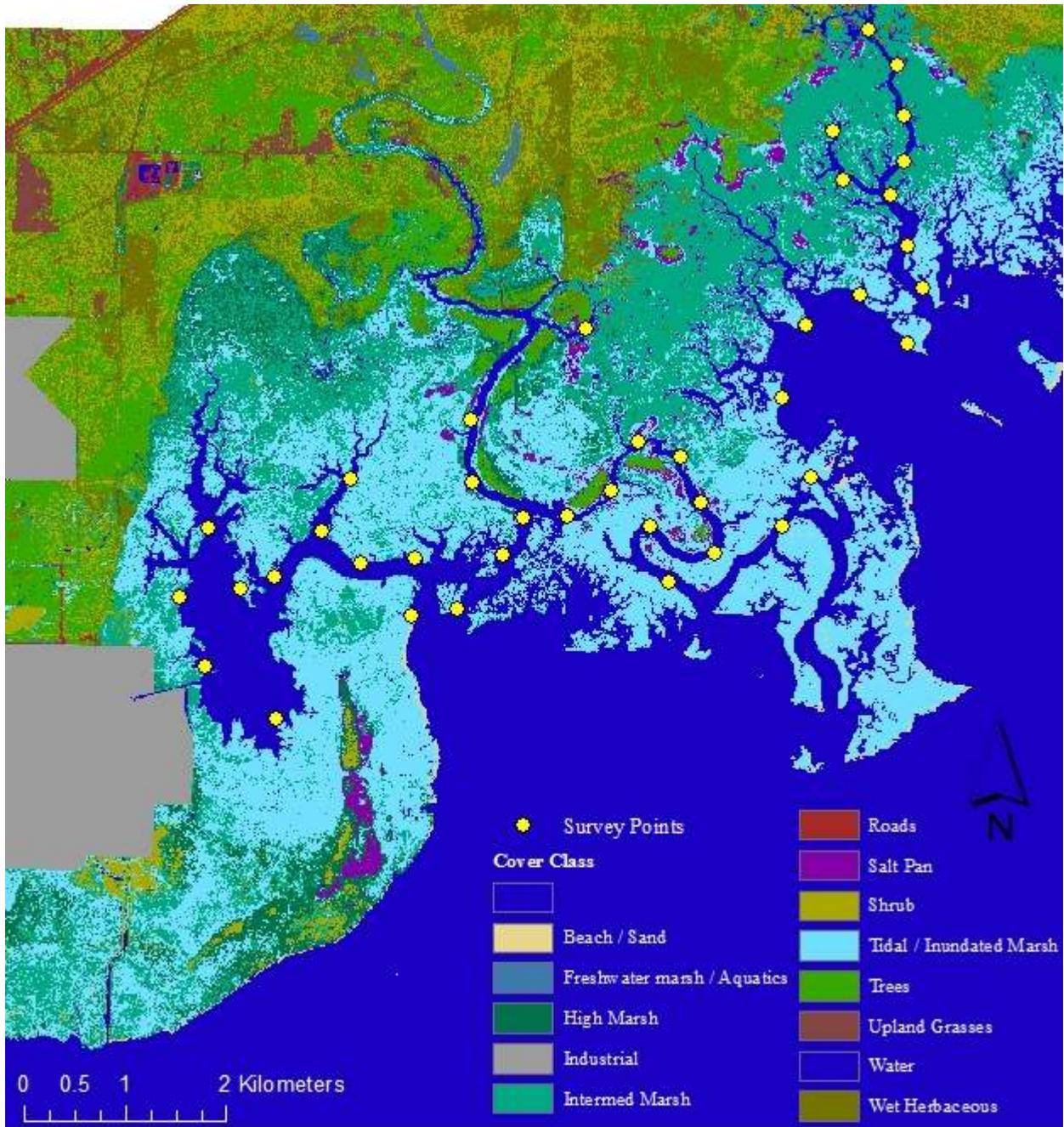


Figure 2.1. Land-cover map used to extract modeling variables, including distribution of marsh bird survey points at the Grand Bay National Estuarine Research Reserve, Jackson Co., MS, USA. Points were established in 2005.

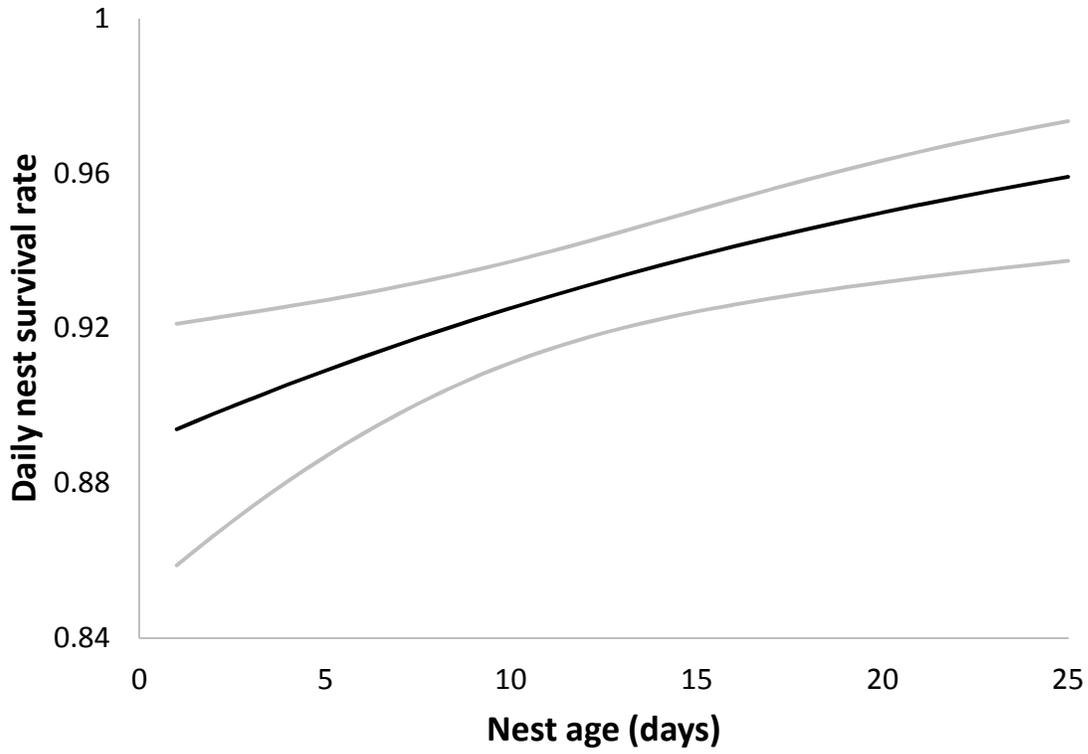


Figure 2.2. Predicted daily survival rate of Seaside Sparrow nests with increasing nest age. Gray lines represent 95% confidence intervals.

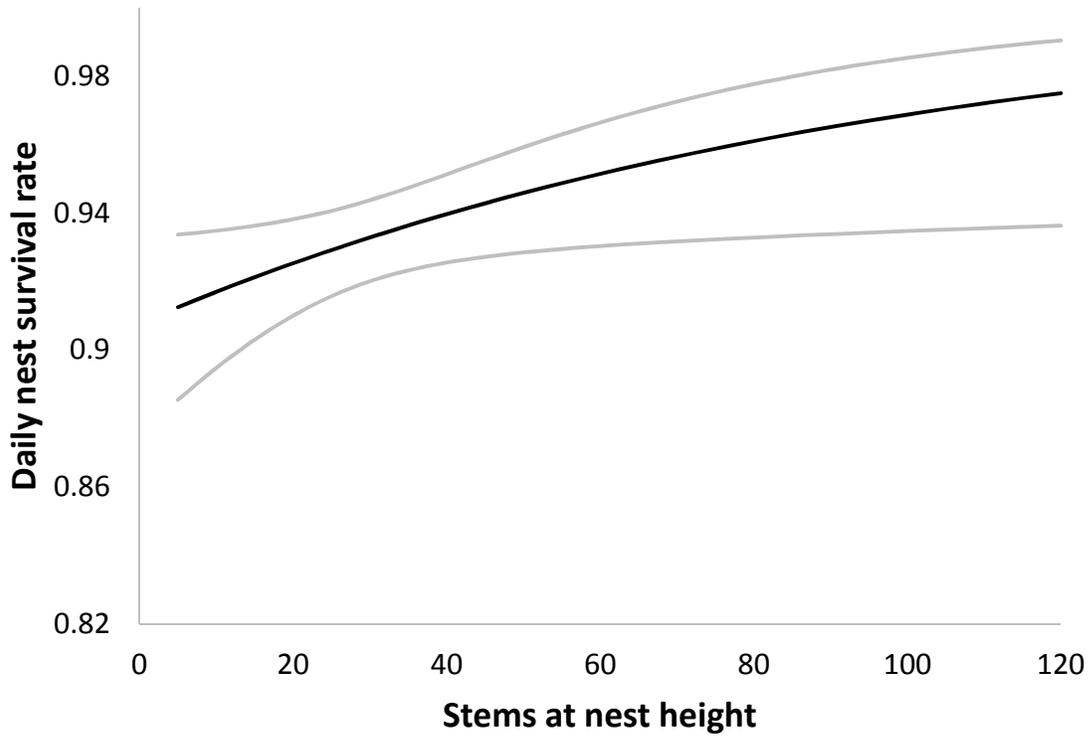


Figure 2.3. Predicted daily survival rate of Seaside Sparrow nests across the observed range of number of stems in the same dm as the nest. Gray lines represent 95% confidence intervals.

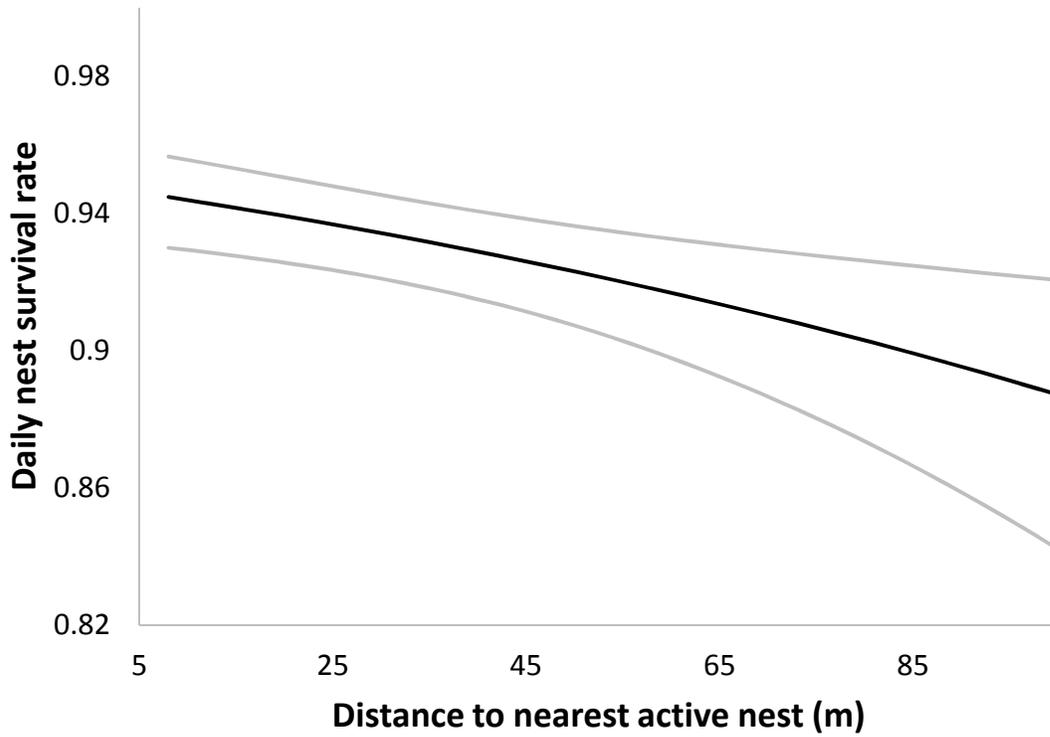


Figure 2.4. Predicted daily survival rate of Seaside Sparrow nests across the observed range of nearest-neighbor distances. Gray lines represent 95% confidence intervals.

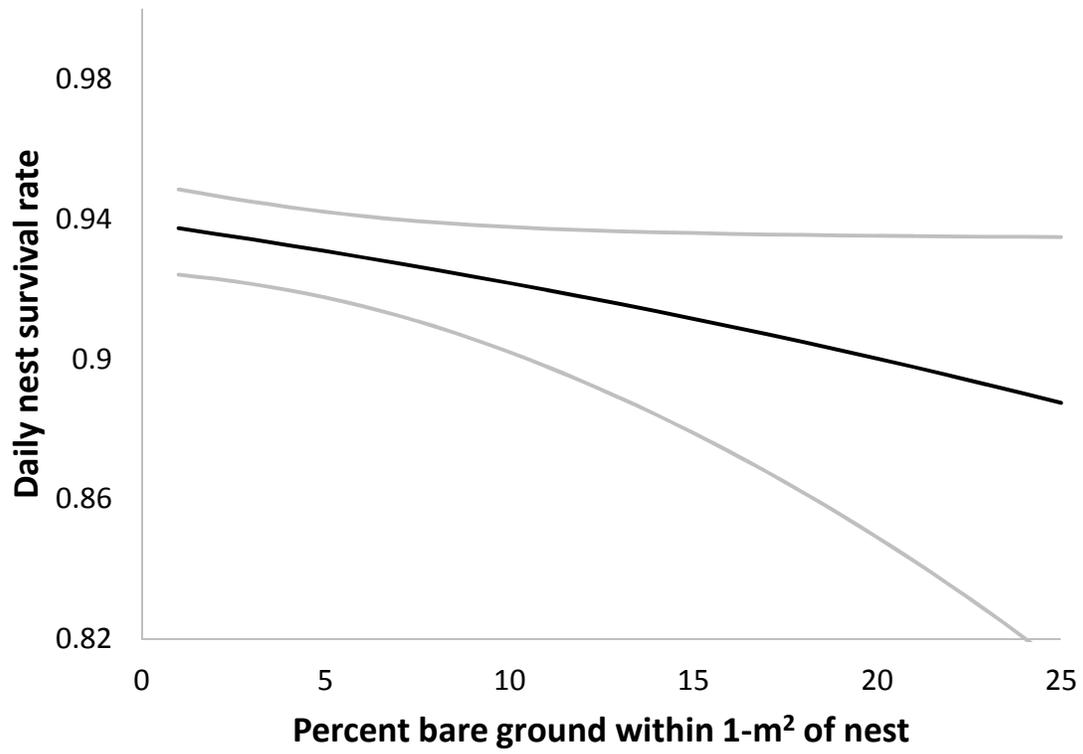


Figure 2.5. Predicted daily survival rate of Seaside Sparrow nests across the observed range of bare ground in a 1-m² centered on the nest. Gray lines represent 95% confidence intervals.

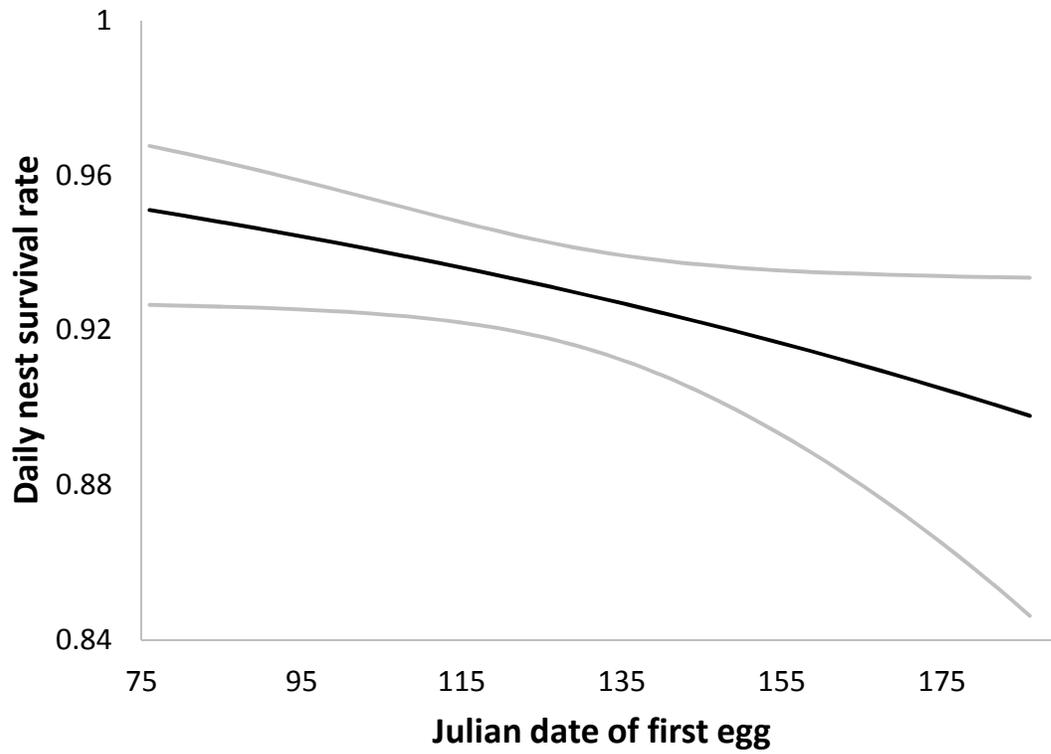


Figure 2.6. Predicted daily survival rate of Seaside Sparrow nests across the range of first egg dates observed during our study. Gray lines represent 95% confidence intervals.

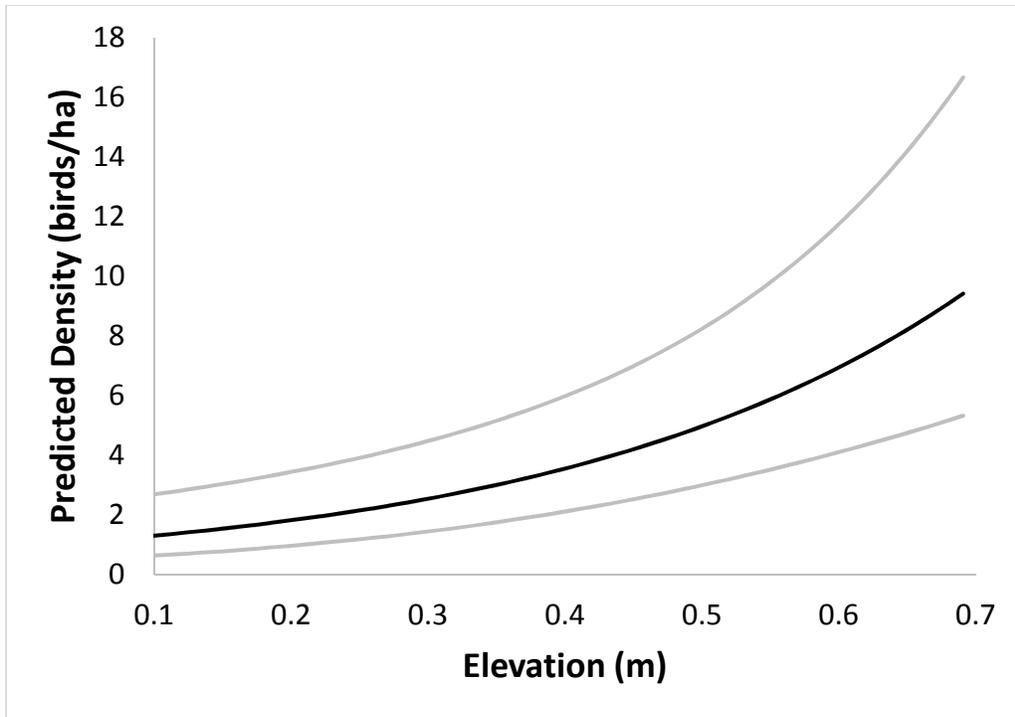


Figure 2.7. Predicted relationship (with 95% confidence intervals) between elevation and density of Seaside Sparrows (*Ammodramus maritimus*) across the range of elevations of survey points. Prediction is based on the top model.

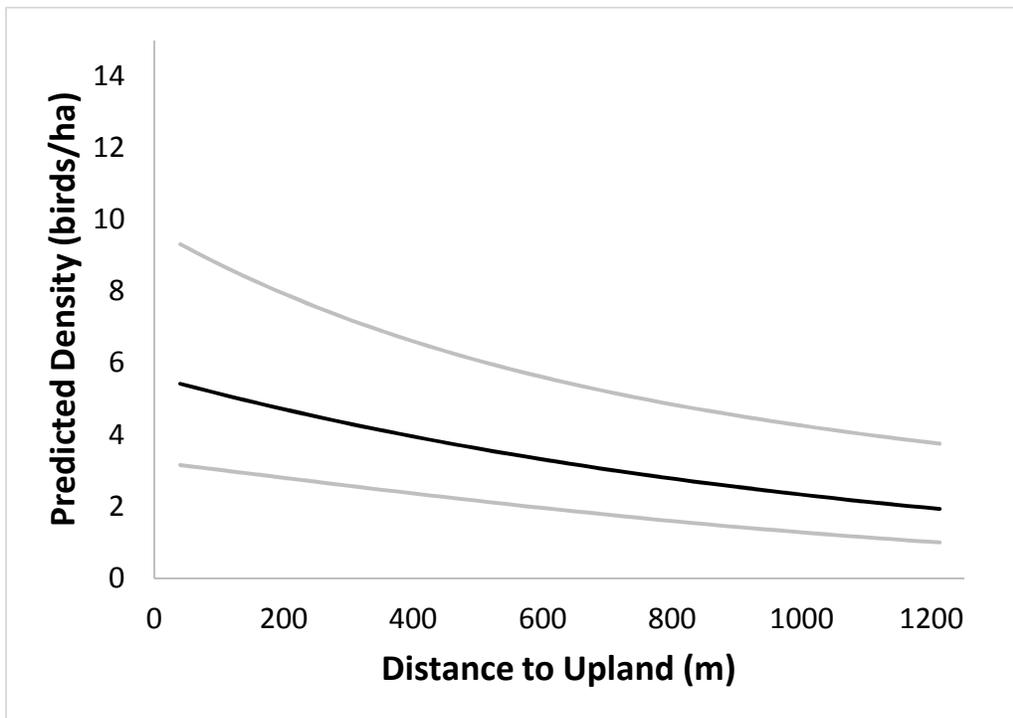


Figure 2.8. Predicted relationship (with 95% confidence intervals) between distance to upland habitat and density of Seaside Sparrows (*Ammodramus maritimus*) across the range of values of survey points. Prediction is based on the top model.

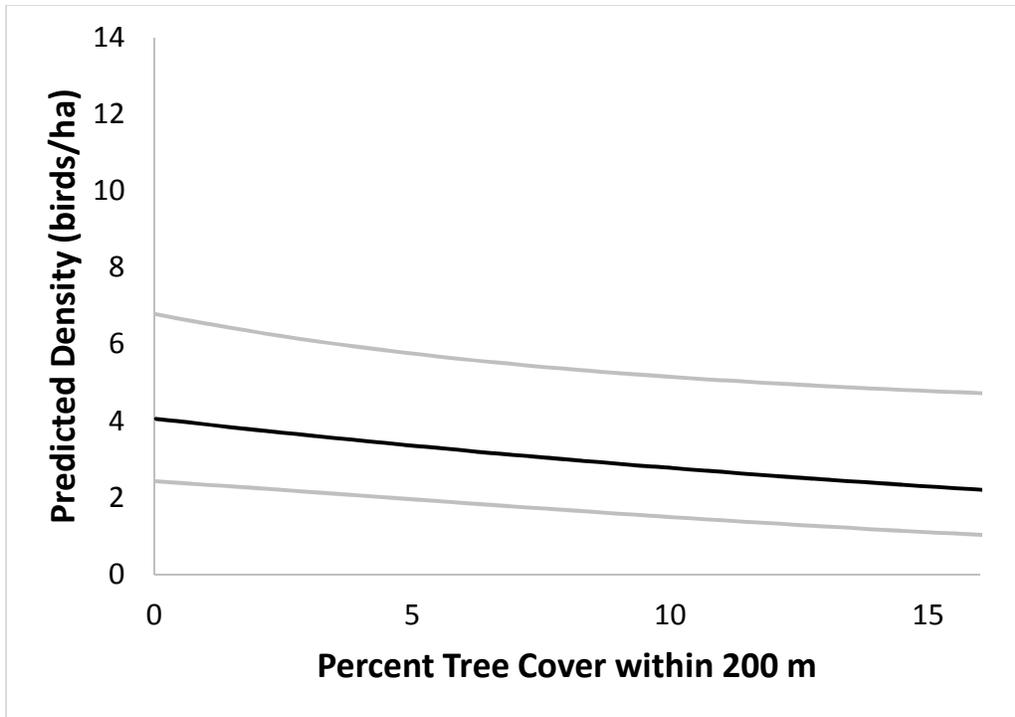


Figure 2.9. Predicted relationship (with 95% confidence intervals) between percent tree coverage within 200 m of a survey point and density of Seaside Sparrows (*Ammodramus maritimus*) across the range of values of survey points. Prediction is based on the top model.

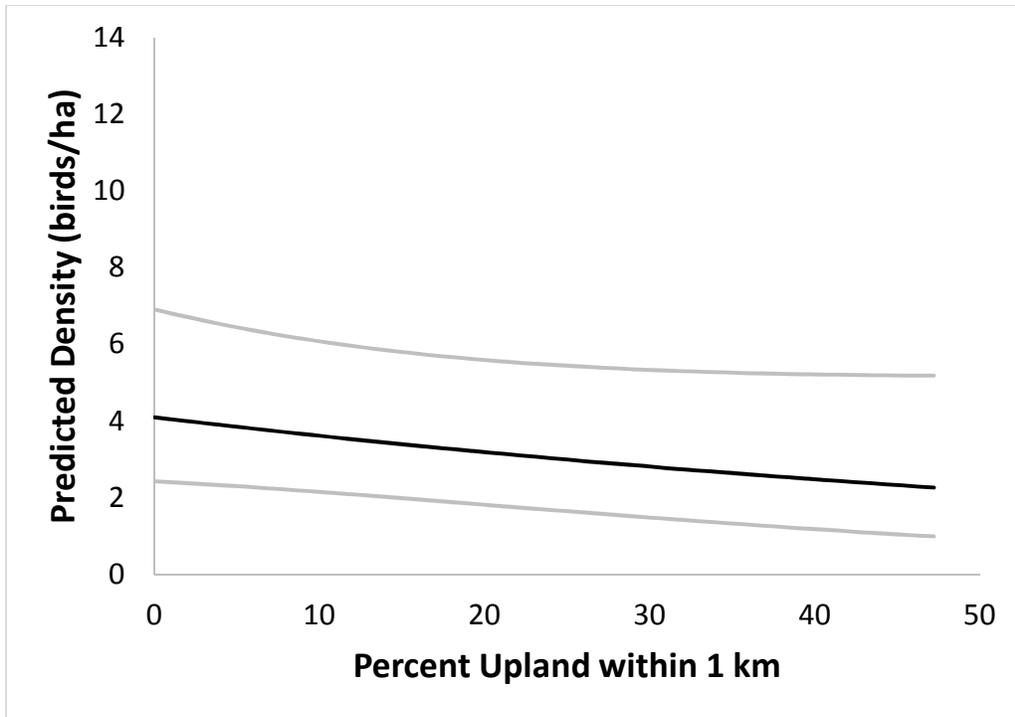


Figure 2.10. Predicted relationship (with 95% confidence intervals) between percent of upland habitat within 1000 m of a survey point and density of Seaside Sparrows (*Ammodramus maritimus*) across the range of values of survey points. Prediction is based on the top model.

Chapter 3

Population Viability Analysis

Population viability analysis (PVA) is a widely-used tool in conservation biology. These analyses allow biologists to assess the current status of a population by predicting its future persistence and identifying current or future threats. While PVAs were initially used primarily to determine the minimum size needed to sustain a population of a threatened or endangered species, they are now used more widely to predict the future status of populations or groups of populations of species of concern. Population viability analyses can also be used to discover which demographic parameters (e.g. reproductive rate, female mortality) a population is particularly sensitive to, which can then be used to guide future research or management efforts.

While SESP populations are generally estimated to be stable through most of their range (Society 2007), future uncertainties and threats to their coastal habitat make further persistence uncertain. With sufficient demographic information, individually-based PVA models can be run to predict the impact of future habitat loss or stochastic environmental events. In individually-based models, discrete animals are born, survive, reproduce, and die according to probabilities and associated standard deviations input by users. The fate of each individual is followed and the size of the entire population is tracked on an annual basis. Users can specify what qualifies as “extinction” for a simulation – generally either when one sex is completely extinct or when the population falls below a pre-determined threshold.

Because there is limited information on SESP in the Gulf, we sought to determine what factors influenced population viability of SESP in our system. Using demographic factors gleaned from this study, as well as published values from other SESP populations, we assessed

the population viability of SESP under a number of scenarios. In addition to assessing population viability, we also conducted sensitivity analyses to see which factors had the greatest influence on population viability and simulated catastrophes to see how SESP may respond to environmental events of increasing frequency and severity.

METHODS

We used program Vortex v. 9.99 (Lacy et al. 2005) to run an individually-based PVA for SESP at the Grand Bay NERR. Program Vortex follows the fate of individuals over time using demographic parameters provided by the user and models the fate of the overall population over a set number of years. The program also allows for the inclusion of stochastic environmental events, with a frequency and severity provided by the user. We defined quasi-extinction as a population size decrease of an order of magnitude over a 100-year period.

Most of the input values were calculated from our own data. For the parameters for which we did not have data, we used values taken from published literature. See Table 3.1 for a complete summary of initial input values.

After running an initial PVA with our calculated demographic values, we performed sensitivity analyses on different model inputs. This allowed us to see which parameters had the greatest effect on the probability of population persistence, which can provide useful information on where to focus future research and perhaps where to focus management efforts.

Using a combination of demographic parameters that allowed for a high probability of population persistence, we then introduced catastrophes in the population to predict the population-level effect of stochastic environmental events of varying frequency and severity. In program Vortex, severity of an event can be represented as the effect on both survival and

reproduction of individuals. We experimented with varying both to simulate events that occurred outside of the breeding season, such as strong hurricanes, and those that may occur during the breeding season, such as storm-induced high tides that may cause flooding-induced nest failures. Finally, we simulated potential future marsh loss due to sea-level rise by including an annual decrease in carrying capacity, representing a loss in marsh area. We modeled a loss of 0.1% to 1% per year over the 100-year simulation period.

RESULTS

Using our initial input values, our simulated population had a 100% probability of extinction over only 15 years. We did not believe this to be true, so we examined the effect of varying the two parameters that we were least confident about: juvenile survival (survival from hatch year – age 1), about which we had no information from our population, and adult female survival. We found that the probability of extinction was extremely sensitive to both of these parameters. Simply setting female survival equal to male survival while leaving juvenile survival unchanged was not enough to make the population viable. When female survival was equal to male survival, in order to reach a 95% probability of persistence over 100 years, juvenile survival had to increase to 0.21. Female passerine survival is generally lower than male survival (Tower and Arbeitman 2009) so we examined how juvenile survival would have to increase as female survival dropped in order to maintain a viable population (Fig. 3.1).

Further sensitivity analyses suggested that if female and juvenile survival were high enough, population persistence was not sensitive to variation in other demographic parameters. For example, if female survival was equal to male survival (79%) and juvenile survival was relatively high (30%), then varying average progeny from 2 to 4 while holding all other factors

constant had no effect on population persistence. However, when female and juvenile survival were both slightly lower (70% and 26%, respectively), varying clutch size over the same range caused the probability of persistence to vary from 0 to 1, with any value below the current estimate leading to a less than 95% probability of persistence.

When we introduced a catastrophe into the simulation, the effect of the catastrophe on survival had a very strong influence on population persistence, while both the effect on reproduction and the frequency of the catastrophe had a much lesser influence (Fig. 3.2). If a catastrophe reduced survival to 80% of the baseline level and occurred on average every ten years, the population had a 25% probability of extinction. To achieve a similar level of extinction risk, a catastrophe would have to reduce annual reproduction to 35% of the baseline level.

A gradual decrease in carrying capacity by itself did not seem to increase the extinction risk of the population unless the rate was fast enough to reduce the carrying capacity below 500 individuals, our threshold for extinction.

DISCUSSION

Rather than providing concrete estimates of extinction probability for our study population, we believe that the results of this preliminary PVA highlight the areas where robust data are still lacking. Individual survival of both adults and juveniles had a stronger effect on population persistence than measures of individual productivity. Adult survival is very high during the breeding season, suggesting that the majority of mortalities occur during the non-breeding season. However, there is a complete lack of data on Seaside Sparrow movement and activity during the fall and winter months. While Gulf Coast SESP are presumably non-migratory, attempts at winter surveys suggest that birds likely move around and may use

different areas of the marsh than are used during the breeding season. A better understanding of habitat use and survival during the non-breeding season will make future PVAs more precise and reliable.

Population persistence was also very sensitive to juvenile survival (defined as survival from hatch year to the following breeding season). When we used juvenile survival estimates from both Atlantic coast and *A. m. mirabilis* populations, our population failed to persist. Most juvenile mortality among passerine species occurs within a short time post-fledging (Sullivan 1989). Therefore, research focused on following juveniles immediately post-fledging could provide valuable survival information to input into future models.

The strong effect of catastrophe severity, measured as the effect of the catastrophe on survival, also highlights a data gap. While catastrophe frequency can be easily measured or predicted, there is much less information on how a catastrophe, such as a hurricane, affects the survival of resident marsh birds. This information would be very difficult to estimate directly, as birds may simply leave the area during a strong storm and may not return to the same location. Long-term monitoring through point-count surveys (or area counts during the non-breeding season; (Roberts and Schnell 2006) could provide estimates of population-level effects of strong storm events and the effect on individual survival could be estimated from those data.

The results of our catastrophe simulations highlight that, in a relatively long-lived songbird such as SESP, factors that affect survival of both individuals and adults have a stronger impact on population persistence than factors affecting reproduction, especially if reproduction is only depressed some years. Long-term reduction in reproductive rates has a strong effect on population persistence, although factors that permanently reduce reproductive output are also likely to reduce survival.

Population viability analyses become more accurate with more reliable data, especially with more accurate estimates of annual variability. While we are confident in the quality of most of the data that we entered into the model, it is only based on two years of field data. Continued demographic monitoring of SESP populations, on a larger scale, will provide continually improved data to input into future PVAs. We believe that a refined ability to predict future population status in the face of a changing environment justifies investment in long-term population monitoring efforts.

TABLES AND FIGURES

Table 3.1. Initial parameters values input into Vortex 9.99 population viability analysis model, along with data source.

Parameter	Value	EV	Source	
# of years	100			
Extinction definition	N < 500			
Age of 1st offspring-females	1		BNA*	
Age of 1st offspring-males	1		BNA	
Max Repro Age	8		BNA	
Max Broods/year	3		data	
Max Progeny per brood	5		data	
Sex ratio	1/1		BNA	
% females breeding	100	0		
Number of broods distribution:				
	0	35	data	
	1	50	data	
	2	14	data	
	3	1	data	
Brood size distribution:				
	1	1.3	data	
	2	6.5	data	
	3	51.4	data	
	4	40.3	data	
	5	0.5	data	
Mortality rates:				
	F 0-1	85	10	BNA (mirabilis)
	F >1	54	9.6	data
	M 0-1	85	10	BNA (mirabilis)
	M >1	21	8.4	data
% males breeding	75			
initial pop size	5100		data (average density * marsh size)	
carrying capacity	17000	500	data (maximum density * marsh size)	
future change in K	none			

*BNA = Birds of North America species account (Post and Greenlaw 2009)

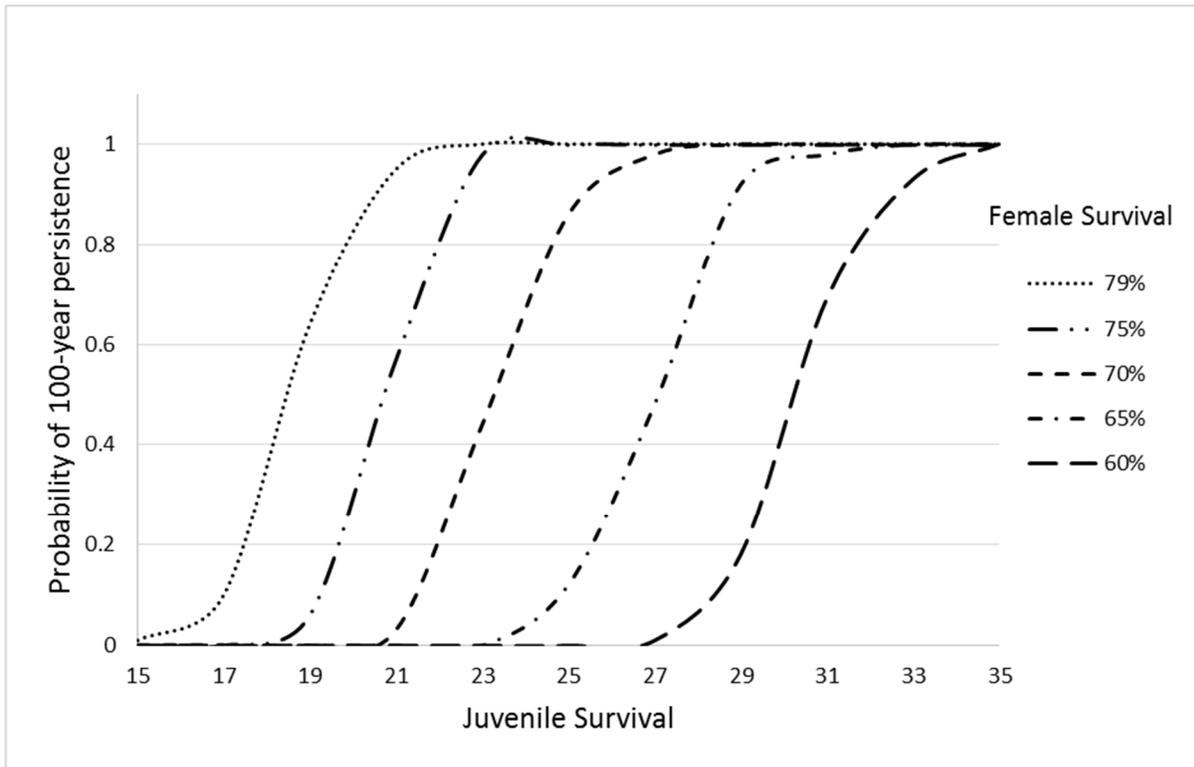


Figure 3.1. The combined effects of varying rates of female and juvenile survival on 100-year population persistence.

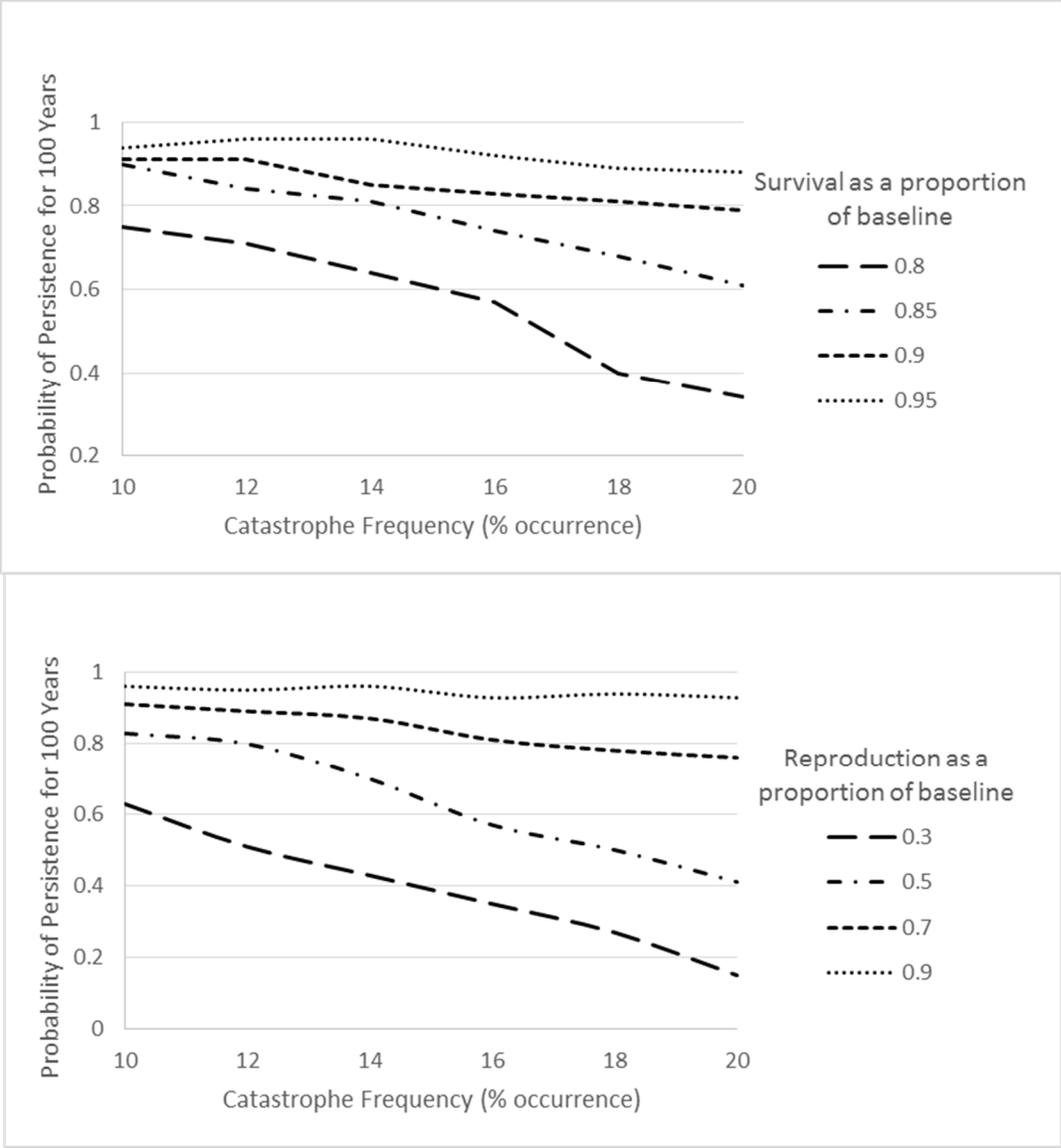


Figure 3.2. Combined effect of catastrophe frequency and severity (measured by effect on survival, top, and reproduction, bottom) on 100-year population persistence.

Chapter 4

Conclusions and Recommendations

Our habitat quality results highlight the importance of using locally-collected data to inform habitat or species management plans. While SESP along the Atlantic coast preferentially nest in smooth cordgrass, in our study area *Juncus roemerianus* and *Spartina patens* were the species predominately used for nest sites. Further, the low-elevation areas preferred by smooth cordgrass had lower SESP density than higher elevation areas with different dominant plant species. If only information from Atlantic coast SESP were considered, managers may incorrectly target areas dominated by smooth cordgrass as preferential SESP habitat. Likewise, the positive relationship inferred between SESP and salinity from surveys at a regional scale may not hold at a more local level and may in fact be contradictory. However, it must be noted that across the Gulf coast, dominant plant communities vary and management may need to be considered and planned for at much smaller scales. Detailed land-cover maps such as that available for the GBNERR are not available for most areas; therefore, we believe that development of such GIS data should be a priority.

We also recommend moving away from using territory size as the basis of calculations for total habitat required. At many of our sites, SESP do not hold well-defined territories and have an activity space much larger than their core use area. We suggest that using density estimates derived from point-counts may be a more suitable metric. Rather than assuming constant densities across the Gulf, we would suggest that point-counts be instituted across a broad range of marshes so that management recommendations can be tailored to individual states or counties.

The conclusions drawn from this research suggest that, at our study sites, SESP may be strong indicators for the presence of healthy intermediate, irregularly flooded marsh. These areas are generally safe from flooding-induced nest failure and also provide suitable nesting substrate. Higher detected densities of SESP may indicate a threshold elevation or the presence of a specific plant community, and bird surveys are likely easier and cheaper to carry out than intensive elevation or vegetation surveys. Similar habitat-density models should be developed across a wider range of marshes along the Gulf coast to look for broad similarities or areas of strong difference.

Continued monitoring of SESP populations in a variety of marsh types could provide more clarity on landscape-level habitat associations. A specific focus on predator identity and density could help increase understanding of the relationship between SESP and upland habitat and how these relationships could be affected by SLR. Seaside Sparrows may exhibit different habitat relationships among marshes and individual marshes may have differing management needs. It is critical that managers consider the individual system in which they are working rather than assuming that broad-scale habitat relations apply to all marshes equally.

We also recommend that demographic studies be continued and/or initiated throughout Gulf coast marshes. The results of our preliminary population viability analysis suggests that any conclusions or recommendations drawn from these analyses are likely to be misleading without the inclusion of accurate survival data. While we are confident in our estimates of male survival, more focused and intensive field work would be needed to accurately predict female and juvenile survival. Once the models are supplied with more robust, we believe that they will be a useful tool for estimating future population response to both predictable and stochastic environmental events as well as potential changes in demographic rates.

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