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DEMOGRAPHIC AND BEHAVIORAL CHARACTERISTICS OF WINTERING SPARROW POPULATIONS IN A SOUTH CAROLINA SALT MARSH

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DEMOGRAPHIC AND BEHAVIORAL CHARACTERISTICS OF WINTERING SPARROW POPULATIONS IN A SOUTH CAROLINA SALT MARSH

A DISSERTATION APPROVED FOR THE

SCHOOL OF BIOLOGICAL SCIENCES

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ABSTRACT

Throughout the world, coastal communities both human and natural face the existential threat of rapidly rising seawater levels resulting from global climate change. Since 2012, my collaborators and I have been monitoring a community of sparrows that overwinter within the extensive salt marshes of Kiawah Island in South Carolina, USA. The three species that comprise this community of "marsh sparrows" are Seaside Sparrow (*Ammospiza maritima*), Saltmarsh Sparrow (*Ammospiza caudacuta*), and Nelson's Sparrow (*Ammospiza nelsoni*), and they can all be readily captured during above-average high-tides during which they are forced to occupy a few salt marsh patches that remain above water. This dissertation documents long-term banding efforts, field experiments, and GIS analyses to assess the current status of the Kiawah Island marsh sparrows, their capacity to cope with environmental changes, and ultimately their prospects for survival over the next 75 years. The three chapters of this dissertation take on each of these subjects in turn.

In Chapter One, I compiled eight years of bird-banding data and used open-population capture-recapture models to estimate annual survival and wintering abundance of the three "marsh sparrow" populations. I employed three different population modeling approaches that included both classical mark-recapture analyses as well as a relatively new spatial modeling approach. To determine which model was best, I simulated bird populations on Kiawah Island as well as the sampling regime (*i.e.*, banding efforts) to see which modeling approach yielded results that best reflected the input parameters for the simulation. Annual survival for all three species generally ranged from 0.5 to 0.8 across all years of the study. Density/abundance estimates indicated that as many as 1,848 marsh sparrows occupy the ~1,650 hectares of salt marsh surrounding Kiawah Island. Although the capture and banding efforts did not fully

conform to the expectations of a mark-recapture analysis, my simulation efforts indicated that a classical Cormack-Jolly-Seber model provided the most accurate estimates of annual survival.

In Chapter Two, we used radio surveillance methods and translocation experiments to study the movement abilities and site fidelity of Nelson's, Saltmarsh, and Seaside Sparrows. The vast majority of translocated birds returned successfully to their initial capture sites (presumed winter home range area), and they generally did so within a few days, regardless of whether they were displaced across fragmented or continuous marsh landscapes. We found no clear evidence that return success differed among species or between landscape treatment (continuous marsh vs. fragmented marsh). Return times did not appear to be significantly influenced by species, landscape treatment, or translocation distance. The high rate and speed of returns following displacement indicates a strong fidelity in marsh sparrows to wintering home ranges and associated high-tide roost sites.

In Chapter Three, we evaluated losses of wintering habitat for marsh sparrows at Kiawah Island under future sea-level rise (SLR) scenarios. We specified four different SLR scenarios in our local models and found that even the most moderate predictions for SLR entailed dramatic losses of salt marsh habitat on Kiawah Island. For the more severe SLR scenarios, our models predicted that Kiawah would not likely sustain overwintering marsh sparrows by the year 2075.

CHAPTER ONE

Annual survival rates and abundances of wintering songbirds in a South Carolina tidal marsh

Keywords:

animal survival; mark-recapture; demography; density; saltmarsh; winter; passerine

Abstract

Studying free-living birds in marsh habitats entails logistic challenges that can limit the application of standard mark-recapture methods for estimating parameters like survival rates and density. We captured and banded three species of marsh sparrows (Seaside Sparrow [*Ammospiza maritima*], Saltmarsh Sparrow [*Ammospiza caudacuta*], and Nelson's Sparrow [*Ammospiza nelsoni*]) over eight consecutive winters in the marsh surrounding Kiawah Island in South Carolina. To capture substantial numbers of birds, our capture efforts coincided with extreme high-tide events, wherein the birds would congregate on a few patches of marsh that remained above water. We applied a traditional mark-recapture analysis to our data, but because of inconsistency in capture effort across the various high tide refugia, we had to subset our data to include only 5 of our 18 capture locations. To make use of the full data set we also applied a newly developed spatially explicit population modeling approach, that allowed for inconsistency in capture effort. Annual survival for all three species generally ranged from 0.5 to 0.8 across all years of the study, and the estimates from the spatially explicit model were mostly higher than

those from the traditional model. Density/abundance estimates indicated that as many as 1848 marsh sparrows occupy the ~1,650 hectares of marsh surrounding Kiawah Island, and this estimate from the spatially explicit model was about twice as high as that of the traditional model. Our study of marsh sparrows is just one of many that is problematic due to conflicts among population-model assumptions and the realities of data collection, and we recommend further development of modeling techniques that can accommodate unusual data-collection scenarios.

Introduction

Research on birds and many other taxa has historically been biased toward the breeding phase of the life cycle while studies of other life history phases (e.g. post-breeding, wintering, migration) have lagged behind (Faaborg et al. 2010). For many species, this bias makes it difficult to assess populations and/or render effective management strategies because factors like non-breeding survival and the potential for carryover effects across seasons are unknown. Calls to investigate full-life histories (Marra et al. 2015) have challenged biologists to shift their research priorities and resources to address knowledge gaps due to biased research foci (e.g., Faaborg et al. 2010, Sherry and Holmes 1995, Marra et al. 1998). To meet this challenge, it is not only necessary to collect data during non-breeding phases of a species' annual cycle, but we must also develop new approaches, both methodological and analytical, to allow us to effectively survey and analyze populations that have shifted from breeding to non-breeding activities.

Estimation of the long-term survival and abundance of bird populations is often accomplished via capture-mark-recapture studies, wherein birds are regularly caught and marked across several seasons, and the rates at which marked birds are recaptured serves as an indication

of detection probability. With detection probabilities established, it is possible to use capture information to estimate basic population parameters such as density and survival. For traditional mark-recapture methods, a robust analysis demands that field data be collected according to a rigorous schedule with regular capture episodes that are equivalent in terms of effort across time intervals. Unfortunately, for many species it is impossible to establish a regimented schedule of capture effort. To address this issue, Efford and Schofield (2020) have derived a spatially explicit population modeling approach that relaxes some of the requirements of traditional mark recapture analysis. This method was initially developed for studies of rodents that involved repeated live-trapping efforts. In this study we attempt, for the first time, to apply this general framework to birds captured on their wintering grounds with mist nets.

In 2012, we initiated a mark–recapture study of three species of sparrows (collectively referred to as "marsh sparrows") that spend the winter (*i.e.*, non-breeding) season in the tidal marsh that surrounds Kiawah Island in coastal South Carolina. We had discovered that these species could readily be captured during the above-average high tides (aka "spring tides" or "King Tides") that occur twice each lunar month, wherein the entire population congregated at a limited number of refugia, which were unflooded habitat patches within the high marsh zone (i.e., roost sites). These dense aggregations (aka "roosts") allowed us, over the course of a few hours, to capture all or almost all of the birds at a given refugium. However, as the seasons passed it proved impossible to maintain a regular schedule of capture effort at Kiawah Island. We were, in fact, only able to sample 6 sites every season, whereas there were 18 sites that were sampled at least once. Hence, we could only employ traditional mark–recapture methods on a subset of < 50% of the data collected. This situation led us to compare traditional mark-recapture

methods and a more recent spatially explicit method that would allow us to include all of our capture data to estimate survival and abundance.

Our study of marsh sparrows was motivated by the need to monitor annual survival rates of marsh sparrows in light of rising seawater levels and ongoing development on Kiawah Island. Both of these activities have the potential to reduce the availability of coastal salt marsh habitat, and the residents of Kiawah Island have a commitment to conservation that includes ensuring the survival of marsh sparrows (Selinger 2021). In addition to examining trends in survival and abundance across winter seasons, the study sought to reveal connections among environmental variables (e.g., severe weather and freezing temperatures) and the survival of each species. We also wanted to better understand the wintering behavior of marsh sparrows including their propensity for high site fidelity across years and how this attachment to specific sites affects survival. Ultimately, we sought information to help us forecast how these species may respond to future changes in their wintering landscape.

The marsh sparrow species we studied were the Seaside Sparrow (*Ammospiza maritima*), the Saltmarsh Sparrow (*Ammospiza caudacuta*), and Nelson's Sparrow (*Ammospiza nelsoni*). They are closely related species (Klicka et al. 2014) that overwinter in salt marshes almost exclusively along the U.S. Atlantic and Gulf Coasts (Greenlaw and Woolfenden 2007, Watts and Smith 2015). Where their wintering ranges overlap, all three sparrows often occur together in loose mixed flocks while foraging throughout the low marsh and while seeking refuge during high tides that flood the low marsh twice a day. Seaside and Saltmarsh Sparrows are habitat specialists restricted to tidal marshes throughout their annual cycle (Greenberg et al. 2006); the former breeds from Texas to southern Maine and includes migratory and non-migratory subspecies (Woltmann et al. 2014, Roeder et al. 2021, Greenlaw et al. 2022). The Saltmarsh

Sparrow is a short- to medium-distance migrant that breeds from northeastern Virginia to southern Maine (Greenlaw et al. 2020). Nelson's sparrow is a medium-distance migrant that breeds in three geographically distinct regions spanning from the northern Great Plains of central Canada to the Maritime Provinces of Canada and northeastern coast of the U.S. (Shriver et al. 2020). Across its breeding range, Nelson's Sparrow uses a variety of wet and dry habitats, including freshwater marshes, wet meadows, coastal salt marshes, and even mesic hayfields (Dechant et al. 2002, Nocera et al. 2007, Shriver et al. 2010). As foraging habitat within the low marsh zone becomes flooded with the regular influx of high tides, all three species move to elevated areas of high marsh until the tide recedes and low marsh is uncovered. The relative abundance and diversity of marsh sparrows encountered at roost sites varies at the regional or local scale (Shaw 2012, Trinkle 2013). Individual marsh sparrows show strong fidelity to roost sites across years and are rarely observed using other roost sites even within a winter season (Michaelis 2009, Winder et al. 2012, Shaw 2012, Trinkle 2013).

To our knowledge, our analyses are the first to apply Efford and Schofield's (2020) spatially explicit capture-recapture model to birds. In so doing, we explore a situation that pertains to a large number of capture-recapture studies (e.g., Doherty Jr. and Grubb Jr. 2002, Johnston et al. 2016, Ruiz-Gutierrez et al. 2016), which is the tradeoff between omitting data to meet the assumptions of a traditional capture-recapture model *vs*. using a model that allows for more data inclusion at the cost of increased sophistication and less generalizable conclusions (*i.e.,* conclusions are more site-specific). Moreover, our results provide much needed estimates of survival and abundance for species that are challenged by a human-altered environment that is experiencing reduction and fragmentation of their natural wintering habitat.

Methods

Study area and capture methods

The project took place within the tidal salt marsh habitat surrounding Kiawah Island (32°36’43.64” N, 80°4'27.51"W) (Fig. 1). Kiawah Island is a ~4,047 ha developed barrier island located approximately 24 miles south of Charleston, South Carolina, USA. The island stretches 16 km in a southwest to northeast orientation, with a width of ~ 2.4 km at its widest point. As a private residential community and luxury beach resort destination, Kiawah Island supports a human population that ranges from ~1,4000 people in the winter to upwards of 10,000 people per day in the summer. Much of the island’s artificial habitat, including golf courses, hotels, roads, and residences, is concentrated within its relatively flat upland areas and interior. Kiawah also contains some 15 different natural habitat types across its terrestrial and aquatic environments, including ocean beach, maritime forest, salt shrub thicket, tidal mudflats, hammock islands, and tidal saltmarsh.

We actively captured marsh sparrows within Kiawah Island’s tidal saltmarsh during eight consecutive non-breeding winters from January 2013 through March 2020. Although we sampled in October, November, December, April, and May of some years, the core of our sampling effort took place from January through March. Sampling occasions took place during daylight hours between sunrise and mid-afternoon (local time) and were scheduled to coincide with above-average high-tides produced by “spring tides” which occur twice a month and coincide with full or new moons when the Moon is closest to Earth. Sampling during these high-water periods allowed us to exploit the fact that the birds are forced to congregate for several hours in relatively small patches of high marsh that are not inundated. Outside the time windows of these spring tides, marsh sparrows are extremely difficult to capture because they can disperse

throughout vast areas of low marsh that are difficult for us to access and maneuver in. Although the frequency and duration of suitable spring tides greatly limited the number of capture opportunities each winter, our capture method maximized catchability and optimized efficiency. Once the low marsh was flooded and birds were settled in their high tide roosting sites, we actively funneled birds toward one to three mist nets placed strategically at one end of the roost site. For larger roost sites (i.e., > 0.2 ha), we used a rope-dragging method to slowly corral and flush birds toward the nets. This process was generally repeated until it was apparent that we had captured all or almost all of the birds at a given roosting location. Once captured, all individual marsh sparrows were identified to species and banded with a uniquely numbered USGS aluminum leg band. For each banded bird, we collected standard morphometric data, including mass, wing chord, and bill length. Whenever possible, birds were aged by plumage or "skulling" and identified to subspecies level based on culmen length and plumage (Pyle 1997, Smith 2011). Across the entire study period we captured birds at 18 unique roost sites. However, due to a number of logistical factors, including site accessibility, availability of personnel, weather, and the timing of spring tides, the sampling effort at each roost varied within and across winter seasons. Hence, the number of roosts sampled within a given winter ranged from 11 to 17, and only 6 of the 18 sites were sampled every winter of the study. Individual roost sites were sampled up to 4 times in a single winter. The number of visits to each site was limited both by logistical constraints as described above and by the need to minimize our impact on the vegetation structure and microhabitats in each roost site.

Methods for estimating survival

Because of inconsistency in the capture sites sampled across years, we could not meet the assumptions of traditional capture-recapture models (e.g., Cormack-Jolly-Seber Models) without omitting large quantities of data from sites that were not sampled in the same manner across years. Newer methods for estimating population parameters allow for inconsistent sampling by employing spatial data to integrate the potential for animal movement into estimates of survival. Their application has been limited to studies of mammals, and there is no precedent for applying them to animals that undergo periodic congregations similar to what we see with marsh sparrows. Therefore, we decided to apply three open-population mark-recapture methods (Table 1) that encompass both traditional and more advanced approaches (i.e., omitting data to meet assumptions and including data in untested analytical methods). All three analyses shared the goal of estimating apparent annual survival probabilities of each marsh sparrow species. Methods 1 and 2 both employed Cormack-Jolly-Seber (hereafter "CJS") models, and method 3 is a spatial analog of the Pradel-Link-Barker model developed by Efford and Schofield (2020). For each method, we used capture histories composed of eight primary capture-mark-recapture periods ("primary sampling occasions").

For method 1, we defined the primary sampling occasion as a three-month period from January through March, and for methods 2 and 3, the primary sampling occasion was composed of a five-month period (November – March) spanning two calendar years. For methods 1 and 2, we pooled banding data from roost locations that were sampled at least once in each of the eight primary sampling occasions. This filtering left us with sufficient data to include only five sites using method 1 and six sites using method 2.

We established four environmental covariates that we reasoned may be related to marsh sparrow survival in a given year (Table 2). These covariates were 1) winter precipitation (total rainfall for November to March; 2) number of freezing days (average temperature of 0° C or less) from November to March; 3) occurrence of one or more winter storms that produced ice or snow (coded as a binary); and 4) occurrence of a flood (coded as a binary). These covariates were chosen based on past research demonstrating the effects of temperature and severe weather on migratory songbirds (e.g., Dugger et al. 2004, Salewski et al. 2013, Wellicome et al. 2014, Rockwell et al. 2017, Woodworth et al. 2017, Hill et al. 2019). We specified constant detectability across all models because sampling effort was consistent across all years. Our sampling method entailed capturing all or nearly all birds at each roost site in each capture session; hence, we had no reason to suspect that detectability varied across years.

Methods 1 and 2 – We compiled data from 2012 – 2020 to generate capture histories from every individual. Each capture history was encoded as a sequence of 1s and 0s that corresponded to whether an individual was captured in each sampling period (season) or not. Repeated captures of an individual in the same season were disregarded. For method 1, we generated capture histories from banding data collected only during the months of January, February, and March for each winter from 2013 to 2020 at five different capture sites. For method 2, we expanded the scope of our analyses to include individuals captured during a five month period from November – March that spanned two calendar years, and there were six capture sites included in the analysis.

We fitted Cormack-Jolly-Seber (CJS) models within Program MARK (White and Burnham 1999) via the RMark package (Laake 2013) in program R 4.2.0 (R Core Team 2022) to estimate annual survival probabilities for Nelson's, Saltmarsh, and Seaside Sparrows. We ran six

models for both method 1 and method 2 wherein survival was allowed to vary with one of the five covariates described above and listed in Table 2. In all analyses, we fit a CJS model to the data sets using the sine-link function. Survival estimates from each model were derived. The R code used for these analyses is posted on the Open Science Framework at https://doi.org/10.17605/OSF.IO/2T94F.

We assessed goodness-of-fit and overdispersion using the Fletcher c-hat parameter calculated by Program MARK for the most parameterized model in each species' model set. When Fletcher c-hat < 1.2, we used AIC_c to rank models from best to worst. When Fletcher c-hat > 1.2 (indicating overdispersion), we corrected for overdispersion on the basis of an adjusted c-hat, and for model comparison we used the quasi-likelihood modified Akaike's information criterion corrected for small sample sizes ($QAIC_c$). Finally, we retained all models for which ΔAIC_c (or $\Delta QAIC_c$) was < 2 and used them to estimate population parameters via model averaging.

Method 3 – We employed spatial Pradel-Link-Barker open-population capture-recapture models (hereafter "open SCR") (Efford & Schofield 2020) using the full data set, including all capture efforts as well as repeated captures of individuals within a winter, to estimate annual survival for each species. This analysis allowed us to incorporate 18 capture sites into the analysis as opposed to five or six, and we were able to include 100–120% more individuals (Table 1). Each species' capture-recapture dataset consisted of data collected during 119 secondary trapping sessions across 8 primary trapping sessions. Secondary sessions corresponded to unique sampling dates between 1 November and 31 March within each of the 8 winter periods (primary sessions). In contrast to methods 1 and 2, capture histories constructed for method 3 included multiple recaptures of the same individual within a winter. Locations

(longitude and latitude) and sampling effort (i.e., number of secondary trapping sessions) for each capture site (roost) were encoded separately into a 'detector layout' file which was combined with the species-specific capture data file to create the final input file. Finally, we incorporated a binary habitat mask that specified whether land cover within the study area was salt marsh or not. The habitat mask was generated from land cover data produced by NOAA Coastal Change Analysis Program (C-CAP). We downloaded the most recent (i.e., 2016) C-CAP data available for our study region (https://coast.noaa.gov/digitalcoast/) and reclassified the land cover types of the raster into two land cover categories representing salt marsh and non-salt marsh habitat. This raster layer was then converted to spatial polygons, from which we isolated salt marsh habitat within the larger geographic area of the study site. We verified the accuracy of data from the newly reclassified land cover map using recent high resolution aerial photographs of the study area captured in 2018 for the Town of Kiawah Island and satellite imagery of Google Earth Pro. All geospatial analysis was performed with Quantum GIS (QGIS) version 3.16.15 (QGIS Development Team, 2022), and R code and associated files are available at https://doi.org/10.17605/OSF.IO/2T94F.

As with methods 1 and 2, we fitted five separate models with differing predictors of survival corresponding to the variables in Table 2, plus one constant survival model. For all six open SCR models, we specified that the detection function intercept (lambda0, λ_0), detection function scale (sigma, σ), and population growth rate (lambda, λ) should be kept constant across models. Hence, only the survival parameter was allowed to vary, whether randomly by year or as function of one of the four environmental covariates. We again used Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002) to rank the six models, and we discarded any models with more than one unidentifiable parameter. We retained

all models for which ΔAIC_c was < 2 and used these models to estimate parameters via model averaging. Model fitting and selection of open SCR models was performed in R using the 'openCR' package (Efford 2022).

Estimating abundance

In addition to estimating survival, we sought estimates of each species' wintering abundance at Kiawah Island. To estimate abundance, we used the spatially explicit JSSAsecrD model in the openCR package for R (Efford 2022) because we wanted direct estimates of time-specific population density (animals per hectare), and this spatial modeling approach allows for open populations as well as multiple recaptures within and across primary sessions (i.e., winter seasons). The alternative, closed-population, approach was not workable because captures that occur across sessions would violate assumptions of independence (Efford and Schofield 2020). We constructed capture data and detector layout data files for each species following the same formatting described above in method 3. We also used the same habitat mask created for fitting the spatial models in method 3.

For each species, we fit two simple JSSAsecrD models: 1) A null model with constant values for the four parameters (φ, $\lambda 0$, σ, and D) across all primary sessions (t), and 2) a model that allowed D to vary among the primary sessions while keeping phi, lambda0, and sigma constant across primary sessions. Models were checked for maximization errors and non-identifiability and then ranked according to AIC_c. We rejected any models with more than one unidentifiable parameter. For each species, the model with the lowest AIC_c and without possible maximization errors was selected as the 'best' model. We present estimates of density from the best-fit model for each species. We also report estimates of species' winter abundance, which we

calculated by multiplying the best model's estimates of density and confidence intervals by the area of available saltmarsh habitat at Kiawah Island (1,648 ha).

Agent-based validation model

To help evaluate the accuracy of survival estimates from the different populations models, we generated a simulation wherein populations of virtual birds were generated and sustained with pre-determined densities and survival rates. These populations were then sampled in a manner that corresponded to the real-world bird-banding effort that gave rise to our dataset. The birds in the virtual populations were distributed among several "zones," that corresponded to the areas surrounding each of our 18 real-world capture sites. For each zone we stipulated a catchment area that corresponded to our best estimate of the extent of the marsh used by the birds linked to a particular high-tide refuge (capture site). The catchment area of each zone was estimated in hectares which ultimately translated into a proportion of a total of 1650 ha of habitat. Each zone also had spatial coordinates that matched the latitude and longitude of each corresponding capture site. For each simulation, an initial population of birds was generated based on a given density value (0.4, 0.8, or 1.2 birds per hectare) and 1650 ha of marsh habitat. The three different density values were chosen to represent the approximate average species' densities estimated for Nelson's, Saltmarsh, and Seaside Sparrows based on the results of our spatially explicit JSSAsecrD models (see above). Each of the virtual birds within the simulated population was apportioned to one of the 18 zones (i.e., capture sites) or was regarded as outside any of the zones according to the size of each catchment area and the remainder of the marsh that was not contained within a zone. This initial population was then projected forward in time with a number of randomly chosen individuals removed each year as determined by a yearly survival

rate. We set survival rates for the first 7 years to 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8. Because the survival rate for year 7 represents the last time interval for which survival can be estimated, we decided to keep the survival rate for year 8 equal to 0.8. Virtual birds were also rearranged among zones (and the area outside the zones) each year as determined by random draws from survivors and a user-defined, year-to-year probability of movement rate, which we set equal to 0.02. For birds selected for movement, their destination was determined by the probability of movement value (0.2), the catchment area of the zone (which was set to 20 ha for each of the 18 zones), and the proximity of other zones.

After simulating a population over the course of 8 years, we simulated banding efforts that corresponded to the dates and locations of the real banding efforts. Each banding effort sampled birds in the zone that corresponded to the capture site, and the number of birds sampled was determined by multiplying the number of birds in the zone by a user-defined capture-probably value based on our estimation of real capture success. For each virtual bird that was sampled, we assigned it a band number and projected that band number forward in time throughout the population data frame, so that "recaptures" could be recognized. Over the course of each banding season, birds could move among zones (and outside zones) according to a daily movement rate; hence the simulation mimicked real instances in which the same bird was captured at different sites in the same year. The result of each simulation was a full record of a simulated population, with known densities and survival rates, as well as virtual bird-banding data from a sampling regime that emulated our real-world banding as precisely as possible. From the virtual bird-banding datasets, we created capture history files for analysis by our three capture-recapture methods. Capture histories for each analytical method were formatted following the same steps as described above in the methods for estimating survival (e.g., capture

histories for Method 1 were generated from banding data collected at five different capture sites during January, February, and March of each winter from 2013 to 2020). In total, we created 9 capture history files from our simulated population datasets (Table 3).

To compare model performance, we applied the CJS and open SCR model approaches used in Methods 1, 2, and 3 on our virtual bird banding data and compared the resulting population parameters with the known parameters that governed our virtual bird populations. For CJS and open SCR methods, we only fitted one model that allowed survival to vary randomly by year (i.e., Phi ~ t) and kept all other model parameters constant across years. We fitted a total of 9 models, one for each of the 9 capture histories generated from the simulated data. Simulations, data formatting, and models were executed in the R programming environment, the relevant R code and associated files are available at https://doi.org/10.17605/OSF.IO/2T94F.

Results

Across all years 8 seasons we processed a total of 2,965 capture events across 18 captures sites, which comprised capture histories for 414 Nelson's, 285 Saltmarsh, and 1,149 Seaside Sparrows. All of these data were used for Method 3 analyses. For method 1, we used capture histories for 187 Nelson's, 126 Saltmarsh, and 421 Seaside Sparrows associated with 5 capture sites; and for method 2, we used capture histories for 210 Nelson's, 156 Saltmarsh, and 522 Seaside Sparrows from 6 capture sites.

Annual survival estimates

Nelson's Sparrow – Method 1, when applied to Nelson's Sparrow, resulted in four models for which $\Delta AIC_c \leq 2$. These comprised the null model, and the models that included winter

precipitation, flood, and winter storm as covariates, respectively. The model-averaged estimates (± SE) of annual survival ranged from a low of 0.47 ± 0.086 (between seasons 4 and 5) to 0.56 ± 0.18 (between seasons 7 and 8). The degree of AIC_c weight allocated to models with severe weather covariates (0.538) suggests that survival of Nelson's Sparrows is linked to local weather conditions. However, within their respective models, effect sizes (β ± 95% CI) of winter precipitation (-0.027 ± 0.043), flood (1.18 ± 2.62), and winter storm (0.41 ± 1.40) all had 95% confidence intervals that included zero.

Method 2 applied to Nelson's Sparrow resulted in five models that were well supported by the data ($\Delta QAIC_c \leq 2$), all of which provided similar survival estimates. These five models included the null model as well as models that included annual survival as a function of freezing days, flood, winter precipitation, or winter storm. We used model averaging to obtain estimates of annual survival, which ranged from 0.48 ± 0.109 between seasons 6 and 7 to 0.53 ± 0.126 between seasons 7 and 8. As with method 1, annual survival appeared to be greatest between the last two winters (2018/19 - 2019/20). Also, with method 2 there was no clear evidence that the environmental covariates influenced survival as the 95% confidence intervals of their effect sizes overlapped zero: Freezing days (β = -0.09 ± 0.21 95% CI), flood (β = 0.56 ± 1.94 95% CI), winter precipitation (β = -0.01 ± 0.04 95% CI), and winter storm (β = -0.27 ± 1.23 95% CI).

The Nelson's Sparrow data analyzed with method 3 yielded higher survival estimates than did the analyses using methods 1 and 2 but was similar, indicating potential effects of winter weather. The best model included winter precipitation as a covariate, and three other models (winter storm, null, and freezing days) were among those with $\Delta QAIC_c \leq 2$. The model-averaged estimates (±SE) of annual survival ranged from 0.54 ± 0.09 between seasons 4 and 5 to 0.78 ± 0.15 between seasons 6 and 7. Hence, not only were the survival estimates from the

spatial modeling approach higher than those from the CJS models, they also did not vary across seasons in correspondence with CJS estimates (Fig 2). Effect sizes ($\beta \pm$ 95% CI) for winter precipitation, winter storm, and freezing days were -0.04 ± 0.05, 1.53 ± 2.49, and 0.15 ± 0.23, in their respective models.

Saltmarsh Sparrow – The Saltmarsh Sparrow capture histories, when analyzed via method 1, resulted in four models with values of $\Delta AIC_c \leq 2.0$. The best model was the one that included winter precipitation as a covariate, and it was followed in AIC_c weight by the null model, the winter storm model, and the freezing days model. Model-averaged survival estimates (± SE) ranged from 0.51 ± 0.11 between seasons 4 and 5 to 0.73 ± 0.15 between seasons 6 and 7 (Fig. 3). As with Nelson's Sparrow, the summed AIC_c weights from models with weather covariates (0.704) suggested an influence of winter weather on Saltmarsh Sparrow survival. Freezing days (β = 0.163 ± 0.14 SE) and winter storm (β = 1.29 ± 1.28 SE) were positively related while winter precipitation (β = -0.04 ± 0.03 SE) was negatively related to annual survival probabilities, but their 95% confidence intervals overlapped zero (freezing days 95% CI: -0.12, 0.44; winter storm 95% CI: -1.22, 3.79; winter precipitation 95% CI: -0.10, 0.01).

Using Method 2, we found five models were well supported by the Saltmarsh Sparrow data ($\Delta AIC_c \leq 2$), with the null model receiving the most support (AIC_c weight = 0.358). The other four models (cumulative AIC_c weight = 0.632) had nearly equivalent support in the data and included an effect of one environmental covariate (winter storm, flood, freezing days, or winter precipitation) on annual survival probability. Although the cumulative weight of the models with environmental covariates was high, we did not find strong evidence for a relationship between annual survival and any of the environmental covariates ($\beta_{\text{winter storm}}$ = 0.54, 95% CI = -0.84, 1.92; β_{flood} = 0.50, 95% CI = -1.22, 2.22; $\beta_{\text{freezing days}}$ = 0.06, 95% CI = -0.14,

0.27; $\beta_{\text{winter precipitation}}$ = -0.01, 95% CI = -0.05, 0.03). Model-averaged estimates of annual survival rates (±SE) were consistent across years, ranging from 0.56 ± 0.069 between the fourth and fifth winter seasons (2015/16 – 2016/17) to 0.61 ± 0.101 between the sixth and seventh winter seasons (2017/18 – 2018/19) (Fig. 3).

The best-supported model for the Saltmarsh Sparrow data set analyzed using Method 3 was the null model (AIC_c weight = 0.58). The second and third ranked models each included an environmental covariate and both models received an equal amount of support (AIC_c weight of = 0.21). The second ranked model included an effect of freezing days on annual survival probability, while the next best model included an effect of winter storm on annual survival probability. Model-averaged estimates of annual survival probability calculated from the top three ranked models were, overall, slightly higher and less variable across years compared to the estimates from Methods 1 and 2, with survival (± SE) ranging from 0.68 ± 0.07 to 0.71 ± 0.05 (Fig. 3). We did not find strong evidence of a relationship between survival and either of the environmental covariates, as their 95% confidence intervals overlapped zero ($\beta_{\text{freezing days}}$ = –0.04, 95% CI = –0.22, 0.14; $\beta_{\text{winter storm}}$ = –0.24, 95% CI = –1.4, 0.92).

Seaside Sparrow – Method 1 applied to Seaside Sparrow resulted in only one model being retained ($\Delta AIC_c \leq 2$) for survival. This top-ranked model, which included the temporal effect of flood on annual survival, had more than four times the AIC_c weight (0.66) as the second-ranked model (0.15), which allowed survival to vary by winter. Annual survival estimated from the top-ranked model suggested a positive effect of winter flooding (β_{flood} = 1.48 ± 0.93 SE, 95% CI = -0.35, 3.30). This means that survivability was higher in the year following a winter with a flood event (0.84 ± 0.13 SE) compared to the years which followed a winter without any flooding event (0.54 ± 0.03) (Fig. 4).

Using Method 2, we found that only two of our six candidate models received strong support when fitted to the Seaside Sparrow data. The top model (AIC_c weight = 0.46) included the temporal effect of flood on annual survival and had only marginally better support than that of the second-best model, which was the null model (AIC_c weight = 0.35). Because two models were well-supported by the data, we used model averaging to generate estimates of annual survival (Fig. 3). Model-averaged estimates (± SE) of annual survival ranged from 0.46 ± 0.10 to 0.58 ± 0.07 during the first six years (2012/13 – 2018/19) and increased to 0.76 ± 0.12 for yearly interval following the second to last winter (2018/19 – 2019/20) (Fig. 4). Like the results of Method 1, we found some evidence of a positive relationship between winter flooding and Seaside Sparrow survival in the subsequent year (β = 1.00 ± 0.57 SE, 95% CI = -0.11, 2.11). There was also evidence of a negative relationship between the third winter period (2014/2015) and survival in the subsequent year ($\beta_{\phi 3}$ = -1.10 ± 0.42 SE, 95% CI = -1.92, -0.28), but we did not find strong support for an effect of any other winter period on survival as their 95% confidence intervals broadly overlapped zero.

Using Method 3 to analyze the expanded Seaside Sparrow data (n = 1,149), our top ranked model (AIC_c weight = 0.40) included the temporal effect of winter storm on annual survival and had only marginally better support than that of the second best model, which was the null model (AIC_c weight = 0.34). There was some evidence that winter storm was positively related to survival in the subsequent year (β = 0.4 ± 0.28 SE, 95% CI = -0.14, 0.95), with model-averaged estimates (± SE) of survival from the top two models ($\Delta AIC_c \leq 2$) slightly higher in post-winter storm years (0.66 ± 0.05) compared to years following winter periods during which there were no snow or ice storms in the study area compared (0.61 ± 0.03) (Fig. 4).

Density and abundance estimates

Analysis of density using capture histories for each species showed that the model with density varying with winter period received overwhelming support (AIC_c weight = 1.0) compared the null model for all three species. Nelson's Sparrow densities (birds per hectare ± SE) ranged broadly across seasons from 0.11 ± 0.03 in the second winter (2013/14) to 0.79 ± 0.61 in the last winter (2019/20). These density estimates translate to total winter abundances ranging from 181.28 (95% CI = 115.36 – 313.12) to 1,301.92 (95% CI = 1,005.28 – 1,697.44). Overall, the wintering population of Nelson's Sparrow increased steadily in abundance over the study period, with the only declines in abundance occurring between the first and second winter periods (2012/13 – 2013/14) and between the sixth and seventh winter periods (2017/18 – 2018/19) (Fig. 5). The largest change in winter abundance happened between the second and third winters, when Nelson's Sparrow experienced a nearly 264% increase in numbers, from 181.28 (95% CI = 115.36 – 313.12) to 659.2 (95% CI = 477.92 – 906.40) individuals (Fig. 5).

Overall, density estimates were higher for Saltmarsh Sparrow compared to Nelson's Sparrow, with a minimum density (± SE) of 0.52 ± 0.14 in the first winter (2012/13) and a maximum density of 1.46 ± 0.32 in the penultimate winter (2018/19). The wintering population of Saltmarsh Sparrow at Kiawah Island showed a similar trend to that of Nelson's Sparrow, with increasing abundance over the study period. However, Saltmarsh Sparrows evinced a large (~70%) increase in total abundance between the winters of 2017/18 and 2018/19, with a peak abundance estimate of 2,406.08 (95% CI = 1,565.6 – 3,708.0) (Fig. 5).

Seaside Sparrows had the highest density estimates which ranged across seasons from 0.85 ± 0.07 SE in the winter of 2014/15 to 1.68 ± 0.14 SE in the winter of 2018/19. Of our three marsh sparrow species, Seaside Sparrow had the largest estimated winter population sizes at

Kiawah Island. Abundance estimates across seasons ranged from 1,400.08 to 2,768.64. The trend toward increasing abundance across seasons was not as apparent in Seaside Sparrows as it was in the other species, with a lower population estimate in the final season (1,796.32; 95% CI = 1,549.12 – 2,092.96) than in the first season (2,241; 95% CI =1,895.2 – 2,653.28) (Fig. 5). Interestingly, our results suggest that both Seaside and Saltmarsh Sparrows experienced relatively large surges in their estimated winter population sizes at Kiawah from 2016/17 to 2018/19 (55% and 72% increase, respectively) before undergoing sharp declines in their winter population sizes (28% and 35% decrease) between the last two years of the study, from 2018/19 - 2019/20 (Fig. 5).

Population data simulation and model performance

Overall, our three capture-recapture analysis methods performed similarly, producing annual survival values lower than the true values for data sets simulated at three different density levels (Figs. 6, 7, and 8). Although all methods tended to underestimated survival, method 2 generally outperformed the other two methods, but this tendency was not always consistent. For example, for the low population density simulation, method 2 provided accurate estimates for some years (2012/13, 2014/15, 2016/17, 2018/19) but not others (2013/14, 2015/16, 2017/18; Fig. 6). Nevertheless, across all simulations method 2 was the most accurate in 11 of the possible 21 survival estimates, which surpasses both method 1 and 3.

Discussion

Traditional capture-mark-recapture (CMR) analyses for open populations (e.g., Cormack-Jolly-Seber model) are generally conceived for data sets that result from rigorous adherence to a set

schedule of capture episodes wherein capture effort is constant across capture efforts. Such a schedule is the ideal for estimating population parameters like apparent survival, but logistical concerns and the unique behavior of the organisms being studied can often make regular sampling impossible. In our long-term study of marsh sparrows, several factors prevented us from adhering to some of the recommended data collection protocols associated with a CMR analytical framework. In particular, the timing and height of spring high tides dictated the timing of our capture efforts, and as a corollary we could not always muster the personnel required for sampling as the availability of volunteer field assistants varied independently of the tides. Finally, weather conditions and the physical condition and/or accessibility of roost sites also reduced our ability to maintain consistency in our banding efforts.

To meet the assumptions of CJS models, we had to omit more that 50% of the data we collected and consider capture histories only from the 5 or 6 sites that we were able to sample every season. Data from 12 or 13 other sites that were not regularly sampled did not contribute to analyses via method 1 or method 2. Our use of a spatially explicit capture-recapture modeling approach (Efford and Schofield 2020) allowed us to incorporate our entire data set into estimating survival and abundance. It is important to note that our study was not inherently designed for spatially explicit capture-recapture analysis. Nevertheless, our data, like that collected in many capture-mark-recapture studies, are inherently spatial. We sampled at multiple spatially distinct roosting locations (patches of high marsh habitat) distributed throughout a geographically closed study area. The spatial open population capture-recapture modeling approach developed by Efford and Schofield (2020:398) “relaxes some assumptions of non-spatial open-population and spatial closed- population models,” allowing us to bring to the

analysis more segments of the overall population of marsh sparrows, leading to more realistic estimates of population parameters.

Survival estimates from methods 1 and 2 were similar, and there was general correspondence between the yearly survival estimates from methods 1 and 2 within each species (Figs 2, 3, and 4). Neither method 1 nor 2 yielded consistently higher estimates than the other. These observations suggest the data from an additional roost site used in method 2 had a negligible effect with regard to survival estimates using CJS models. However, analyses of our simulated populations suggest that method 2 was superior to method 1. The survival estimates from method 3 were higher than those of methods 1 and 2 in all three species and across almost every season. Given that inclusion of all banding data essentially casts a broader net for recapturing individuals, higher survival estimates for method 3 could be regarded as an expected result. The differences between method 3 (spatial PLB model) and the CJS model results beg the question as to which provides a better estimate of survival. We think that the spatial PLB model is preferred because it conditions on the number of individuals observed during the study (n) rather than times of the first detection. There were no evident trends in survival across seasons, although methods 1 and 2 registered an unusually high survival rate for the last season of data collection (Figs 2, 3, and 4).

Although the results from method 3 yielded reasonable results, there are several factors that call for caution in accepting our estimates. Foremost, is that our data are not ideally suited to the spatially explicit model because recaptures of individuals across different roost sites were relatively rare. The model requires detections of individuals moving across capture sites to estimate the detection function scale (i.e., σ) which describes how the detection probability decreases with distance from an original capture site (Smith et al. 2020). We captured > 150

individuals at more than one site, but they represented a small proportion (< 1%) of the number of individuals captured overall. Secondly, when looking at the results of our data simulation analyses, both model types (spatial PLB and non-spatial CJS) generally underestimated survival rates for the simulated data sets, suggesting that our real-world survival estimates for Nelson's, Saltmarsh, and Seaside Sparrows might also be low.

Models with environmental covariates (e.g., flood, winter storms, etc.) were frequently included among the best models generated by all three of our analytic methods, yet there was no clear evidence that survival was meaningfully affected by these factors. Generally speaking, beta values for environmental variables in models with covariates were trivial (i.e., their 95% confidence intervals overlapped zero). Given that survival across years was minimal, there is not much variation that could be attributed to any of the covariates.

Abundance estimates indicate a clear stratification among the three species wherein Nelson's Sparrows are the least common and Seaside Sparrows are the most common. This conclusion is supported by general observations of the marsh sparrows in the area (WFO and AMG, pers. obs.). Over the course of the study there appears to be a trend toward increased density and abundance in Nelson's Sparrows and Saltmarsh Sparrows. There may be a similar trend among Seaside Sparrows, but a somewhat high estimate of density in the first season of the study and a relatively low density estimate in the last season obscure this result.

One thing that may have resulted from the low number of recaptures across sites is a discrepancy between total captures and the density and abundance estimates for Saltmarsh Sparrows and Nelson's Sparrows. The abundance estimate for Saltmarsh Sparrows was consistently higher than that of Nelson's Sparrows (Fig 5); although we captured considerably more Nelson's Sparrows (414) than Saltmarsh Sparrows (285). The total number of recaptures

for the two species were similar (Nelson's Sparrow: 109; Saltmarsh Sparrow: 105) indicating a higher proportion of recaptures for Saltmarsh Sparrow. However, 10.8% of Saltmarsh Sparrows were captured at more than one site, whereas only 5.3% of Nelson's Sparrows were captured at 2 sites (no birds of either species were captured at 3 or more sites). These interspecific differences likely affected the detection function scale (Sigma) in the model. Estimates of sigma are compromised when there are few or no detections in different locations. Captures across sites were rare for both species, but they were especially rare for Saltmarsh Sparrows.

Marsh sparrows on Kiawah Island and similar coastal areas in the region face a dual threat of rapid sea-level rise and established human developments. Whereas gradual shifts in sea-level within an undeveloped landscape would likely have sustained marsh habitats with some upslope or downslope shifts in the marsh boundaries, sea-level rise in a developed landscape does not allow for marsh habitat to spread inland. Hence, loss of habitat and habitat fragmentation are major concerns with regard to the sustainability of marsh sparrows in coastal South Carolina and the surrounding region.

Given these ongoing threats to marsh sparrow populations, there is a need to improve monitoring methods. Our work has focused on capturing relatively large numbers of birds at tidal refugia during high tide events. Although it is possible to capture marsh sparrows at low tide when they are dispersed across the salt marsh, these capture efforts generally require large teams of field workers and yield many fewer birds than high-tide efforts. Nevertheless, capturing birds at low tide may allow for a better assessment of how birds move throughout the marsh. Perhaps a combination of low-tide and high-tide capture effort could provide a full perspective on the population, wherein high-tide work generates a robust sample of the population, and low-tide work reveals potential biases in data that come from a limited number of refugia.

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Tables

Table 1. The types of capture-recapture survival models, months, number of winters, and number of roost sites used in methods 1 – 3 of the present study. (NESP = Nelson's Sparrow; SALS = Saltmarsh Sparrow; SESP = Seaside Sparrow)

					Number of individuals		
Method	Model type	Months	Number of winters	Number of roosts	NESP	SALS	SESP
1	CJS	Jan - Mar	8	5	187	126	421
2	CJS	Nov - Mar	8	6	210	156	522
3	Spatial PLB	Nov - Mar	8	18	414	285	1,149

[a] CJS = Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). [b] Spatial PLB = spatial analog of the Pradel-Link-Barker model (Efford and Schofield, 2020)

Table 2. Definitions of each covariate used to model the annual survival for Nelson's, Saltmarsh, and Seaside Sparrows.

Variable	Definition
t	Time or winter period; 'primary session' in spatial openCR model
Flood	Binary environmental variable representing whether there was a coastal flooding event that winter at Kiawah Island, SC
Winter storm	Binary environmental variable representing whether there was a snow and/or ice storm that winter at Kiawah Island, SC
Winter precipitation	Environmental covariate representing the total precipitation (cm) during that winter (1 Nov – 31 Mar) in Charleston, SC
Freezing days	Environmental covariate representing the number of days in Charleston, SC that winter (1 Nov – 31 Mar) with a mean temperature $\leq$ 0°C

Table 3. The number of simulated individuals produced under three different population densities that were used in our three different methods of capture-recapture analysis.

Simulated population density	Method 1	Method 2	Method 3
Low	213	268	549
Medium	405	513	1030
High	599	785	1544

Figure legends

Figure 1. Map of the 18 primary high-tide roost sites where wintering marsh sparrows were sampled during the 8-year study period (2012/13 – 2019/2020) at Kiawah Island, South Carolina. Green areas denote intertidal saltmarsh, blue is open water, and all other habitat/landcover is brown.

Figure 2. Estimates (± SE) of annual survival for Nelson's Sparrow from three methods of open population capture-recapture analysis. Methods 1 (*n* = 187) and 2 (*n* = 210) used a standard Cormack-Jolly-Seber (CJS) modelling approach, while method 3 (*n* = 414) applied a spatially explicit modeling approach.

Figure 3. Estimates (± SE) of annual survival for the Saltmarsh Sparrow from three methods of open population capture-recapture analysis. Methods 1 (*n* = 126) and 2 (*n* = 156) used a standard Cormack-Jolly-Seber (CJS) modelling approach, while method 3 (*n* = 285) applied a spatially explicit modeling approach.

Figure 4. Estimates (± SE) of annual survival for the Seaside Sparrow from three methods of open population capture-recapture analysis. Methods 1 (*n* = 421) and 2 (*n* = 522) used a standard Cormack-Jolly-Seber (CJS) modelling approach, while method 3 (*n* = 1,149) applied a spatially explicit modeling approach. The first 6 winters were "flood-free", while the 7th winter had at least one flooding event.

Figure 5. Estimates of abundance (± 95% CI) of marsh sparrow species each winter season (November – March) at Kiawah Island, SC from 2012/13 to 2019/20. Abundance estimates were calculated by multiplying density estimates (individuals per hectare of saltmarsh) by the total available area of saltmarsh within the study area (~1648 ha). Density estimates were generated by the best-fit JSSAsecrD model for each species. (NESP = Nelson's Sparrow; SALS = Saltmarsh Sparrow; SESP = Seaside Sparrow).

Figure 6. Annual survival probability (95% CIs) estimated by fitting non-spatial CJS (Methods 1 and 2) and spatial PLB (Method 3) models to simulated data from a population simulated at "low density" (0.4 animals/ha). Dark red diamond symbols denote the true survival values.

Figure 7. Annual survival probability (95% CIs) estimated by fitting non-spatial CJS (Methods 1 and 2) and spatial PLB (Method 3) models to simulated data from a population simulated at "medium density" (0.8 animals/ha). Dark red diamond symbols denote the true survival values.

Figure 8. Annual survival probability (95% CIs) estimated by fitting non-spatial CJS (Methods 1 and 2) and spatial PLB (Method 3) models to simulated data from a population simulated at "high density" (1.2 animals/ha). Dark red diamond symbols denote the true survival values.

Figures

Figure. 1

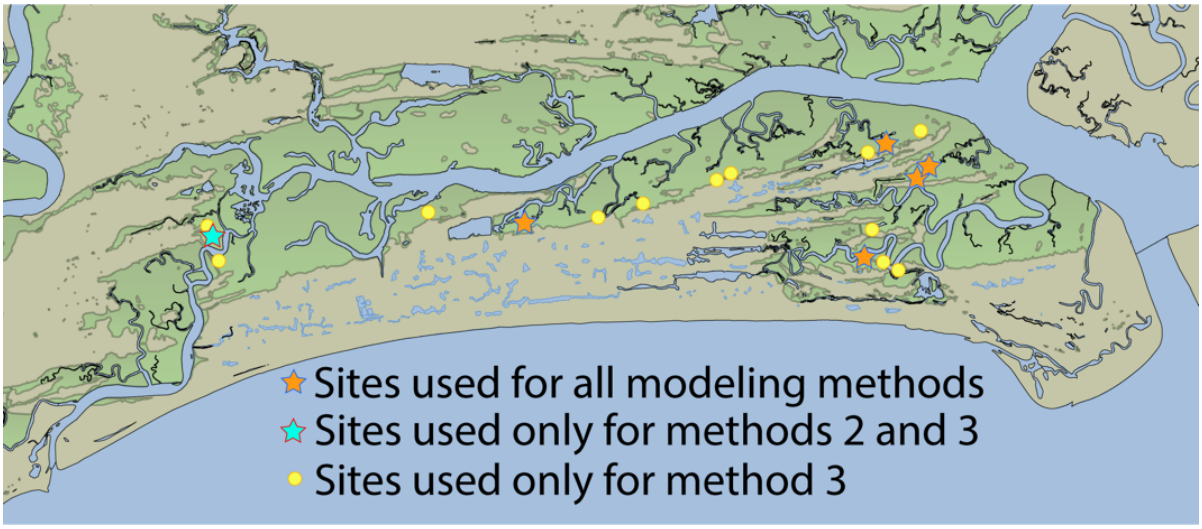


Figure 2.

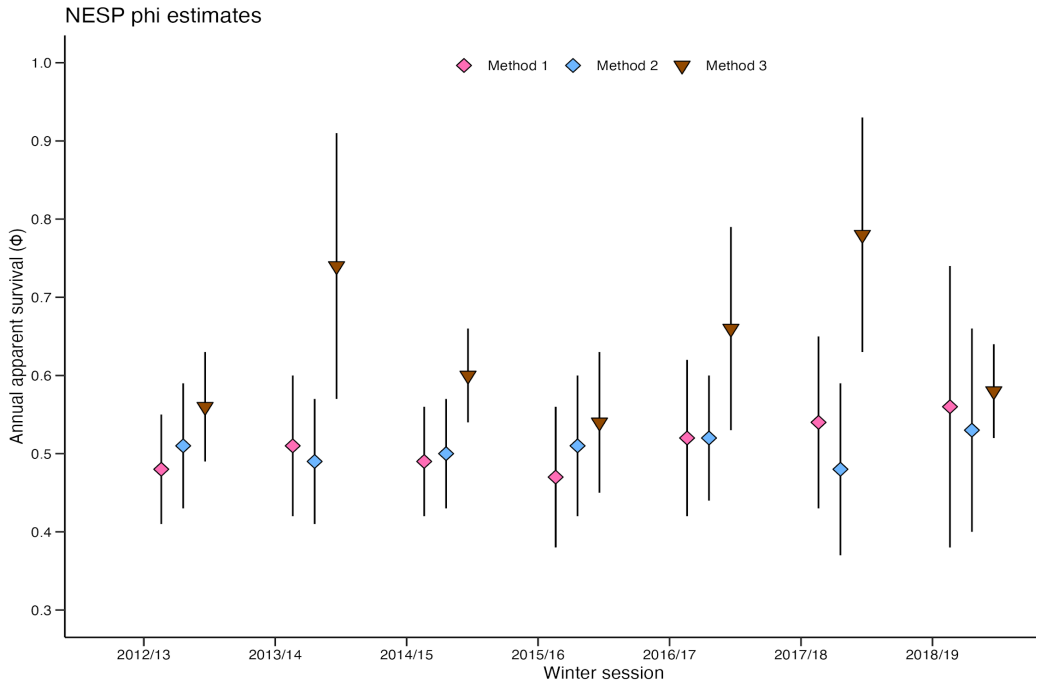


Figure 3.

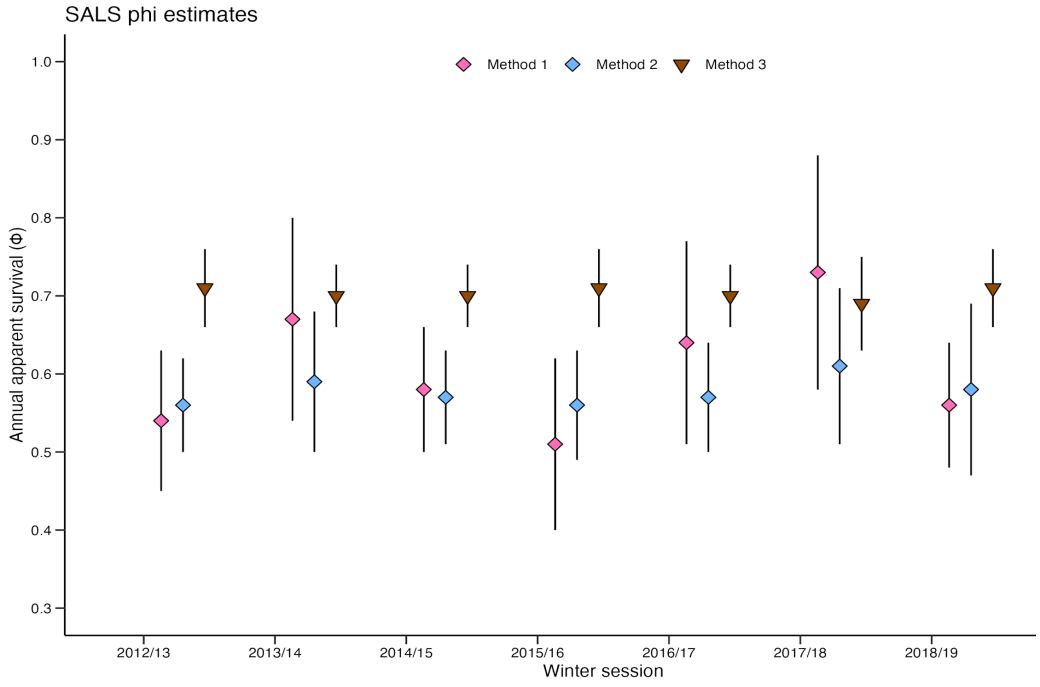


Figure 4.

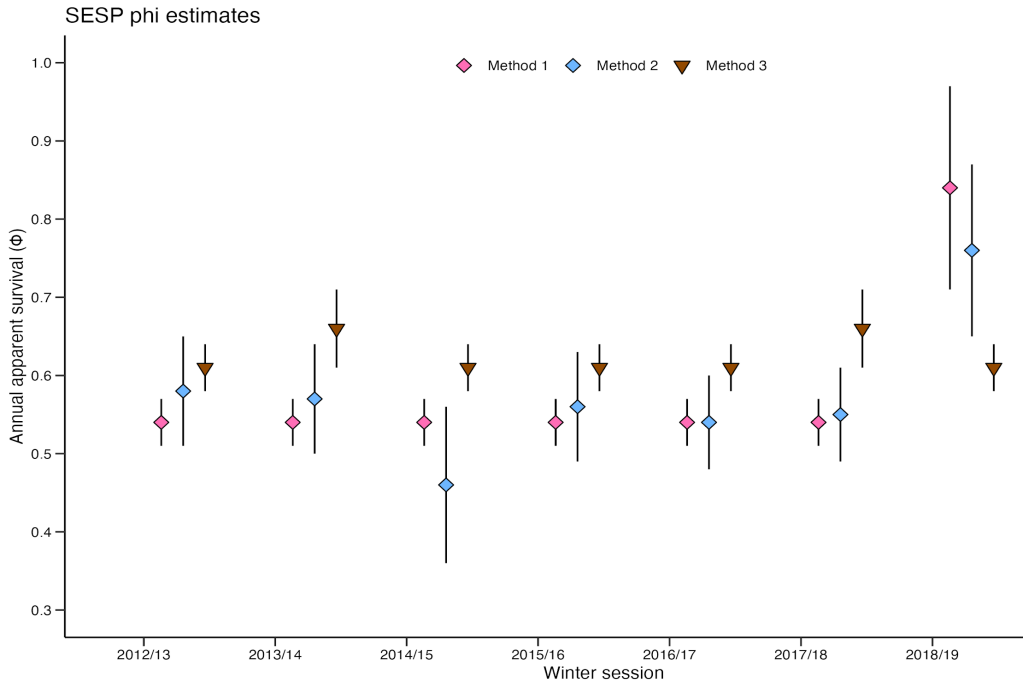

SESP phi estimates
Method 1
Method 2
Method 3
Annual apparent survival (Φ)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
2012/13
2013/14
2014/15
2015/16
2016/17
2017/18
2018/19
Winter session

Figure 5.

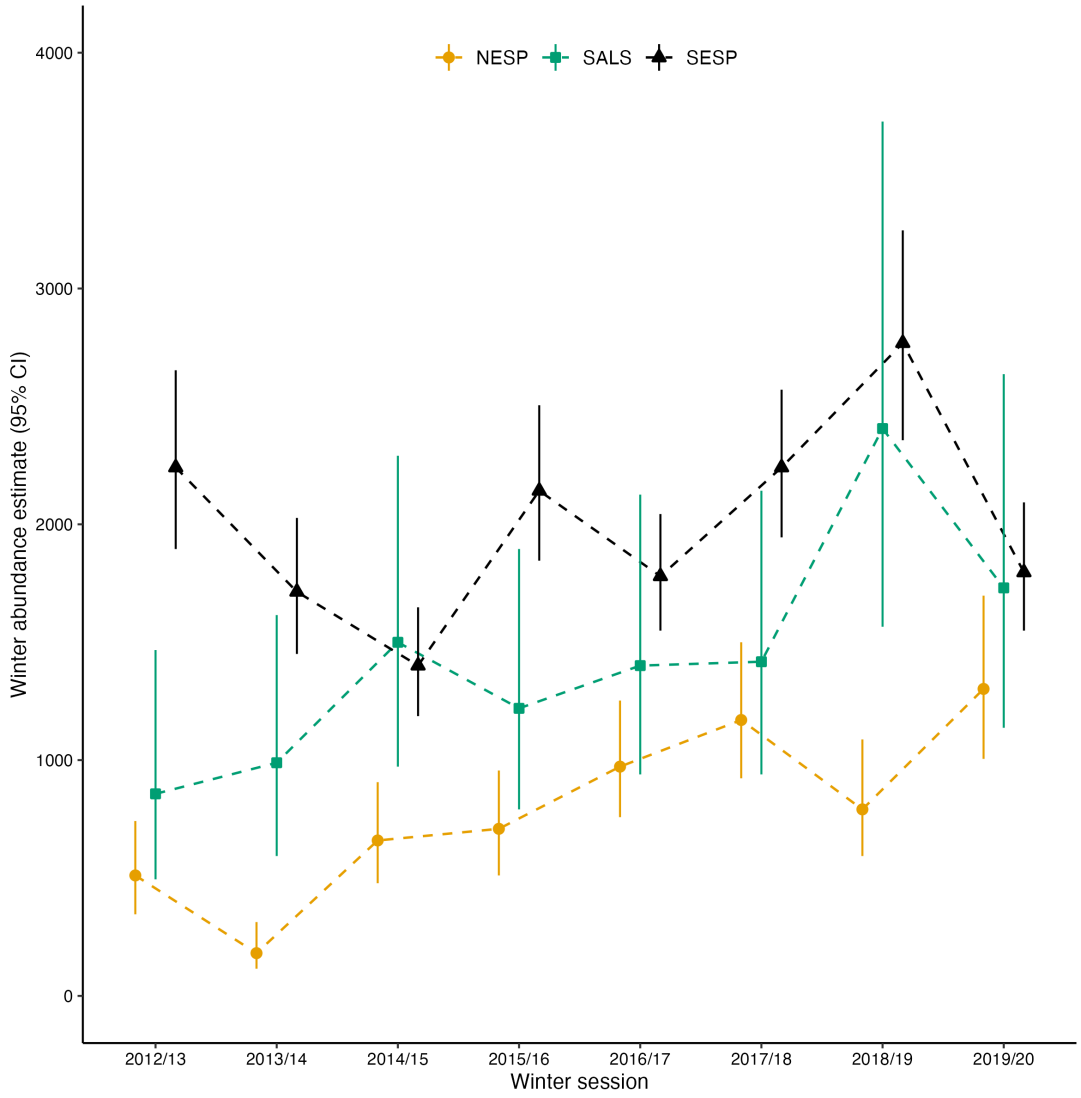

NESP
SALS
SESP
4000
3000
2000
1000
0
Winter abundance estimate (95% CI)
2012/13
2013/14
2014/15
2015/16
2016/17
2017/18
2018/19
2019/20
Winter session

Figure 6.

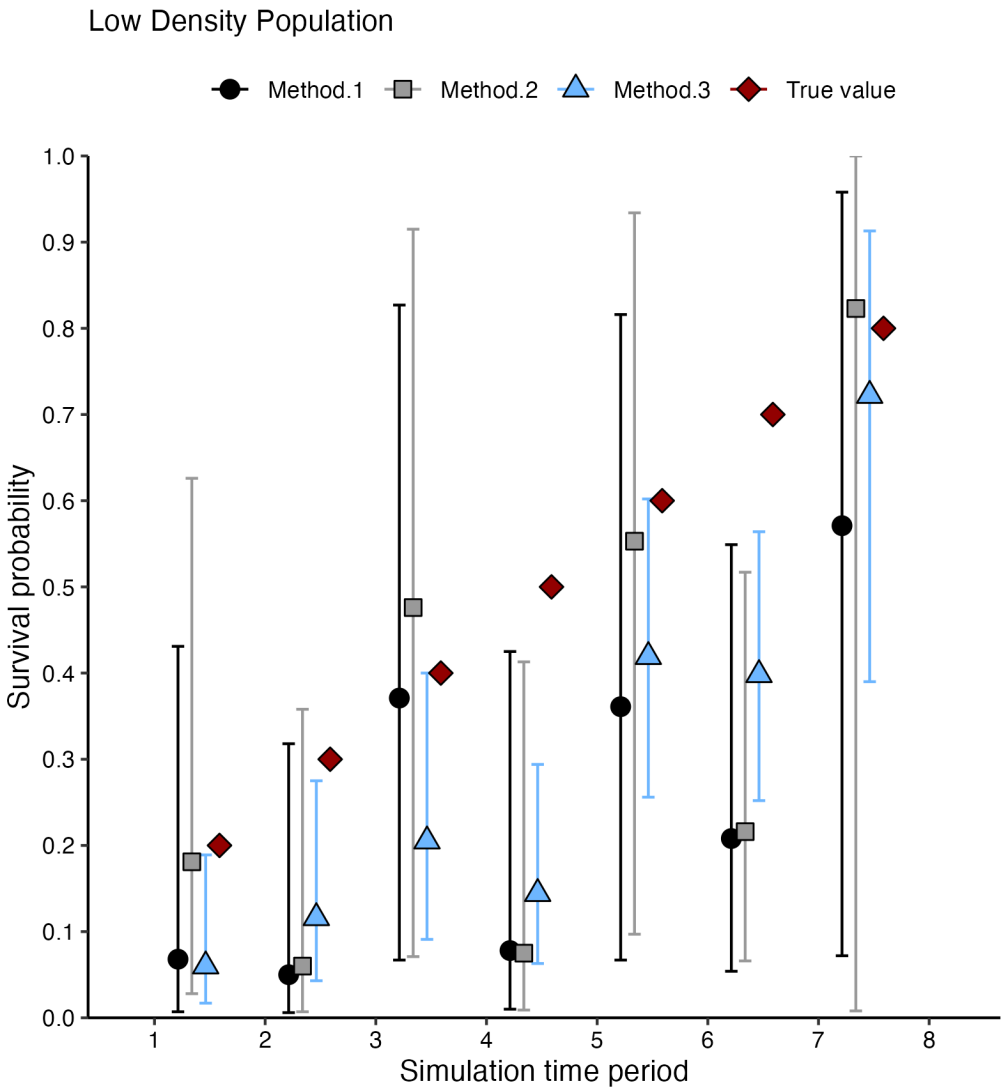

Low Density Population
Method.1
Method.2
Method.3
True value
Survival probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
Simulation time period

Figure 7.

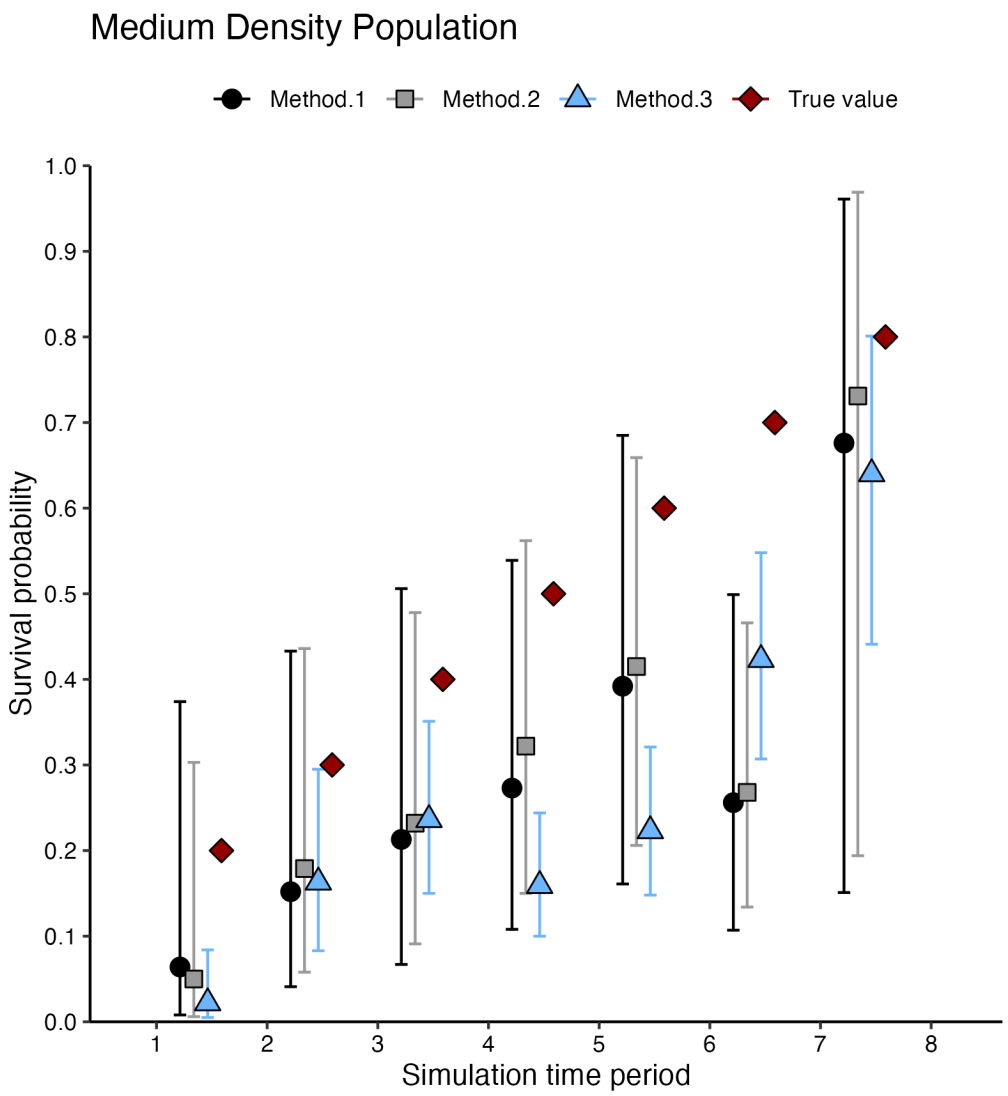
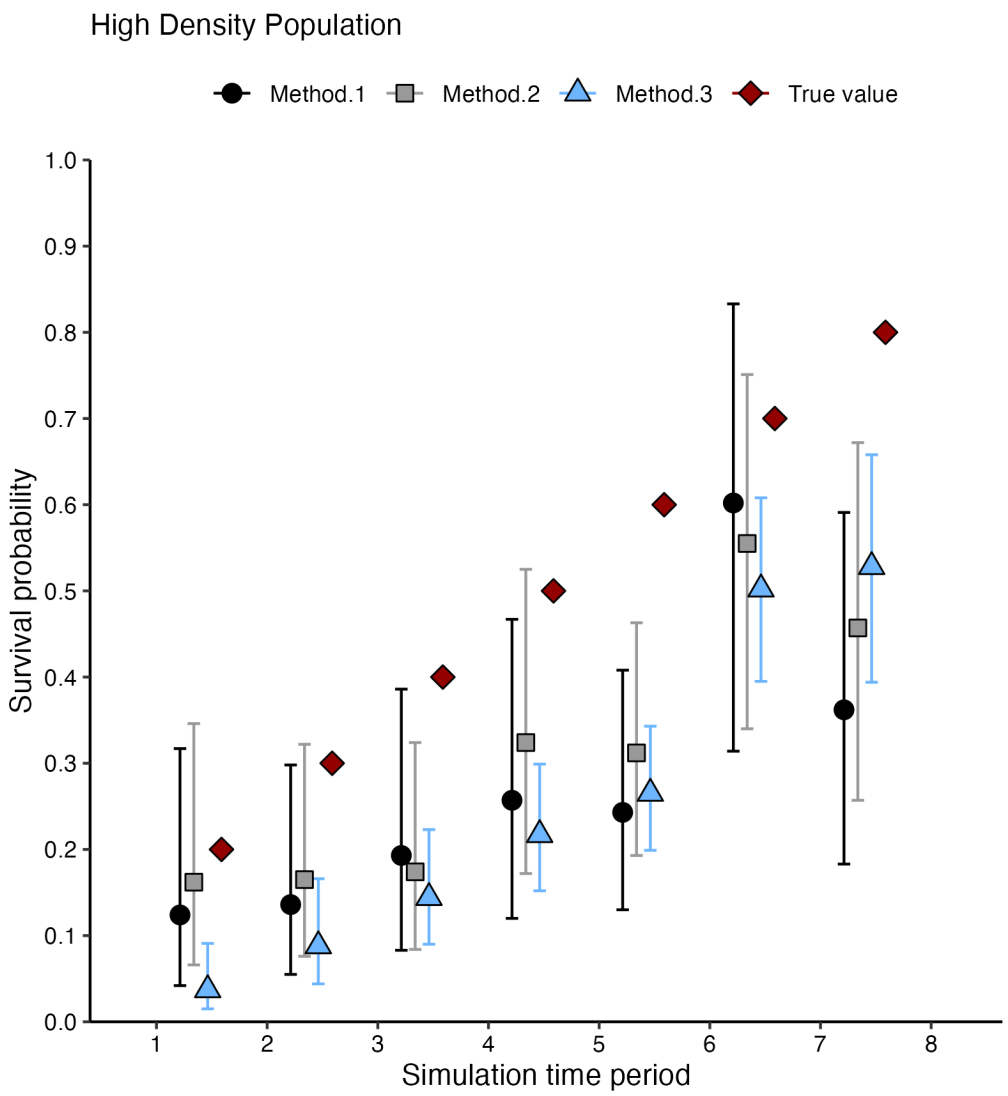

Medium Density Population
Method.1
Method.2
Method.3
True value
Survival probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
Simulation time period

Figure 8.


High Density Population
Method.1
Method.2
Method.3
True value
Survival probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
Simulation time period

CHAPTER TWO

Functional connectivity of a coastal landscape for three tidal marsh songbirds: a translocation experiment

Keywords:

animal movement, translocations, ornithology, salt marsh, habitat fragmentation

Abstract

Predicting species' responses to environmental changes requires assessments of site fidelity as well as an understanding of how individuals move through habitats that may become heterogenous and/or fragmented. We used translocation experiments to evaluate the functional connectivity of a heterogenous saltmarsh landscape for three coastal marsh songbird species during the non-breeding winter season. We tested whether species differed in their movement abilities and if landcover type and translocation distance had any influence on movement. Over two consecutive winter seasons, we radio-tagged and experimentally translocated Seaside Sparrows (*Ammospiza maritima*; n = 42), Nelson's Sparrows (*A. nelsoni*; n = 10), and Saltmarsh

Sparrows (*A. caudacuta*; n = 6) 0.26 – 2.3 km across two different landscape types (i.e., continuous marsh vs. fragmented marsh) and monitored their return success and times. Overall return success was high (72% of 57), but we found no clear evidence that return success differed among species or between continuous and fragmented marsh. Return times did not appear to be significantly influenced by species, landscape treatment, or translocation distance. Our findings indicate a strong fidelity in all three species of marsh sparrow to wintering home ranges and associated high-tide roost sites. This strong homing instinct may have led to the surprising result that wintering marsh sparrow movements are not significantly impacted by habitat fragmentation.

Introduction

Salt marshes support a wide variety of animal species adapted to the tidal dynamics of these ecologically productive and economically valuable coastal wetlands (Barbier et al. 2011; Costanza et al. 2008; Greenberg et al. 2006; Taylor et al. 2018). Over the past several centuries, the impacts of human settlement and land use practices within coastal zones have greatly reduced the quality and extent of saltmarshes around the world (Gedan et al. 2009; Lotze et al. 2006). Consequently, populations of vertebrates restricted to these intertidal habitats have declined, resulting in a disproportionate number of endangered, threatened, or conservation-priority species and subspecies (Greenberg et al. 2006). Accelerated rise in sea level associated with climate change is predicted to reduce the extent of saltmarsh habitat in some regions (Hunter et al. 2017; Rosencranz et al. 2018; Kirwan et al., 2016; Schuerch et al. 2018), which will compound the observed and predicted impacts of increased human settlement in many coastal areas (Carter et al. 2014; Dame et al. 2000; Powell et al. 2017). The combined impacts of human

activities and sea-level rise undoubtedly will transform what are now isolated areas of contiguous saltmarsh into fragmented landscapes of saltmarsh and matrix (non-saltmarsh) habitats. It remains to be seen how saltmarsh species will cope with contraction and fragmentation of their habitat, although we might expect to see reductions in survival, gene flow, population persistence, and dispersal.

Little is known about how tidal marsh songbird species move and settle within their winter landscape. Studies on forest and grassland birds have shown that fragmentation and loss of preferred habitat can create behavioral barriers that influence movement abilities and site fidelity across the landscape (Bélisle and Desrochers 2002, Harris and Reed 2002; Knowlton et al. 2017; Krištín and Kaňuch 2017; Volpe et al. 2016). Such barriers are significant because movement and site fidelity influence habitat selection, and, ultimately, a species' spatial distribution, genetic structure, and population persistence.

Translocation (displacement) experiments give us a powerful and logistically efficient way to study how birds and other animals move across landscapes and how the composition and configuration of different landscape features influence those movements (Betts et al. 2015). Translocation studies typically involve: (1) capturing site-faithful/territorial individuals, (2) uniquely marking them so they can be monitored and detected later, (3) releasing them at new sites at across gradients of habitat loss and/or fragmentation, and (4) tracking them back to their capture site or attempting to detect them later at their capture site. Return time (homing time) and the probability of return (return success) are used as indirect measurements of landscape connectivity, with long return times and low probabilities of return typically associated with landscapes of low connectivity (permeability). Some features such as habitat corridors may

facilitate a species' movement across the landscape, whereas other features such as habitat matrix, rivers, and roads may restrict a species' movement.

We used translocation experiments to investigate connectivity of a heterogenous coastal landscape for three bird species, henceforth collectively referred to as marsh sparrows: the Seaside Sparrow (*Ammospiza maritima*), Saltmarsh Sparrow (*A. caudacuta*), and Nelson's Sparrow (*A. nelsoni*). Individuals were captured and moved different distances across two landscape treatments: 1) landscapes comprising continuous salt marsh ("continuous marsh") between capture and release site, and 2) landscapes composed of a mosaic of salt marsh fragmented by human-modified habitats. We then released the birds and used radio telemetry to monitor if and when birds returned to their point of capture.

Using this translocation paradigm, we tested several predictions about return success and return time in relation to displacement distance, landscape treatment, and species. First, we predicted that marsh sparrows would show lower probabilities of return and slower return times as translocation distance increased. In addition, we predicted that individuals would return more quickly and successfully through the continuous marsh landscape relative to the fragmented marsh landscape. We reasoned that birds displaced across the fragmented treatment landscape would be unwilling to cross unsuitable habitats (Harris and Reed, 2002), such as roads and open water, forcing them to carry out lengthy and complex movement paths to return to their capture sites (Gillies and St. Clair, 2008; Knowlton et al. 2017; Tremblay and St. Clair, 2011) or to find and establish a new home range for the remainder of the winter. Alternatively, individuals returning across fragmented marsh may have shorter return times because taking shortcuts through unfamiliar habitat, where they move more directionally (and thus more quickly).

All three of our target species are restricted to tidal marshes during the non-breeding season, but only Nelson's Sparrow has variable breeding habitat associated with tidal marshes, with some breeding in inland marshes and others in coastal systems (Dechant et al. 2002; Nocera et al. 2007). Nelson's Sparrow also migrates farther than Saltmarsh and Seaside Sparrows, with some populations undergoing inland migrations from the Gulf Coast of the United States to breeding locations around James Bay and Hudson Bay in Canada and throughout the Great Plains of northcentral United States and western Canada (Shriver et al. 2020). These life-history traits led us to predict that Nelson's Sparrow will more readily navigate back to its winter home range following displacement. We predicted that Saltmarsh and Seaside Sparrows would not differ in return success or time across either landscape treatment.

Methods

Study area

Our study took place within an approximately 39 km^2 area encompassing Kiawah Island, South Carolina (Fig. 1; 32°36'43.64" N, 80° 4'27.51"W), a developed barrier island located on the Atlantic Coast of the Southeastern United States. Kiawah Island (hereafter "Kiawah") contains some 15 different habitat types, including intertidal beach, maritime grassland, maritime shrub thicket, maritime forest, salt shrub thicket, and intertidal salt marsh. Maritime forest dominates the upland and interior areas of the island. However, over the last several centuries, much of the Kiawah's upland dry land has been transformed by human activities, including agriculture and real estate development. The most significant changes have happened over the past 50 years with the establishment and growth of a private beach resort community which now extends across much of the island and even into the island's salt marsh. Kiawah is immediately surrounded by

~8.3 km^2 of intertidal salt marsh that is flooded and exposed twice daily by the tide. Most of that salt marsh covers the island's protected landward side where many of our translocations took place. The salt marsh community at Kiawah can be roughly divided into three zones based on elevation (height above mean sea level), salinity, and tidal height: (1) low marsh, (2) high marsh, and (3) upland border. The twice-daily flooded low marsh is the dominant zone within the salt marsh system at Kiawah, and it is dominated by smooth cordgrass (*Sporobolus alterniflorus* or *Spartina alterniflora*). The high marsh zone typically receives less than two hours of high-tide flooding each day, but it will get completely flooded during storm surges and by above-average high tides produced from twice-monthly "spring tides". Plant diversity increases in the high marsh zone and includes a mixture of Virginia glasswort (*Salicornia depressa*), saltgrass (*Distichlis spicata*), black needlerush (*Juncus roemerianus*), lavender thrift (*Limonium carolinianum*), turtleweed (*Batis maritime*), saltmeadow cordgrass (*Spartina patens*), and sea oxeye daisy (*Borrichia frutescens*). The upland marsh border zone lies between the high marsh zone and upland habitats (e.g., maritime forest, scrub/shrub thicket), where inundation from salt water rarely occurs. The two main plants in this zone are marsh elder (*Iva frutescens*) and sea oxeye daisy (*Borrichia frutescens*). While some areas of the island's interior and surrounding salt marsh are protected under conservation easements, much of the barrier island's landscape is susceptible to the impacts of ongoing human-related activities, including residential and commercial development.

Study species

Seaside, Saltmarsh, and Nelson's Sparrows are closely related species (Klicka and Spellman, 2007) that winter in salt marshes almost exclusively along the U.S. Atlantic and Gulf Coasts

(Greenlaw and Woolfenden, 2007; Watts and Smith, 2015). Seaside and Saltmarsh Sparrows are habitat specialists restricted to tidal marshes throughout their annual cycle (Greenberg et al. 2006); the former breeds from Texas to southern Maine and includes migratory and non-migratory subspecies (Post and Greenlaw, 2020; Woltmann et al. 2014), the latter is a short- to medium-distance migrant that breeds from northeastern Virginia to southern Maine (Greenlaw et al. 2020). Nelson's sparrow is a long-distance migrant that breeds in three geographically distinct regions spanning from the northern Great Plains of central Canada to the Maritime Provinces of Canada and northeastern coast of the U.S. (Shriver et al. 2020). Across its breeding range, Nelson's Sparrow uses a variety of wet and dry habitats, including freshwater marshes, wet meadows, coastal salt marshes, and even hayfields (Dechant et al. 2002; Nocera et al. 2007; Shriver et al. 2010).

Analyses of mark-recapture data collected over eight consecutive winters at Kiawah suggest that marsh sparrows are largely settled in our area from 1 November until the end of March. Our findings are similar to those made in North Carolina by Winder et al. (2012), who collected and analyzed multiple years of wintering marsh sparrow mark-recapture data. The species co-occur within the low and high marsh zones (Watts and Smith, 2015; Winder et al. 2012). During spring tides and storm surges, all three species move to elevated patches of high marsh and remain there until water recedes. The relative abundance and diversity of marsh sparrows encountered at roost sites varies at the regional or local scale (Shaw, 2012; Trinkle 2013). Individual marsh sparrows show strong fidelity to roost sites across years (Michaelis, 2009; Shaw, 2012; Trinkle, 2013; Winder et al. 2012), and they are rarely observed using other roost sites even within a winter season.

Translocation experiments

We performed translocation experiments during two successive winters. The first season ran from 28 November 2018 to 14 March 2019 (median capture date: 26 December), and the second season ran from 10 January to 10 March 2020 (median capture date: 14 January). The dates spanning each field season correspond to the period (1 November – 31 March) when nonbreeding populations of marsh sparrows in the region have settled for the winter (Winder et al., 2012), and we presumed that individual birds had established stable winter home ranges by no later than 1 November. Climatic conditions in our study area were similar across both nonbreeding winter periods. For example, the average minimum daily temperature for each season was nearly identical (mean + 1 SD: Season 1: 46.1 + 9.5 F; Season 2: 46.7 + 10.4 F), and the average daily precipitation total (inches) was also similar between seasons (mean + 1 SD: Season 1: 0.12 + 0.34 inches; Season 2: 0.13 + 0.37 inches).

Birds were captured at 14 different roost sites between 0730 and 1330 h during spring tides when larger than average high tides forced birds to concentrate for 2-4 hours in their roost areas. Once the low marsh was completely flooded, we actively funneled birds toward one to three mist nets placed strategically at one end of the roost site. For larger roost sites (i.e. > 0.2 ha), we used a rope dragging method to slowly corral and flush birds toward the nets. The frequency and duration of these suitable high tides greatly limited the number of capture opportunities. However, without these larger than average tides, marsh sparrows are extremely difficult to capture because they can otherwise spread and move about in areas of low marsh that are difficult for us to access and maneuver in. We banded each marsh sparrow with a unique U.S. Geological Survey aluminum band and recorded the bird's age (when possible), wing chord, fat score, and body weight. Individuals selected for translocation experiments were fitted with a

radio transmitter using a figure-eight leg-loop harness system, as described by Streby et al. (2015). Harnesses were made from a very thin (0.5mm) elastic sewing thread (Gütermann) and super glued directly to the transmitter body. The combined weight of the harness and radio transmitter did not exceed 3% of a bird's body weight. Each radio-tagged bird was also banded with one plastic colored leg band to facilitate identification if it was recaptured, particularly if the bird's transmitter fell off prematurely. To maintain statistical independence, all individuals (with one exception) were translocated only once. The exception was one Seaside Sparrow that was translocated twice in one season, and we used only data from its first translocation for our analyses. Birds selected for translocation were placed separately into cloth bags and transported by car to distances between 265 m and 2,331 m (mean + 1 SD: 1,056.21 + 481.7 m) from their capture site across continuous or fragmented marsh landscapes to pre-designated release areas within the high marsh (Fig. 2). We chose release sites far enough away from presumed winter home ranges in order to reduce the potential influence of release-site familiarity on return time and success (Betts et al. 2015). Potential release areas were selected before the start of each season based on site visits and satellite imagery. To avoid non-independent returns within the same field season, we released individuals at least 50 m from each other. During both seasons, we observed each translocated bird during its release for up to 5 minutes to ensure that it exhibited normal flight capability. During the second field season, we observed each radio-tagged bird inside a large, wired bird cage prior to its translocation and release. This method allowed us to more easily observe and address any issues related to harness fit before releasing the bird back into the marsh. To standardize the motivation to return, we released all translocated birds in salt marsh patches that were as similar as possible to each other in their vegetation characteristics and proximity to non-salt marsh habitats.

We identified successfully homed marsh sparrows by detection of radio tag signals within capture site areas. Radio surveys began 5-7 hours upon release, and if individuals were not detected as same-day returns, then we carried out radio surveys at the relevant capture sites based on the following schedule: daily for the first two weeks following release (Season 1) or daily for the first 7 days, followed by day 9, day 11, and day 14 after release (Season 2). When birds had not homed within 7 days of translocation, we also surveyed their release site areas at least once up to 13 days post-translocation. If a bird did not return within 14 days, we continued to monitor their capture and release sites weekly until the bird returned, the transmitter failed, or until the study period ended. As constraints permitted, we searched for any individuals suspected of having settled outside their capture and release areas. All surveys took place between 0630 and 2230 on days when the weather permitted (i.e. no heavy rain). Each capture site was surveyed within a radius of approximately 25 - 330 m by a single observer equipped with a hand-held receiver and directional antenna. The observer thoroughly patrolled the search area, stopping occasionally to listen for tag(s) of any potentially returned bird(s). Once a signal was detected, the observer would home in on the tag until the bird's presence or absence within the specific capture site area could be recorded with confidence. We searched for translocated birds for a minimum of 10 mins, but the search period was extended in situations where there were multiple target birds at one site, during low tides when more potential habitat was exposed around the site, and also based on general capture site patch size. Return time was calculated as the number of days between release and first detection at the capture site. Two birds that returned on the same day were given a return time of 0.5 days. Return success was determined by radio-based presence/absence surveys for all birds except one. This one exception, which we included in our

analyses, was a Nelson's Sparrow that had not been detected as a same-day return but was recaptured in a mist net the following morning at its original site.

In addition to the birds that were translocated, we radio-tagged two individuals each field season that were released at their capture site. We used these birds primarily as "controls" to evaluate the efficacy of detecting birds using radio telemetry, but we also monitored these "control" birds to better understand the wintering home range sizes and natural movements of our species. We followed the same search protocols with these birds as we did for translocated individuals, and we used the resulting re-location rate to evaluate bird detectability. Three of the control birds were Seaside Sparrows and were detected 100% of the time (two birds: 10 detections in 10 attempts; 1 bird: 15 detections in 15 attempts). The fourth control bird was a Nelson's Sparrow, and we detected it ~87% of the time (13 detections in 15 attempts). Our overall detection rate for control birds was 96% (48 detections in 50 attempts).

Statistical analyses

As environmental conditions in our study area were similar across years (see Translocation Experiments), we combined translocation data from both field seasons in all analyses. To test for differences in return success among species and between landscape treatments, we used log-likelihood ratio (G-test) tests of independence with Williams' correction for 2x2 and 2x3 contingency tables. As an additional strategy for dealing with our small sample size and as a way to validate the results of our G-tests, we used a Bayesian framework to draw inference about whether return success differed by species or landscape treatment. More specifically, we built Bayesian analogs for G-tests of independence and used the Bayesian 95% density credible intervals (HDI) for estimates of proportions of successful returns to determine whether return

success differed among species or between treatment groups tested. For example, if credible intervals broadly overlapped among our three species, we could comfortably say that return success did not differ among the species. Lastly, we tested whether return success was related to translocation distance based on a univariate logistic regression model with distance as the only covariate and return success as the binary response variable (0 = did not return, 1 = returned). The fit of our logistic regression model was evaluated by comparing it to the null model using a likelihood ratio test.

We applied two different time-to-event analyses to identify which of our predictor variables, if any, significantly influenced the return time of translocated birds. In the first analysis, we applied a non-parametric method (Kaplan-Meier survival curves and log-rank tests) to visualize and test for differences in return time between and among groups of our categorical variables. For this analysis, we focused on testing two null hypotheses: (1) all three species survival curves are equal, and (2) both landscape treatment survival curves are equal (all species data combined). We used log-rank tests to compare survival curves (Harrington and Fleming, 1982; Kleinbaum and Klein, 2012). For our second analysis, we used the semi-parametric Cox proportional hazards (PH) regression approach to determine whether return time was influenced only by translocation distance. For the univariate Cox PH model, the response variable was the number of days between translocation and first detection of marked individuals at their capture site area within the same winter season. The time-to-event analysis techniques are commonly used in animal translocation studies and homing experiments to test for differences in 'survival time' (i.e., return/homing time) between certain groups or treatments (Bélisle et al. 2001; Capaldi and Dyer, 1999; Sheller et al. 2006; Smith et al. 2011). In our study, a terminal event occurred when an individual returned to its original capture site before the end of the winter field season.

Those individuals that were not detected to return to their capture sites within the same winter season that they were translocated (i.e., non-successful return) were treated as Type I, right-censored data.

All statistical analyses were performed in R v. 3.6.3 (R Core Team 2020). We used the *stats* package to fit and evaluate logistic regression models. The *GTest* function in *DescTools* package (Signorell et al. 2021) was used to analyze contingency tables, while all Bayesian models used to analyze contingency tables were built in JAGS (Plummer 2003) and run via R using *rjags* package (Plummer 2016). We used the *survival* package (Therneau 2020) to analyze time-to-event (return time) data with Kaplan-Meier and Cox PH modeling approaches, with additional plotting and graphical diagnostics performed with the *survminer* package (Kassambara et al. 2021). For our Cox PH modeling, ties in return time were handled using Efron's approximation, and we used statistical and graphical approaches based on scaled Schoenfeld residuals to verify the assumption of proportional hazards (Kleinbaum and Klein, 2012).

Results

Return success

Combining data from both seasons, most of the marsh sparrows (72% of 57) returned to their capture site. Return success was similar across both seasons, with 70% (21 of 30) and 74% (20 of 27) of birds returning in seasons one and two, respectively. However, we found no evidence that return success of individuals differed among species ($G = 1.03$, df = 2, $p = 0.60$; Fig. 3b). The lack of difference in return success among species was supported by the results of our Bayesian analysis which showed broadly overlapping credible intervals for estimates of proportion of successful returns (Fig. 4). The proportion of individuals returning to their home

site was high for each species, with 73% of 41 Seaside Sparrows returning, compared to 60% of 10 Nelson's Sparrows and 83% of 6 Saltmarsh Sparrows (Fig. 3b). Return success did not appear to be associated with landscape treatment, with 78% of the 23 translocated sparrows returning from the continuous marsh treatment and 68% of 34 sparrows returning from the fragmented landscape treatment ($G = 0.75$, df =1, p = 0.39, Fig. 3a). The lack of association between return success and landscape treatment was also supported by our Bayesian analysis, which showed broadly overlapping credible intervals for estimates of proportion of successful returns for both landscape treatments (Fig. 4). As for the effect of translocation distance, there was a general trend of decreasing return rates with increasing distance, but the probability of return was not significantly associated with translocation distance, regardless of species or landscape treatment type, (2(1) = 3.3, p = 0.067).

Return time

Overall, birds that successfully returned did so rather quickly, regardless of landscape treatment. When data for all three species was combined, we found that 61% of the 41 birds detected back at their capture sites returned within four days of being displaced ($\overline{x} \pm 1$ SD = 5.7 $\pm$ 7.5 days; median = 3.0 days). The return times for all successfully homed birds (N = 41) ranged from half a day to 42 days. In our Cox proportional hazards regression analysis, translocation distance (m) was not significantly related to overall return time for marsh sparrows (p = 0.51). We did not find differences in comparing Kaplan-Meier survival curves for species ($\chi 2 = 1.5$, df = 2, p = 0.5) or for landscape treatment ($\chi 2 = 3.1$, df = 1, p = 0.08), indicating that return time was not influenced by the species or landscape treatment type. On average, Seaside Sparrows took more than twice as long to return to their capture sites ($\overline{x} \pm 1$ SD: 6.9 ± 8.4 days) compared to Nelson's

and Saltmarsh Sparrows (Table 1), which had mean return times of 2.0 ± 0.63 days and 2.9 ± 2.0 days, respectively, and this difference was apparently driven by a strong response by Seaside Sparrows to fragmented marsh. When displaced across fragmented habitat Seaside Sparrows took approximately three times as long to return ($\overline{x} \pm 1$ SD: 9.5 ± 9.9 days) than the other species (Nelson's: 2.0 ± 0.0 days; Saltmarsh: 3.8 ± 3.6 days). When translocated across continuous marsh, return times for Seaside Sparrows were similar to those of the other species. Although not a significant difference, birds translocated across continuous marsh landscapes returned almost three times as fast as birds exposed to fragmented marsh treatment (Table 1, $\chi 2 = 3.1$, df = 1, p = 0.08).

Discussion

The marsh sparrows we studied had a robust response to translocation. The vast majority of translocated birds returned successfully, and they generally did so within a few days. Our predictions were mostly unsupported by the observed responses to translocation. First, we did not see any effect of translocation distance. Both return rates and return times were not influenced by variation in displacement distance. Similarly, there was limited evidence that birds were affected by displacement across fragmented marsh as opposed to continuous marsh. Return rates did not differ between these two treatments, and return times differed for only one species. Finally, our prediction that Nelson's Sparrow, the long-distance migrant and habitat generalist, would be more adept at homing behavior was not supported (Fig. 3).

The high rate and speed of returns following displacement indicates a strong fidelity in marsh sparrows to wintering home ranges and associated high-tide roost sites. We speculate that this strong tendency to maintain a limited wintering home range has been the overwhelming

driver of the results we observed. Even our most extreme displacements of ~2.5 km were, in many cases, quickly countered by the homing instincts of the birds. Displacing the birds even farther was a possibility, but we did not have any precedent for doing so before the study began, and it would have been logistically challenging given the difficulty of accessing more distant release sites in the saltmarsh/tidal-creek system within our study area. We are confident our translocation distances were sufficient to reduce the potential confounding effect of release-site familiarity on return time and success (Betts et al. 2015). Studies of landscape connectivity involving translocation experiments with forest songbirds used displacement distances similar to those used in our study (Geoffroy et al. 2019; Gillies and St. Clair, 2008; Gobeil and Villard, 2002; Jones et al. 2017; Kennedy and Marra, 2010; Tremblay and St. Clair, 2011). We are unaware of any similar translocation experiments with songbirds in salt marshes or other intertidal wetlands.

Of the 57 birds that were translocated, 16 were not detected back at their capture site during the season in which they were moved. There are several potential explanations for these missing birds. First, it is possible that some birds emigrated from the study area, although it is unlikely. Multi-year banding studies at our study location and at similar locations within the region (i.e., the Carolinas) indicate that non-breeding marsh sparrows remain closely tied to their wintering grounds by November and remain through April (Winder et al. 2012). It is also possible that transmitter loss or failure contributed to the number of unsuccessful returns. One transmitter was not functioning when we recovered it from a translocated bird; this individual was excluded from all analyses. Moreover, transmitter signals were strongly attenuated when they were in contact with water, which was probably common in our marsh habitat. Our continued radio detections of “control” birds (i.e., tagged birds that were not displaced) suggests

that our use of radio telemetry was a robust relocation method. Some of the displaced birds may have died before they could return to their wintering sites, but there is a general lack of information on within-season mortality for the marsh sparrows we studied. We suspect that these species face few direct threats to their survival during the winter, and the list of potential predators is short, with Northern Harrier (*Circus hudsonius*) likely at the top of the list, followed by American mink (*Neovison vison*) and Raccoon (*Procyon lotor*). We have no reason to suspect that within-season mortality rates would differ significantly among locations across the species' wintering range because marsh sparrows wintering in our study area regularly occupied sites that bordered roads, forest, and even residential houses.

The robust homing abilities and site fidelity of Nelson's, Saltmarsh, and Seaside Sparrows are potentially both beneficial and detrimental to conservation strategies for marsh sparrows. That they recover quickly from displacement implies that they can cope with short-term disturbance. Even so, the small and specific winter home ranges maintained by these species may create conflicts with ongoing human activities that would leave the species vulnerable to rising sea water levels. Marsh sparrows show relatively high year-to-year site fidelity to winter sites in our study area and within the region (A. Given, unpublished; Shaw, 2012; Trinkle, 2013; Winder et al., 2012). It remains unknown how these species will respond if they find their wintering home range has been developed or inundated.

The stationary non-breeding (wintering) phase of avian life histories is understudied compared with the breeding phase (Marra et al. 2015), even though conditions and events during the wintering period are known to have important impacts on individuals and populations during subsequent periods of the annual cycle (Cooper et al. 2015; Norris et al. 2004; Paxton and Moore, 2015; Reudink et al. 2009; Rockwell et al. 2015; Studds et al. 2007). Further research

into the wintering behavior of birds in tidal marshes is warranted not only for the sake of understanding but to develop management strategies that can ensure the survival of coastal populations under the dual threat of sea-level rise and encroaching human development. One potential management recommendation, for example, would be to maintain or create wide buffered upland edges along the saltmarsh to allow the saltmarsh to naturally migrate inland as sea levels rise. This strategy, however, poses a problem on Kiawah Island and in other coastal communities where most of the saltmarsh is bordered by private residences and/or land parcels awaiting development. Under the threat of accelerated sea level rise, homeowners and real estate developers may install hard structures such as revetments and bulkheads adjacent to the saltmarsh to protect their property. This shoreline hardening approach is commonly used along sheltered coastlines to fight the impacts of sea level rise, storm surges, and erosion (Dugan et al. 2011; Gittman et al. 2015), but it eliminates the potential for the marsh to migrate inland as sea levels rise (Titus et al. 2009) and will also reduce the extent of high marsh habitat that would be available for marsh sparrows to use when their preferred habitat is inundated. As a result, the prospects for many local populations are not good, unless alternative shoreline stabilization strategies (e.g., living shorelines; Currin 2019) are used in place of the traditional hard structures. Conservation of undeveloped land adjacent to the saltmarsh's upland border will still a premium, and we recommend land managers and conservation groups work to identify and protect inland migration routes for marshes in their areas, and where possible, restore lost and degraded marsh habitat.

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Tables

Table 1. Mean number of days + 1 SD since translocation when birds were detected back at their original capture site.

Variable	Category	Return time	*n*
Species	Nelson's Sparrow	2.0 ± 0.6	6
	Saltmarsh Sparrow	2.9 ± 2.9	5
	Seaside Sparrow	6.9 ± 8.4	30
Landscape treatment	Continuous marsh	2.8 ± 2.1	18
	Fragmented marsh	8.0 ± 9.3	23

Figure legends

Figure 1. Map of the study area (Kiawah Island, South Carolina; 32°36'43.64" N, 80° 4'27.51" W) showing where experimental translocations took place during two consecutive winter seasons (2018/2019 – 2019/2020) and its approximate location on the Atlantic Coast of South Carolina, USA.

Figure 2. Examples of translocation trials conducted within continuous salt marsh habitat (solid lines) and across salt marsh landscapes fragmented by a range of human-dominated and natural land cover types (dashed lines).

Figure 3. Plots of cumulative percent of birds detected back at their capture site and their return time following experimental translocation based on the following conditions: A. landscape treatment, and B. species (Nelson's Sparrows (NESP), Saltmarsh Sparrow (SALS), and Seaside Sparrow (SESP)).

Figure 4. Results of a Bayesian comparison of return success among species and between landscape treatments. Each line segment represents the estimated proportion of successfully returned individuals (black square) and 95% Bayesian highest density credible intervals (HDI) for a given species or treatment. Credible intervals overlap broadly among species and between marsh landscapes, indicating that return success did not differ among marsh sparrows or between landscape treatment.

Figures

Figure 1.

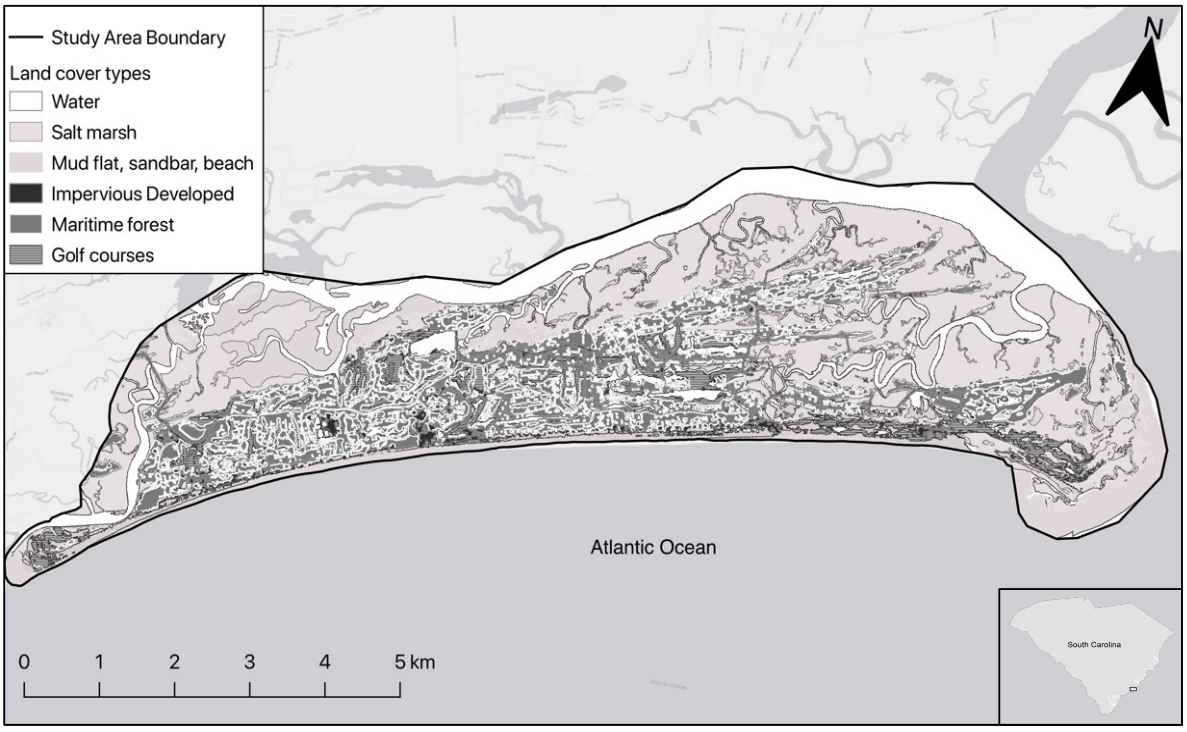


Figure 2.

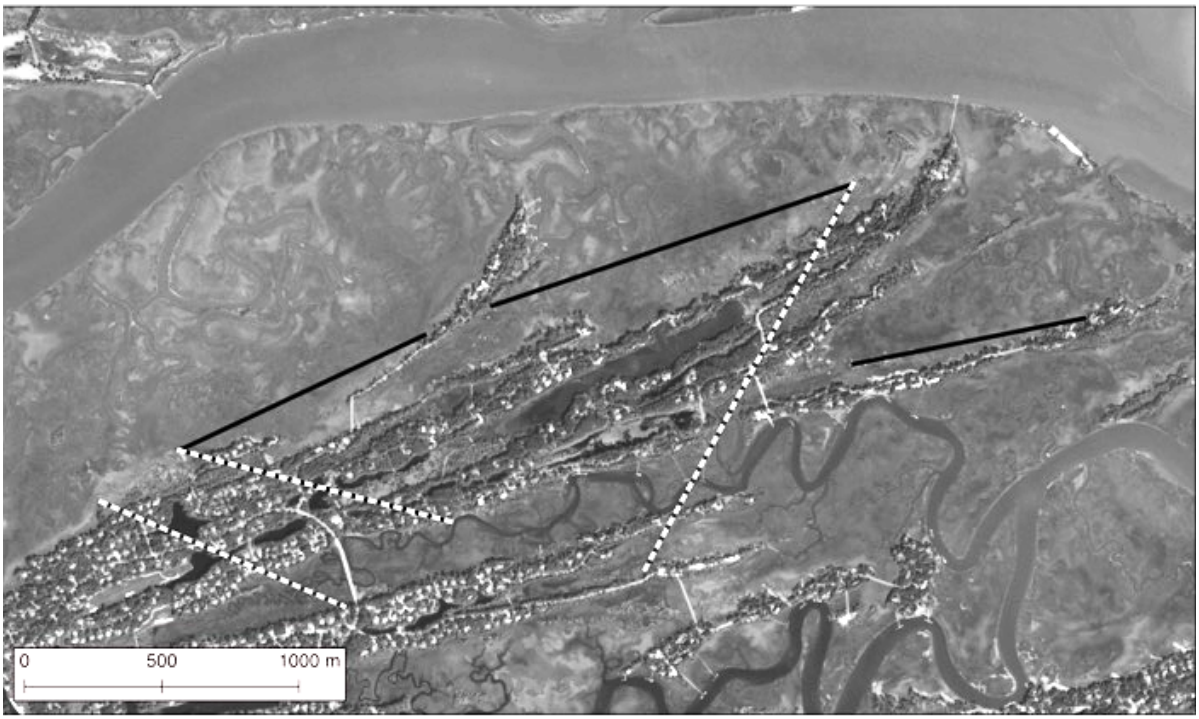


Figure 3.

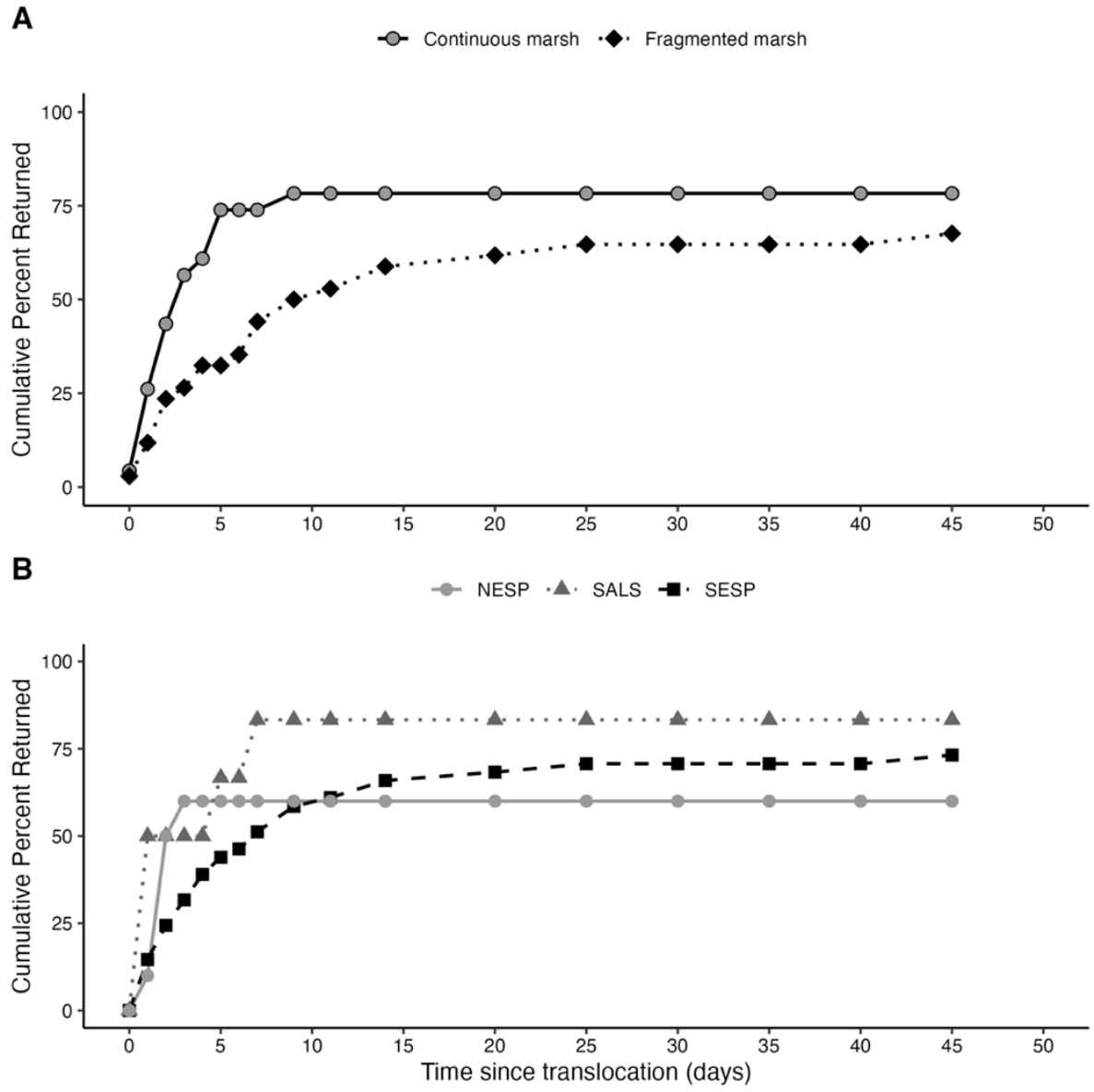
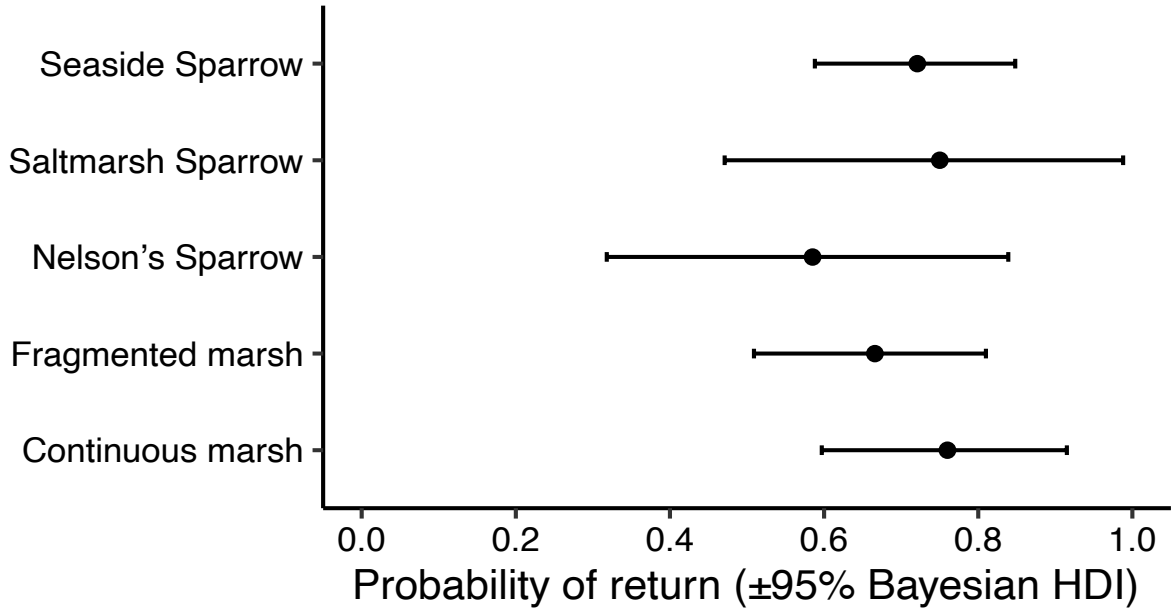

A
Continuous marsh
Fragmented marsh
Cumulative Percent Returned
100
75
50
25
0
0
5
10
15
20
25
30
35
40
45
50
B
NESP
SALS
SESP
Cumulative Percent Returned
Time since translocation (days)

Figure 4.


Seaside Sparrow
Saltmarsh Sparrow
Nelson's Sparrow
Fragmented marsh
Continuous marsh
0.0
0.2
0.4
0.6
0.8
1.0
Probability of return (±95% Bayesian HDI)

CHAPTER THREE

An Uncertain Future for Overwintering Populations of Tidal Marsh Songbirds in Coastal South Carolina

Keywords:

habitat loss, marsh birds, salt marsh, sea level rise, climate change, SLAMM, coastal wetlands

Abstract

Rising sea-levels are a major threat to salt-marsh habitats, and coastal areas in the Eastern United States are expected to experience some of the most dramatic changes in sea levels in the world. The consequences of sea-level rise to wildlife that depend on salt marshes could be devastating. In 2012, we initiated a study of three species of "marsh sparrow" that overwinter on Kiawah Island in South Carolina. Eight years of monitoring data indicated stable populations of all species, but this monitoring did not take into account potential losses of salt marsh habitat in response to sea-level rise. Here we used a Sea Level Affecting Marshes Model (SLAMM) to evaluate losses of wintering habitat for marsh sparrows. In addition, we evaluated the effects of sea-level rise on high-water refugia (i.e., specific patches of elevated high marsh habitat) used by the birds during above-average high tides. We specified four different sea-level rise scenarios in our models and found that even the most moderate predictions for sea-level rise entailed dramatic losses of salt-marsh habitat on Kiawah Island. For the more severe sea-level rise

scenarios, our models predicted that Kiawah would not likely sustain overwintering marsh sparrows by the year 2075. Fortunately, there are conservation measures that can mitigate these effects, and the human residents of Kiawah Island are actively engaged in long term measures to preserve salt marsh habitats.

Introduction

Tidal salt marshes are unique and dynamic ecosystems that support a substantial amount of biodiversity on almost every continent. They are also one of the most vulnerable land cover types to increases in sea level. This vulnerability is particularly pronounced when coupled with human development of coastal areas. Salt marshes typically respond to changes in sea level rise by shifting inland as previously dry areas are inundated, but dikes and other landscaping fortifications generally prevent this introgression. The resulting loss of marsh habitat warrants careful consideration of the risks posed to plants and wildlife that rely on coastal salt marshes. When we can appreciate these risks we can more wisely devise conservation strategies and allocate resources to both hold off extirpation/extinctions and promote coexistence among human and natural communities.

Salt marshes in the eastern United States are of great concern to conservationists both because of the biodiversity they support and because of the density of the human population in the region. Among the many species that depend on these east-coast salt marshes are three species of sparrow: Seaside Sparrow (*Ammospiza maritima*), Saltmarsh Sparrow (*Ammospiza caudacuta*), and Nelson's Sparrow (*Ammospiza nelsoni*). Each of these species appears to be dependent on salt marshes for wintering habitat as they are rarely found in any other landcover type. On Kiawah Island in South Carolina, these three species have been the subject of long-term

population monitoring, which has yielded estimates of survival rates and population density (Chapter 1). Additional studies on the same population have revealed a high degree of site fidelity in all three species (Chapter 2), which suggests that individuals have limited ability to disperse to other locations in response to habitat loss. These studies set the stage for a marsh-sparrow risk assessment that is centered around sea-level rise projections and the associated loss of marsh habitat Kiawah Island. Although Kiawah Island is a relatively small part of the east coast, it is arguably representative of much of the surrounding region both in terms of natural land cover and human development.

This study employs a Sea Level Affecting Marshes Model (henceforth SLAMM) to forecast losses of marsh habitat around Kiawah Island at different time points and under four sea-level rise (SLR) scenarios. We then combine these habitat losses with density estimates for each marsh sparrow species to evaluate the prospects for future populations. In addition, we use sea-level data from NOAA's models of mean high tide data to assess the fates of specific high-water refugia (*i.e.*, patches of marsh that remain above water at high tide). These refugia are important for the marsh sparrows because they congregate to these areas when the remainder of their habitat is inundated. This study seeks to motivate conservation initiatives that can mitigate losses of tidal marshes and/or make new areas available for marsh dependent species.

Methods

Study system

Kiawah Island (32°36'43.64" N, 80°4'27.51"W) is a ~4,047 ha barrier island that stretches 16 km in a southwest to northeast orientation and is about 2.4 km across at its widest point. It is located approximately 24 miles south of Charleston, South Carolina, USA, and hosts a private residential

community and a luxury beach-resort industry. The human population on Kiawah Island ranges from ~1,400 people in the winter to upwards of 10,000 people in the summer. The flat upland areas in the interior of the island are dominated by artificial habitat (*e.g.*, golf courses, hotels, and residences) and maritime forest. Outside these upland areas, Kiawah contains some 15 different terrestrial and aquatic habitat types including intertidal beach, maritime grassland, salt shrub thicket, intertidal mud/salt flats, and salt marsh.

Habitat used by all three marsh sparrows is almost exclusively limited to salt marsh. The salt marsh system can be divided into two zones based on variation in flooding and elevation: the high marsh zone, which abuts the upland border (aka transitional marsh) and is flooded with salt water for only one to two hours each day, and the low marsh zone, which spans the lower elevation areas from tidal creek bank to high marsh and is covered with salt water for half of the day. The birds move between these two zones in response to the twice-daily ebb and flow of tides, foraging primarily within the low marsh when it is exposed at low tides and then retreating to high marsh areas when the incoming tide floods the low marsh. At extreme high tides (*i.e.*, spring tides), marsh sparrows congregate in high densities on the few patches of marsh habitat that remain above water. These refugia are likely a critical landscape feature for marsh sparrows, as it is unclear how they would cope with spring tides if these refugia were not available.

Marsh sparrow populations on Kiawah Island were monitored for eight years (the winters of 2012/13 to 2019/20), by capturing and banding birds at their high-tide roost sites during spring tides (Chapter 1). This work indicated that the local population was stable, with no evidence of dramatic changes in density for any of the three species. However, densities for Nelson's Sparrows were low in some years, with population estimates as low as 181 individuals within the ~16,500 ha of salt marsh habitat currently associated with the island. The population monitoring

occurred at 18 patches of high marsh habitat (aka roost sites or high-tide refugia), which likely hosted most of the marsh sparrow population during spring tides. However, there were other known and suspected refugia that were not used as banding sites, mainly because they were too difficult to access and/or difficult to sample using our capture methods. The eight years of population monitoring indicated high rates of within-winter fidelity to roost sites among all three marsh sparrow species, and low rates of movement among roost sites between winters. Of the 706 birds that were captured two or more times, 77% were recaptured at their original roost site (Chapter 1), and a translocation study involving these same species documented individual birds rapidly returning to their preferred high tide refugia following displacements of up to 2 km (see Chapter 2).

Forecasting marsh habitat loss using SLAMM – To predict the impacts of SLR on wintering marsh sparrow habitat at Kiawah Island, we use SLAMM (version 6.7 beta; https://warrenpinnacle.com/) in conjunction with ArcGIS Pro 3.1.2 (ESRI 2023). SLAMM interpolates the impact of changes in sea level on marsh habitats by combining a digital elevation model (DEM) with a map of land surface types and then simulating a persistent decrease in land surface elevation (rather than increasing sea level). The resulting product is a map of land surface types derived from the original map but altered to account for relatively higher water levels. SLAMM is widely used as a predictive tool for evaluating the potential environmental and economic effects of SLR within coastal areas (e.g., Craft et al. 2009, Fernandez-Nunez et al. 2019, Hunter et al. 2017, Woodland et al. 2017).

For this study, we used the most recent 2017 LIDAR DEM data available for our study area (OCM Partners, 2023: 2017 SC DNR Lidar DEM: Coastal Counties (Berkeley, Charleston and Williamsburg Counties), https://www.fisheries.noaa.gov/inport/item/57112), which was

downloaded from NOAA's Digital Coast website (https://coast.noaa.gov/digitalcoast/data/). This high-resolution (i.e., 1-m spatial resolution, and 0.06-m vertical accuracy) DEM data was originally produced for the NOAA Office for Coastal Management's Sea Level Rise and Coastal Flooding Impacts Viewer (https://coast.noaa.gov/digitalcoast/tools/slr.html). The original data used the world geodetic coordinate system and had a cell size of 2.69×10^{-5} degrees. Using ArcGIS Pro 3.1.2 (ESRI, Redlands, California, USA), we reprojected and resampled the DEM data to generate a new DEM with a 2.68-m spatial resolution, which was subsequently clipped to a 1-km boundary area centered around Kiawah Island. In addition to the DEM, SLAMM requires a corresponding grid of slope values, which we generated using the *Slope* tool in the Spatial Analyst toolbox in ArcGIS Pro. We downloaded 2017 National Wetland Inventory wetland distribution data from the National Wetlands Inventory, which is made available by the United States Fish and Wildlife Service (USFWS 2017). These data were originally rendered as a shape file, and we used ArcGIS Pro to convert it to gridded data that matched the extent and resolution of the DEM and slope raster. The three raster maps were converted from raster format to the required ASCII text format for SLAMM using the *Raster to ASCII* conversion tool in ArcGIS Pro.

For our SLAMM simulation, we ran four different SLR scenarios with a fixed rise of 0.72, 1.18, 1.62, and 2.11 meters by the year 2100, and we refer to these scenarios as 'Intermediate Low,' 'Intermediate,' 'Intermediate High,' and 'High,' respectively. For each of these scenarios, our SLAMM simulations generated maps of spatial distribution of relevant coastal wetland habitats for the years 2050, 2075, and 2100 (Table 1). We selected these four SLR scenarios based on the most recent projections of relative SLR from NOAA (Sweet et al., 2022) for the nearest available location (i.e., Charleston, SC).

We used tidal datums and SLR trend data from a tide station in nearby Charleston, SC (station ID# 8665530) to assign values for several site parameters within SLAMM. These data include historic trend of SLR, Great Diurnal Tide Range (GT), and elevation correction based on the mean tide level. The historic trend of SLR in the study area is based on monthly mean sea level data for the period of 1901–2022 from the tide station in nearby Charleston, SC (station ID# 8665530; https://tidesandcurrents.noaa.gov/). This SLR estimation was 3.44 mm/yr. We used a mean vertical accretion rate for salt marshes which we calculated from estimates reported for South Carolina (Crotty et al. 2020). These estimates ranged from -3.97 to 9.62 mm/yr. Finally, we used a Great Diurnal Tide Range (GT) value of 1.757 m, which we obtained from the tide station in nearby Charleston, SC.

In addition to quantifying changes to landcover distributions with SLAMM, we evaluated how rising water levels would affect the availability of high-water refugia which marsh sparrows seem depend on during spring tides. We used aerial photos in conjunction with field observations to identify high-water refugia currently available to marsh sparrows at Kiawah Island, and we manually generated a polygon around each refuge in ArcGIS Pro. We then obtained SLR data produced by NOAA's Office for Coastal Management (OCM) for their Sea Level Rise Viewer web mapping tool (https://coast.noaa.gov/digitalcoast/tools/slr.html). This data is used to display the extent of inundation due to SLR from 0-10 feet above mean higher high water (MHHW), which is defined as the average of the higher high water height of each tidal day observed over the National Tidal Datum Epoch (~19 years). Data were available in 1-foot increments from 0-10 feet above MHHW for Charleston, SC, and we generated inundation maps (i.e. sets of polygons representing the extent of surface water) for eight SLR scenarios from 1 to 7 feet. Because these maps show inundation relative to MHHW, we could use them to determine both the total area of

high tide refugia that would persist under the different SLR scenarios as well as which specific refugia would become inundated and thus no longer be available to marsh sparrows.

To analyze refuge persistence, we imported the polygons generated for each refuge into R along with the sea-level-rise data from NOAA, and we cropped the sea-level-rise polygons to a 1000m buffer around Kiawah Island. For each potential refuge, we cropped the sea-level-rise polygons again to the area surrounding the refuge and converted the cropped polygons to a 1x1 meter raster. We then set the raster values to 1 for land and 0 for water and used the extract function in the R package raster (citation) to count the number of land pixels in each refuge polygon. We used the zero sea-level-rise inundation map as a baseline to calculate the current number of refugia and their collective area. From this baseline we calculated losses of refugia and refuge area across the other sea-level-rise scenarios.

Results

SLAMM analysis for all sea level rise scenarios predicted dramatic losses of salt marsh habitat, ranging from losses of 55% to nearly 100% by the year 2100 (see Table 2). We note that for all scenarios except ‘Intermediate Low’ over 90% of the Kiawah salt marsh will be lost by 2100 according to SLAMM. In the absence of mitigation efforts or behavioral adaptations in the bird species, it is likely that wintering marsh sparrow populations on Kiawah Island will cease to exist under all but the least severe water-rise scenario. The only question is, “When will it happen?” Even the ‘Intermediate Low’ water-rise scenario will entail loss of more than 50% of the salt marsh by 2100, which calls into question the viability of the marsh sparrow population. SLAMM results for ‘Brackish Marsh’ similarly showed dramatic declines in surface area, with more than 90% lost by 2100 under the “Intermediate,’ ‘Intermediate High,’ and ‘High’ scenarios.

For the analysis of high-water refugia persistence at Kiawah Island, we identified 85 potential refugia, ranging in area from 53 m^2 to 32,437 m^2 (Fig 4). According to the NOAA sea-level rise data, an increase in sea level of just 1 foot would inundate over 40% of the area currently available as high water refugia, although only two refugia would be lost entirely (Table 3). The effects of a three-foot increase in seal level include the loss of 58 individual refugia (68% of the current 85) with the total area reduced by about 95%. Under the 6 and 7-foot scenarios, only 3 and 2 refugia would remain above water at high tide respectively, and they would amount to less than 1% of the total area now available.

Discussion

Results from the SLAMM analysis and the analysis of high-water refugia persistence forecast major habitat losses for overwintering marsh sparrows at Kiawah Island. Even the mildest projections for sea-level rise are associated with losses of more than 50% of Kiawah Island's marsh habitat and high-water refugia by the year 2100. Under the more severe sea-level rise scenarios extirpation of the marsh sparrow populations is likely barring any conservation efforts to preserve or expand salt marsh. Although the scope of our analysis is limited to Kiawah Island, it is reasonable to assume similar effects of sea level rise on salt marshes throughout the region. Kiawah Island is representative of many coastal communities where the pressures of development and human activity … Infrastructure, such as revetments and bulkheads, meant to stabilize shores and protect human interests (e.g., homes, roads) from storm surges and coastal flooding will likely reduce the extent of future marsh sparrow habitat by limiting the ability of the salt marsh to migrate back (landward) as sea level rises (Titus et al. 2009). If we extrapolate

the situation from Kiawah Island to the larger coastline, it becomes clear that the risk to marsh sparrows is substantial.

Quantifying reduction in marsh sparrow populations in response to losses of marsh habitat requires several assumptions regarding how the birds respond to fragmentation and the amount of continuous marsh required by the marsh sparrow species for successful foraging. Also, it is important to account for the birds' need for high water refugia. In short, it is important not just to consider the amount of suitable habitat that is available, but also how much of the habitat actually meets the needs of the birds. While home range and territory sizes for marsh sparrows during the breeding season are relatively well known (Shriver et al. 2010; Greenlaw et al. 2022), is not clear how much tidal marsh habitat is required for a single marsh sparrow during the non-breeding wintering period (i.e., November – March). An examination of unpublished GPS tracking data from four individual Seaside Sparrows indicated that wintering home ranges for this species in our study area ranged from nearly 1 ha to a little more than 5 ha, and that these birds demonstrated very little movement across the larger landscape during the winter (Appendix C). Similarly, multi-year mark-recapture efforts (see Chapter 1) and a translocation study (see Chapter 2) indicated high levels of site fidelity to specific locations within the salt marsh system for all three marsh sparrow species within and between winter seasons, and little propensity for individuals to explore or exploit the larger tidal marsh landscape. Hence the prospect of marsh sparrows moving among small, isolated patches of habitat seems unlikely, and large expanses of contiguous salt marsh will be critical for sustaining marsh sparrow populations. Unfortunately, large patches of marsh will become increasingly rare as the sea level rises (Fig 3). Therefore, we are led to suggest that declines in marsh sparrow populations will outpace losses of marsh

habitat, and that Kiawah Island may become unable to support wintering marsh sparrows within the next 50 years in the absence of conservation/restoration efforts.

Loss of habitat will be gradual, which may afford time for the birds to develop behavioral responses to habitat loss. These responses could include inland shifts in wintering areas and use of forests or other non-marsh habitat. It remains to be seen whether the response to marsh habitat loss will be dominated by selection (i.e., decreases survival of birds that persist in current habitat preferences) or behavioral adaptation (i.e., birds adjusting to habitat change by broadening the types of habitats used). Continued monitoring of Kiawah's marsh sparrow populations is needed to establish whether behavioral adaptations and/or selection for reduced site fidelity are occurring.

An important limitation to long term predictions about marsh habitat loss is uncertainty about the degree of sea level rise that will occur. Sea level rise projections for coastal South Carolina differ among studies. Strauss et al (2014) predict an increase of 1.22 m by the year 2100, which is an average of model estimates that range from 0.55 m to 1.98 m of increase by 2100. Morris and Renkin (2020) predict a more moderate sea level increase 0.65 m by 2100. A full range of models is presented by Sweet et al (2022) with sea level increases of 0.6 m to 2.2 m by 2100. These scenarios are linked to projections for global temperature increases, which remain labile and dependent on the success of international cooperation on climate change mitigation strategies. Unfortunately, even the most optimistic scenarios with regard to sea-level rise will have dramatic effects on the salt marsh habitats of Kiawah Island.

The residents and local leadership of Kiawah Island are well aware of the threats posed by sea-level rise. In response to those threats, the Town of Kiawah Island (TOKI) Planning Department has initiated a Comprehensive Marsh Management Plan "as an effort to consolidate

existing marsh-related needs and recommendations across the Kiawah entities to guide future marsh management on the island" (Town of Kiawah Island, 2022).

There are potential management actions that can counter some of the habitat loss affecting marsh sparrows. As water levels rise, problems with flooding and infrastructure maintenance could devalue some of the developed areas on Kiawah Island, which may present an opportunity for marsh restoration. In addition, maintenance of high-water refugia could be a relatively simple yet valuable measure for sustaining marsh sparrows. Currently, these areas remain above water during spring tides and provide the only marsh patches available. To counter rises in sea level that threaten to inundate these refugia, ____. The refugia are generally not very large, so the cost of maintaining them would not be overwhelming.

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Tables

Table 1. Data inputs, site parameters, and SLR scenario options for Sea Level Affecting Marshes Model (SLAMM) simulation.

Model simulation inputs	
NWI photo date (year)	2017
DEM date (year)	2017
Direction offshore of DEM	South
Slope date (year)	2017
Spatial resolution (m)	5
SLR by 2100 (m)	0.72, 1.18, 1.62, 2.11
Projected time periods (years)	2050, 2075, 2100
Great diurnal tide range (m)	1.757
Historic trend (mm/yr)	3.44
MTL - NAVD88 (m); the elevation correction based on the mean tide level	-1.05
Salt marsh accretion (mm/yr)	2.41

Table 2. Areas (hectares) of coastal wetland habitats at Kiawah Island, SC under four different sea level rise scenarios for four different time periods.

Scenario	Year	Salt marsh	Brackish marsh	Intertidal shore	Mud flat	Open water	Scrub-shrub	Percent loss in salt marsh
Current Condition	2017	79.9	7.5	8.1	0.2	52.7	1.7	*NA*
Intermediate Low	2050	70.2	7.2	6.3	9.2	55.7	1.5	12.2
	2075	62.7	4.9	5.3	18.1	58.4	0.8	21.6
	2100	35.8	1.4	4.6	45.1	62.8	0.2	55.2
Intermediate	2050	66.8	6.7	5.9	12.8	56.6	1.2	16.5
	2075	34.0	1.9	4.7	47.1	62.0	0.3	57.4
	2100	5.4	0.1	4.3	68.8	71.4	0.1	93.3
Intermediate High	2050	61.4	5.5	5.5	19.0	57.8	0.9	23.2
	2075	12.5	0.3	4.4	67.1	65.6	0.1	84.4
	2100	0.7	0.0	3.7	41.8	103.8	0.0	99.1
High	2050	47.4	3.8	5.1	33.8	59.3	0.6	40.7
	2075	5.0	0.1	4.3	65.5	75.1	0.1	93.8
	2100	0.1	0.0	1.0	6.2	142.7	0.0	*NA*

Table 3. Effects of sea-level rise on high-tide refugia required by marsh sparrows during coastal floodings. Percentage columns refer to remaining refugia and cumulative area compared to the present situation (year 2017). Water levels are measured in meters above mean higher high water (MHHW).

	Number of high-tide refugia		Cumulative Area	
Water level (m)	Count	Percentage	hectares	Percentage
0	85	100	40.55	100
0.30	83	97.65	24.10	59.41
0.61	54	63.53	6.74	16.63
0.91	27	31.76	1.89	4.66
1.22	15	17.65	0.49	1.2
1.52	8	9.41	0.10	0.25
1.83	3	3.53	0.026	0.06
2.13	2	2.35	0.0059	0.01

Figure Legends

Figure 1. Study area (Kiawah Island, South Carolina; 32°36’43.64” N, 80° 4’27.51” W) with main coastal wetland habitats at under current conditions (i.e., year 2017).

Figure 2. Percent losses in salt marsh area at Kiawah Island predicted under four sea-level rise scenarios (Intermediate Low: 0.72m; Intermediate: 1.18m; Intermediate High: 1.62m; High: 2.11m). Percent losses at each time period were calculated relative to the year 2017, defined above as “Current Condition”.

Figure 3. Simulated maps of spatial distribution of coastal wetland habitats within a 1-km buffer of Kiawah Island, SC under four different relative SLR scenarios at three time periods (2050, 2075, 2100).

Figure 4. Locations of established and potential high tide refugia for Nelson’s, Saltmarsh, and Seaside Sparrows overwintering at Kiawah Island. (Established refugia are represented by white polygons; potential refugia are represented by yellow polygons).

Figures

Figure 1.

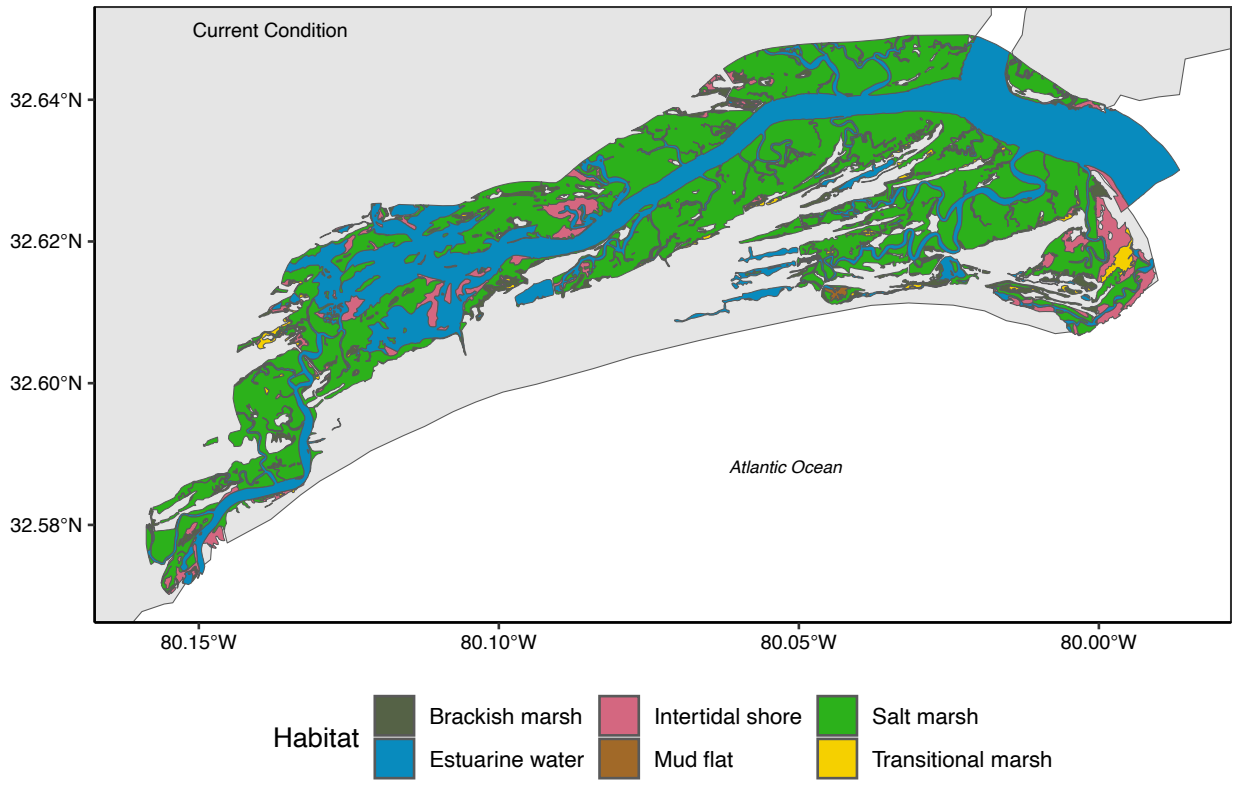


Figure 2.

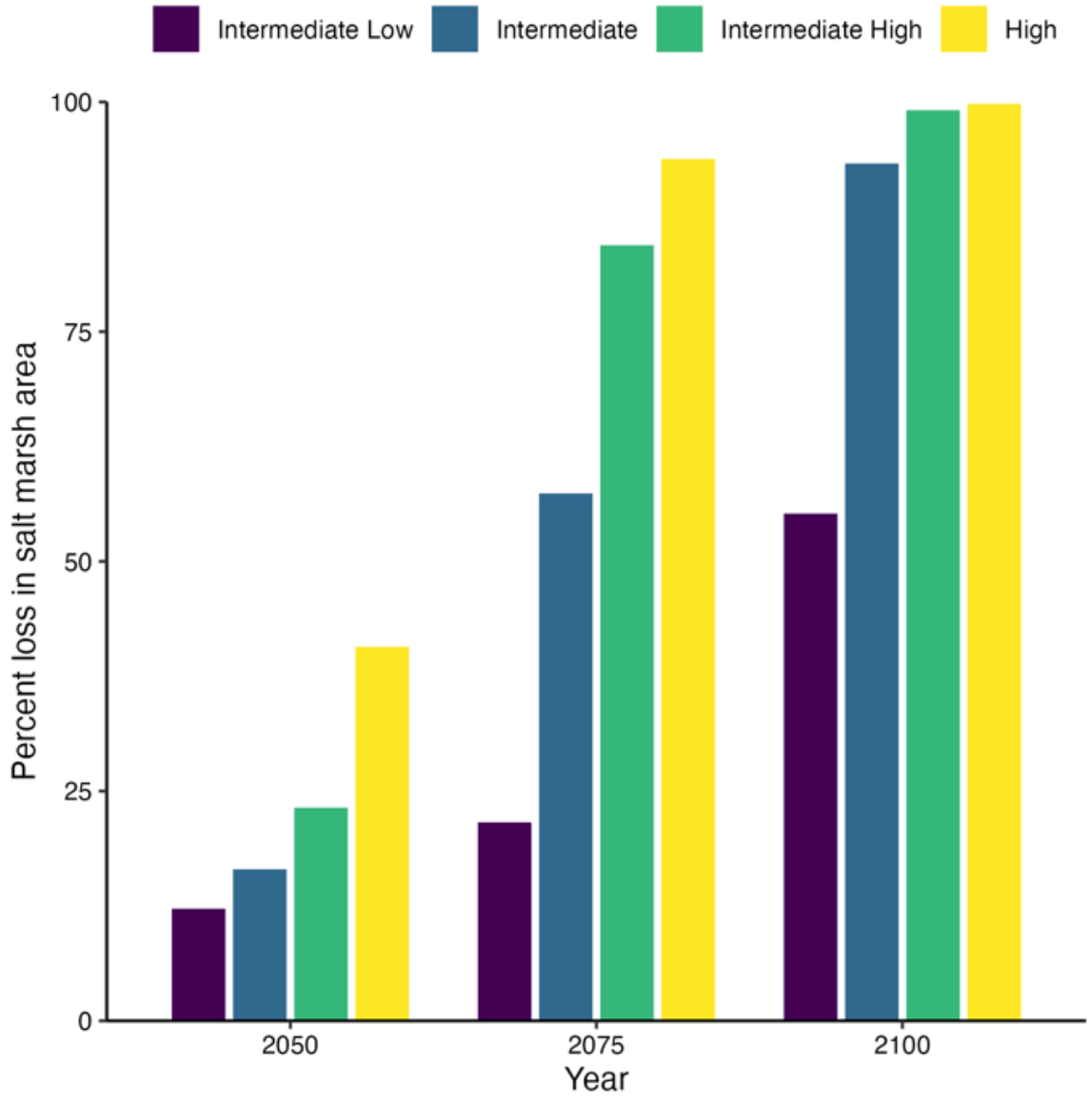

Intermediate Low
Intermediate
Intermediate High
High
100
75
50
25
0
Percent loss in salt marsh area
2050
2075
2100
Year

Figure 3.

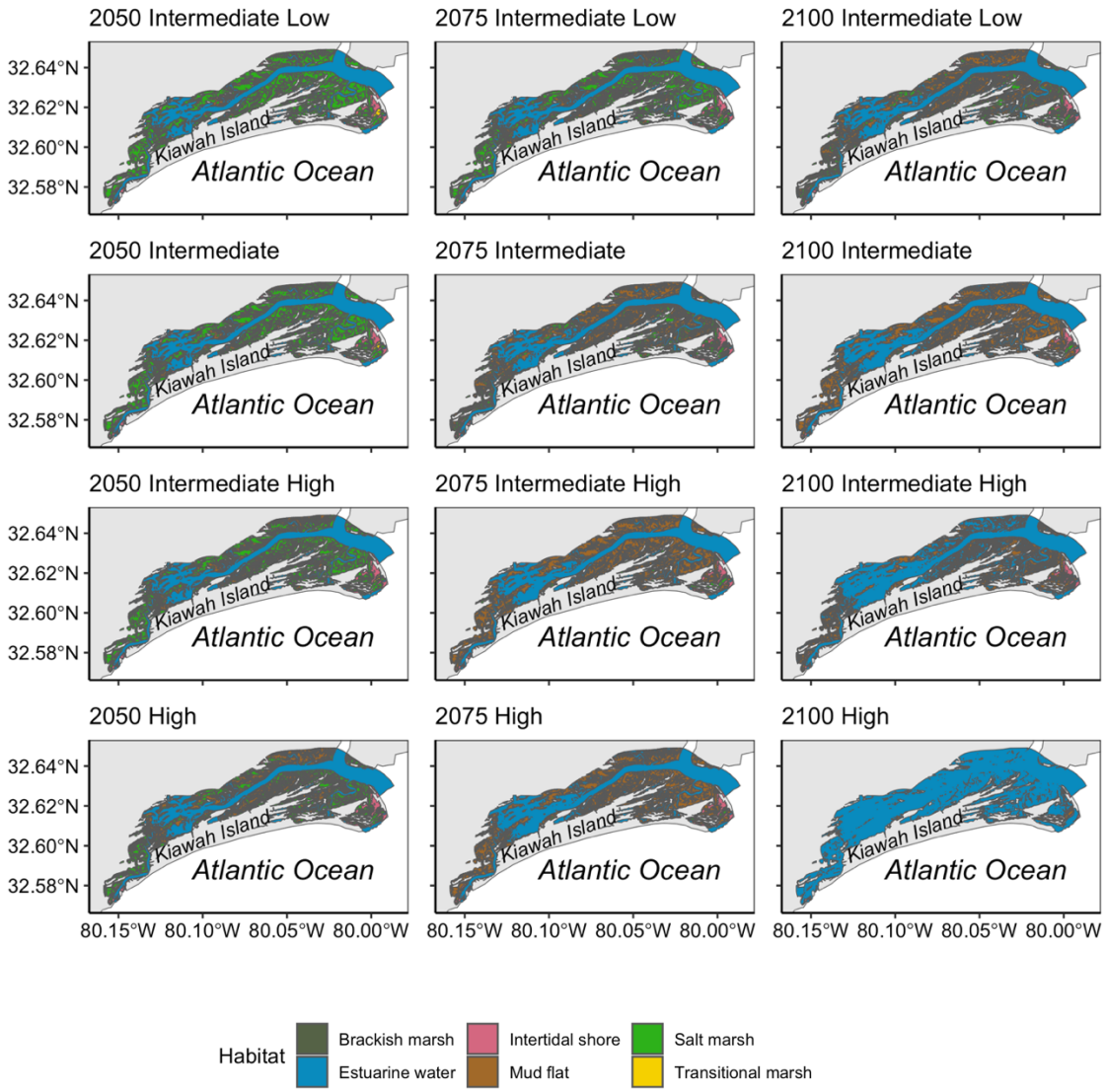
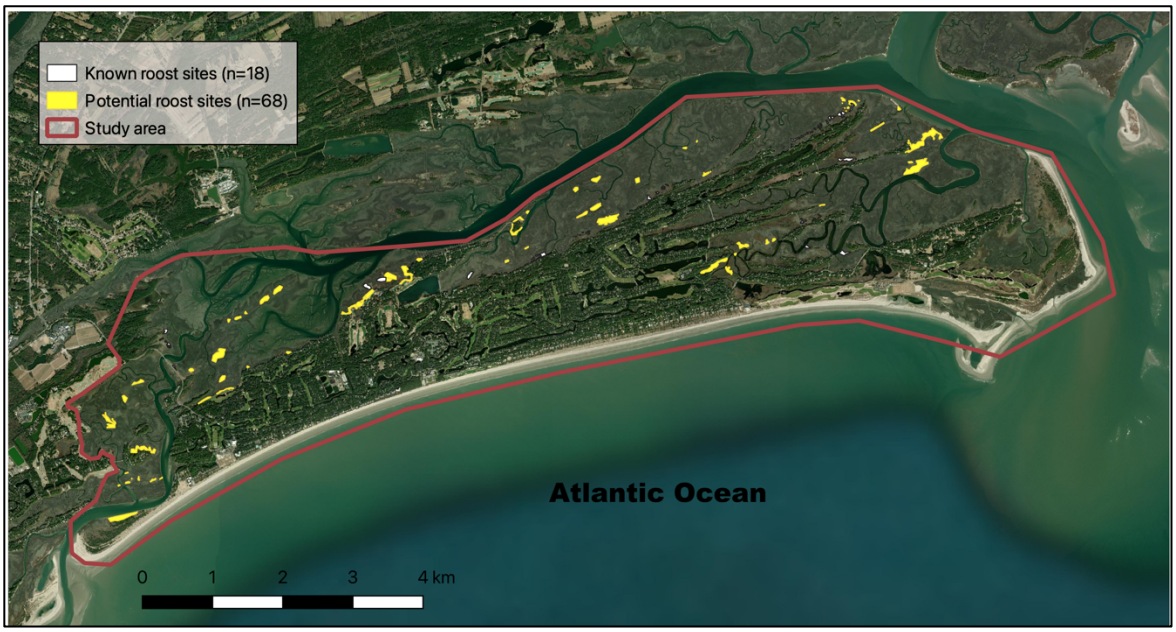

2050 Intermediate Low
2075 Intermediate Low
2100 Intermediate Low
2050 Intermediate
2075 Intermediate
2100 Intermediate
2050 Intermediate High
2075 Intermediate High
2100 Intermediate High
2050 High
2075 High
2100 High
32.64°N
32.62°N
32.60°N
32.58°N
Kiawah Island
Atlantic Ocean
80.15°W
80.10°W
80.05°W
80.00°W
Habitat
Brackish marsh
Estuarine water
Intertidal shore
Mud flat
Salt marsh
Transitional marsh

Figure 4.


Known roost sites (n=18)
Potential roost sites (n=68)
Study area
Atlantic Ocean
0
1
2
3
4 km