CONSERVATION ECOLOGY OF TIDAL MARSH SPARROWS IN NEW JERSEY

by

Rebecca A. Kern

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology

Spring 2015

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Rebecca A. Kern

Approved: _____
Jacob L. Bowman, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: _____
Mark W. Rieger, Ph.D.
Dean of the College of Agriculture and Natural Resources

Approved: _____
James G. Richards, Ph.D.
Vice Provost for Graduate and Professional Education

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: _____

W. Gregory Shriver, Ph.D.
Professor in charge of dissertation

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: _____

Jacob L. Bowman, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: _____

Kyle P. McCarthy, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: _____

Brian J. Olsen, Ph.D.
Member of dissertation committee

ACKNOWLEDGMENTS

Throughout the past four and a half years, this work has been influenced, directed, and occasionally wrestled from stagnation by numerous individuals; although space prevents me from fully acknowledging and appreciating your crucial roles, please know this process truly would not have been possible without you! First and foremost, my deepest thanks to my advisor, Greg Shriver. Thank you for giving me the opportunity to join SHARP (Saltmarsh Habitat and Avian Research Program) and for your excellent mentorship throughout two advanced degrees. Thank you for challenging me to think critically and creatively, to present clearly and confidently, and to passionately pursue conservation. I also thank my dissertation committee, Dr. Jake Bowman, Dr. Kyle McCarthy, and Dr. Brian Olsen, for their input and guidance. My excellent field technicians deserve special acknowledgement for their diligence and great senses of humor throughout long and hot summers: A. Anholt, N. Banet, D. Faith, M. Grasso, A. Mankofsky, T. Pitcher, M. Rhode, and J. Warner. The staff at Edwin B. Forsythe NWR provided invaluable support for field work with trucks, boats, and housing. Forsythe NWR staff P. Castelli, B. Crouch, V. Turner, J. Heise, and M. Schvetz were especially key to the success of this project. I thank the graduate students, past and present, in the Department of Entomology and Wildlife Ecology for their support and for providing a great community in which to spend these past seven years. Many thanks also goes to the members of SHARP, whose cooperative collaboration has made this process more fulfilling, enriching, and exciting than I ever expected. Being a part of this "extended lab group" has truly been a highlight of my

graduate career! Finally, a very special thanks to Whitney Wiest, fellow Shriver-labmate, co-instructor, and saltmarsh enthusiast since 2008. This experience has been infinitely more constructive, educational, humorous, and memorable because you've been a part of it. There's no one else I would rather have shared this wild ride with!

This work would not have been completed without the support and love of my family and friends. Thanks, Mom and Dad, for always encouraging me, checking in about "the paper," and helping me to stay grounded through it all. I'm grateful for the wonderful community at Evangelical Presbyterian Church of Newark, which has been like a second family to me. Thank you, Jon, Meghan, and Olivia for your support and for helping me take time to relax. And special thanks to Anne for your steadfast friendship and comradery.

This dissertation is dedicated in memorium to Dr. Russell Greenberg and Dr. William Glanz, who made invaluable contributions as early committee members. Their passion and ideas provided the foundation for my thinking in many of the following chapters, and they will be deeply missed in the conservation community.

Funding for the research was provided by a Competitive State Wildlife Grant (US-5-R-1) via Federal Aid in Sportfish and Wildlife Restoration to the states of Delaware, Maryland, Connecticut, and Maine.

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ABSTRACT

From 2011 – 2013, I studied breeding populations of Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) sparrows on Edwin B. Forsythe National Wildlife Refuge, New Jersey, to inform conservation and management efforts. I compared nesting ecology and reproductive success of these endemic tidal marsh birds, evaluated the role of a nest flooding vs. nest predation tradeoff in shaping nest-site selection, described tidal marsh resiliency to a stochastic disturbance, and quantified the ability of management actions to improve sparrow population viability given sea-level rise impacts. Using data from 465 sparrow nests, I estimated nest flooding and nest predation probabilities using Markov chain models, and quantified a nest-site niche for each species as a 7-dimensional hypervolume. Counter to predictions, Seaside Sparrows had a 3.5 times lower nest flooding probability and a 1.6 times lower nest predation probability than Saltmarsh Sparrows, as well as a 66% larger nest-site niche. A flooding vs. predation tradeoff does not appear to be the primary influence on nest-site niche. Instead, time since marsh colonization may play a larger role, as the ancestral species, Seaside Sparrows, occupied a larger nest-site niche and had higher overall nest success.

Stochastic disturbances, such as storms, affect tidal marsh habitats and endemic species, but factors influencing species' responses are not well-understood. Hurricane Sandy made landfall on October 29, 2012 in New Jersey and had devastating impacts on human-dominated landscapes. Using pre- and post-storm measurements, I evaluated the short-term resilience, defined as a resistance to change

or a rapid return to pre-storm conditions, of vegetation cover/composition, meadow vole (*Microtus pennsylvanicus*) abundance, and Saltmarsh and Seaside sparrow abundance and reproductive success. By comparing measurements taken three to six months pre-storm with seven to 11 months post-storm, I found a high degree of resilience to Hurricane Sandy. Vegetation cover/composition and sparrow abundance and nest success remained largely similar between 2012 and 2013. Although meadow vole abundance was 1.5 – 19.2 times lower following the hurricane, I detected a rapid increase from June to July 2013, indicating resiliency in the population. Vole recolonization of the marsh may have been facilitated by proximity to upland refugia.

Sea-level rise (SLR) poses the most severe and immediate threat to endemic tidal marsh birds in North America. To inform managers of the relative benefit of management actions for tidal marsh birds given SLR impacts, I conducted a population viability analysis of Seaside Sparrows. I quantified the upper (0.75 m of SLR) and lower (0.35 m of SLR) bounds of probable SLR effects on Seaside Sparrows over 42 years, and compared the relative benefit of improving nest success and reducing habitat loss given SLR impacts. A total population decline of up to 70% was highly likely (mean likelihood = 0.96) under 0.75 m SLR, and improving nest success had a greater benefit than reducing habitat loss. Improving nest success under 0.75 m SLR resulted in a population decline that was equivalent to the decline predicted by 0.35 m SLR. To maintain viable populations of tidal marsh breeding birds over the short-term, management actions should focus on increasing nest success via predator exclusion or flood mitigation.

Chapter 1

AVIAN ADAPTATION TO TIDAL MARSHES: NICHE DIMENSIONS AND TRADEOFFS

Introduction

The niche has been a fundamental concept in ecology for over half a century, and continues to provide the foundation for our understanding of how species adapt to, evolve in, and compete for resources. Niche concepts provide an implicit connection between various fields of ecology, such as linking limiting factors with population dynamics in population ecology or explaining species distribution by environmental constraints in biogeography (Leibold 1995). Early ecologists focused on the environmental requirements (Grinnell 1917) and the environmental impacts (Elton 1927) of a niche, and Hutchinson (1957, 1978) combined these ideas into the fundamental and the realized niche. Although the contemporary ecological community disagrees on a precise niche definition, most acknowledge that it is shaped by numerous factors and is, therefore, inherently multidimensional (Hutchinson 1957, Hutchinson 1978, Pianka 1981, Tokeshi 1999). All biotic and abiotic factors influencing the persistence of a species can be incorporated into an "*n*-dimensional hypervolume" (Hutchinson 1957) that can take any shape or size, and can change over evolutionary or ecological time (Tokeshi 1999).

Within tidal marsh ecosystems, niches are shaped by a unique combination of physical and biotic factors. Tidal marshes form the dominant ecotone between terrestrial and marine ecosystems in eastern North America, and experience challenges

of both environments, such as water availability (flooding challenges terrestrial organisms and drying challenges marine organisms) and salinity (Bertness 1999, Mitsch and Gosselink 2000). Relatively few plants have adapted to these constraints, resulting in a low-diversity vegetation community that is dominated by herbaceous species (Mitsch and Gosselink 2000). Elevation, tide and salinity gradients, and competition and nutrient inputs, generally structure the plant community into two distinct zones that dominate most tidal marshes (Bertness and Ellison 1987, Bertness 1991, Levine et al. 1998, Emery et al. 2001); the high marsh zone (*Distichlis spicata* and *Spartina patens*) floods during monthly high tides, and the low marsh zone (*S. alterniflora*) floods during daily high tides (Bertness and Ellison 1987, Bertness 1991). The physical conditions of tidal marshes present adaptive challenges to terrestrial vertebrate species, resulting in the dominance of endemics, such as Saltmarsh (*Ammodramus caudacutus*) and Seaside (*A. maritimus*) sparrows (Greenberg and Maldonado 2006).

Saltmarsh Sparrows breed on tidal marshes from Maine to Virginia and are sympatric with Seaside Sparrows south of Connecticut (Greenlaw and Rising 1994). The breeding range of Seaside Sparrows extends throughout the southeast Atlantic and Gulf coasts (Greenlaw and Rising 1994, Post and Greenlaw 1994). Although they are closely related (Zink and Avise 1990, Chan et al. 2006), Saltmarsh and Seaside sparrows differ in many behavioral and life history traits. Saltmarsh Sparrows are promiscuous breeders, and males do not defend territories or provide parental care, while Seaside Sparrows form monogamous breeding pairs with established territories (Woolfenden 1956, Post and Greenlaw 1982, Greenlaw and Rising 1994, Post and Greenlaw 1994). Saltmarsh Sparrows have one of the highest documented rates of

multiple paternity of any bird species (Hill et al. 2010), while Seaside Sparrows have one of the lowest rates of extra-pair paternity in New World sparrows (Hill and Post 2005). These species also differ in nest-site selection, with Saltmarsh Sparrows building nests in the high marsh zone 8 – 16 cm off the ground, and Seaside Sparrows typically nesting in the low marsh zone 14 – 28 cm off the ground (Post et al. 1983, Marshall and Reinert 1990, Gjerdrum et al. 2005, Humphreys et al. 2007). However, each species exhibits plasticity in nest placement (Post and Greenlaw 1982), leading to questions about the bounds of suitable nesting habitat and the adaptive significance of nest-site selection. Defining a "nest-site niche" provides a method for quantifying these bounds, as well as the extent of nest-site overlap between the species, and investigating what characteristics of the marsh environment may have acted as selective forces on nest-site selection.

Nest-site niche can be influenced by environmental constraints, as well as interspecific interactions, such as competition (Gause 1934, Pianka 1981). Natural selection should produce nest-site niches that maximize reproductive output given these constraints. For tidal marsh sparrows, the majority of nest losses come from either flooding or predation (Greenberg et al. 2006, Reinert 2006), so nest-site niche may be shaped and driven by adaptation to these two forces. Building nests as high as possible theoretically minimizes the risk of flooding, but marsh vegetation offers relatively little vertical structure, so elevated nests could be more visible to predators. The opposing forces of flooding and predation create a paradox for terrestrial tidal marsh breeders (Marshall and Reinert 1990, Reinert 2006), which may face a tradeoff between these causes of nest failure (Greenberg et al. 2006). If there is a tradeoff that shaped nest-site niche, I predict that each species minimized nest losses due to one

cause at the expense of the other (Saltmarsh Sparrow minimized predation; Seaside Sparrow minimized flooding).

The role of flooding and predation in shaping Saltmarsh and Seaside sparrow nest-site niches can be further described by comparing the best predictors of nest flooding and predation for each species. If the niches evolved primarily in response to flooding and predation, I predict that nest-site features will be stronger predictors of flooding and predation probability than non-spatial, environmental variables (e.g. timing). Previous studies have demonstrated that the relative importance of nest-site features versus other environmental variables for predicting nest flooding and predation remains equivocal. Environmental variables, including the timing of nest initiation within the tide cycle, clearly influence nest flooding for both species (Marshall and Reinert 1990, Shriver et al. 2007), but the effects of nest-site features, such as height, are inconsistent and warrant further evaluation (Gjerdrum et al. 2005, Humphreys et al. 2007, Shriver et al. 2007, Bayard and Elphick 2011). Most research to date has focused on the effects of flooding on nest survival, so little is known about the factors that influence nest predation, particularly for Saltmarsh Sparrows (but see Post and Greenlaw 1982, DeRagon 1988, DiQuinzio et al. 2002, Gjerdrum et al. 2005).

Given their potential impact on reproductive success, evolution, and conservation, I studied the role of nest flooding and predation in Saltmarsh and Seaside sparrow ecology. The first objective was to calculate a multi-dimensional hypervolume nest-site niche for each species and determine how niche size and uniqueness varied between Saltmarsh and Seaside sparrows. The second objective was to determine whether a tradeoff existed between nest flooding and nest predation,

and if the tradeoff influenced nest-site niche partitioning. I then compared the relative importance of nest-site niche components and other environmental variables on the probability of nest flooding and nest predation for both species.

Methods

Study Area

I studied Saltmarsh and Seaside sparrows on the U.S. Fish and Wildlife Service's Edwin B. Forsythe National Wildlife Refuge (Forsythe NWR), New Jersey. Forsythe NWR spans 64 km of coastline and contains over 12,200 ha of tidal marsh, which is dominated by meadow cordgrass (*Spartina patens*), smooth cordgrass (*S. alterniflora*), spikegrass (*Distichlis spicata*), and Jesuit's bark (*Iva frutescens*; U.S. Fish and Wildlife Service 2004). In 2011, I established three study sites on Forsythe NWR based on management history, landscape context, and bird abundance (Figure 1). The AT&T site (14 ha; 39.697191° N -74.214032° W) and the Oyster Creek site (18 ha; 39.504815° N -74.426283° W) were historically managed with grid-ditching and open marsh water management (OMWM), while the Mullica Wilderness site (17 ha; 39.536166° N -74.438021° W) was within a federally designated wilderness area and contained no ditching or OMWM. The sites also spanned a gradient of proximity to non-marsh habitat. Using landcover data from the National Oceanic and Atmospheric Administration's Coastal Change Analysis Program (NOAA CCAP; National Oceanic and Atmospheric Administration 2014), I quantified the proportion of landcover types within 500 m and 1000 m buffers of each study site in ArcGIS. The percentage of vegetated, non-tidal marsh land (including upland forest, scrub/shrub, grassland, agriculture, and forested wetland) at both scales was 98 – 99%

greater at AT&T than at Mullica Wilderness (500 m: 19.2% versus 0.40%; 1000 m: 36.2% versus 0.24%) and 81 – 82% greater at AT&T than at Oyster Creek (500 m: 3.5%; 1000 m: 7.0%). The percentage of developed (non-vegetated) land showed the same trend, with AT&T having 100% more than Mullica Wilderness (500 m: 1.3% versus 0.0%; 1000 m: 1.9% versus 0.0%) and 63 – 83% more than Oyster Creek (500 m: 0.5%; 1000 m: 0.3%). Lastly, the sites contained relatively equal abundances of Saltmarsh and Seaside sparrows, allowing conclusions to be drawn without sample size constraints for either species.

Field Methodology

I monitored Saltmarsh and Seaside sparrow nests on all study sites from 15 May – 30 August, 2011 – 2013. Nests were primarily located by observing adults flushing from the nest site or carrying food. I marked each nest using a GPS and with two wire stake flags, placed on opposite sides of the nest, two meters and four meters away, respectively.

To quantify nest-site niche, as well as features that influenced nest fate, I estimated nest structure and nest-site characteristics. Nest structure attributes (nest height and nest canopy cover) were recorded on the day of discovery for nests with eggs or chicks. For nests discovered during construction, I delayed recording nest structure measurements until after egg-laying had begun. I determined nest height by measuring the distance from the marsh surface to the bottom of the nest cup. I measured nest canopy cover by placing a white paper disc (6.5 cm in diameter) in the nest cup and estimating the percent of the disc that was visible from directly above. Within one week of nest termination, I estimated percent cover of all vegetation cover classes (*Spartina alterniflora* — hereafter "low marsh" —, *S. patens* and *Distichlis*

spicata — hereafter "high marsh" —, bare ground, and open water) within a 1-m^2 quadrat centered on the nest. I also took the following measurements at the center and the midpoint of each side of the 1-m^2 quadrat: thatch depth (dead vegetation lying parallel to the marsh surface) and vegetation height (as the vegetation stood naturally without being straightened).

I visited each nest every 2 – 4 days and recorded the nest contents, female activity, and nest condition, such as disturbed, damp, or submerged. I assigned each nest one of five possible fates. *Fledged* (or successful) nests had at least one live chick leave the nest after reaching ≥10 days of age, counting hatch-day as day one (Martin and Geupel 1993, Greenlaw and Rising 1994, Post and Greenlaw 1994). I considered nests fledged if, on the visit when the chicks were ≥10 days old, I found a well-worn, empty nest (sometimes with fecal material in/around the nest), and no sign of disturbance. Failed nests were placed into one of three categories: *flooded, depredated,* or *failed unknown cause*. I assigned a fate of *flooded* if, following a high tide or heavy rain event: 1) all nest contents were lost and the nest was damp or completely submerged, 2) intact eggs or dead chicks without evidence of external injury were found within a few meters of the nest, or 3) intact cold and dirty eggs were present in the nest and subsequently fail to hatch (Bayard and Elphick 2011). I assigned *depredated* if: 1) all nest contents were lost and the nest structure was disturbed, 2) egg fragments or dead chicks with external injuries were present in or near the nest, or 3) all nest contents were lost on a day when tides could not have accounted for the loss. *Failed unknown cause* was assigned if there was conflicting evidence for flooding and predation (i.e. a nest was found empty after a high tide, but was not damp or disturbed) or if a nest appeared to have been abandoned. The fifth

possible nest fate was *unknown* and was typically assigned if chicks disappeared when they were 9 days old. It was unknown whether 9-day-old chicks could have survived after leaving the nest.

Data Analysis

I estimated and compared the nest-site niches for Saltmarsh and Seaside sparrows by constructing hypervolumes from seven nest-structure and nest-site variables. Using package 'hypervolume' (Blonder et al. 2014) in program R (version 3.1.0; R Core Team 2014), I inferred the hypervolume from the nest structure and nest-site observations using a thresholded multidimensional kernel density method (Blonder et al. 2014). This package computed high-dimensional hypervolumes using box kernels, importance-sampling Monte Carlo integration, and recursive tree partitioning, which overcame computational inefficiencies that limited previous hypervolume creation methods to low-dimensional systems (Broennimann et al. 2012, Petitpierre et al. 2012, Blonder et al. 2014). A full stochastic description of the hypervolume was produced from known point density and volume, as well as random points generated within the box kernels surrounding each known point (Blonder et al. 2014).

The seven nest-structure and nest-site variables included nest height, nest canopy cover, thatch depth, and average vegetation height and cover of high marsh, bare ground, and open water within 1 m^2 of the nest. These variables have been found to be important components of Saltmarsh and Seaside sparrow nests in other studies (e.g. Post 1981, Marshall and Reinert 1990, DiQuinzio et al. 2002, Gjerdrum et al. 2005, Humphreys et al. 2007, Gjerdrum et al. 2008, Bayard and Elphick 2011, Kern et al. 2012). I evaluated all covariates for collinearity and excluded low marsh cover

from the hypervolume calculations because it was negatively related with high marsh cover (adjusted $r^2 = 0.81$, $P < 0.001$). I normalized all covariates using z-scores to enable hypervolume axes comparisons. For the hypervolume estimation, I used a bandwidth of 0.64, calculated using the Silverman estimator (Silverman 1992), generated 5,000 random points within each box kernel, and used a quantile threshold of 0% (all points included in the final estimation). I compared the volume, intersection, and unique components of the Saltmarsh and Seaside sparrow hypervolumes. The intersection and unique components were calculated using an *n*-ball test, in which a "ball" of a set radius is drawn around each point and points with overlapping balls constitute the intersection (Blonder et al. 2014).

To describe the magnitude of differences between Saltmarsh and Seaside sparrow nests for the seven vegetation variables, I used *t*-tests or Mann-Whitney U tests when non-normally-distributed data were indicated by D'Agostino's K-squared tests (Zar 1999). I controlled for the experiment-wise error rate using the Holm-Bonferroni correction with $\alpha = 0.05$ and $n = 7$ comparisons (Dean and Voss 1999, Zar 1999).

I used Markov Chain models in a competing risks framework to estimate the probability of nest flooding and nest predation for Saltmarsh and Seaside sparrows, and to determine covariates that best predicted nest fate. The Markov Chain algorithms were packaged in a standalone program (MCestimate; Etterson et al. 2007a, Etterson et al. 2007b) that linked daily cause-specific failure probabilities with covariates using a multinomial logit. This method presented an advantage over other types of nest failure estimators because it allowed multiple fates to be modeled as separately estimated parameters rather than as covariates to a single failure estimate

(Etterson et al. 2007a). Prior to analysis, I censored all observations for which the nest was found empty or had chicks that were old enough to fledge (≥10 days) to avoid misclassification of nest fate (Stanley 2004, Etterson et al. 2007a). A secondary result of this censoring was the exclusion of all nests that were only seen active on one visit because MCestimate required at least two active visits per nest to model failure. I also considered all nests with unknown fate to have fledged (n = 7 for Saltmarsh Sparrow, n = 11 for Seaside Sparrow).

I modeled the effect of covariates (see below) on nest flooding and predation, and compared models based on Akaike's information criterion corrected for small sample size (AIC_c) and model weights (w_i; Burnham and Anderson 2002). I considered models with $\Delta AIC_c < 2.0$ to be equivalent and calculated model-averaged parameter estimates among equivalent top-ranked models. To determine the relative importance of each covariate in predicting nest failure, I calculated the cumulative model weight by grouping models by their flooding or predation covariate and summing the model weights within each group (Burnham and Anderson 2002).

To determine the factors that best predicted sparrow nest flooding, I modeled the effect of six covariates for each species (Table 1). Nest-site covariates included nest height and high marsh or low marsh cover, while non-habitat covariates included year, date, site, and days post new moon. Prior to modeling, I evaluated covariates for collinearity and found that percent cover of high marsh and low marsh were negatively correlated (adjusted $r^2 = 0.82$, $P < 0.001$) for Saltmarsh Sparrows (all other adjusted $r^2 = -0.006 – 0.128$, $P = 0.99 – 0.001$). Thus, I included only high marsh in the Saltmarsh Sparrow models and only low marsh in the Seaside Sparrow models for both flooding and predation.

Each covariate had a specific prediction regarding its impact on flooding probability. Nest height was predicted to be inversely related to flooding. I predicted that the percent cover of high marsh (for Saltmarsh Sparrows) had a negative relationship because it typically flooded only during monthly high tides, while low marsh (for Seaside Sparrows) had a positive relationship because it flooded during daily high tides (Bertness 1999, Mitsch and Gosselink 2000). Due to the large between-year variation in tide height and precipitation, year was modeled as a categorical covariate and I predicted that it had a random relationship with flooding. I modeled date as an ordinal covariate that varied within nests (most other covariates were constant within nests). Flooding was predicted to decrease with date because tide height generally decreased through the breeding season (NOAA / National Ocean Service 2013) and because tidal marsh sparrows experience less nest flooding after achieving synchrony with the tidal cycle following an early nest loss (Shriver et al. 2007). I modeled the effect of study site to capture the known differences in landcover and management history, and because I observed differences in site flooding rate and severity.

Saltmarsh Sparrows experienced extensive nest flooding during new moon tides in other parts of their breeding range, so I modeled the effect of days between nest initiation and the most recent new moon (Shriver et al. 2007, Bayard and Elphick 2011). I calculated nest initiation date by subtracting four days (average length of nest construction; Shriver et al. 2007) from the first egg date. I used three methods for estimating first egg date, depending on the stage of the nest cycle in which I observed the nest. For nests observed during laying, I assumed that one egg was laid per day and counted backwards to determine the first egg date (Greenlaw and Rising 1994,

Post and Greenlaw 1994, Gjerdrum et al. 2005). For nests observed during the nestling stage, I estimated hatch date based on chick age and subtracted 15 (a site average clutch size of four plus a 12-day incubation period, beginning on the day of clutch completion) to determine the first egg date. To determine the first egg date for the remaining nests that were found during incubation but failed to hatch, I subtracted a site by year average discovery difference from the date of nest discovery. The average discovery difference was the average nest age at the day of discovery, calculated using nests found with full clutches that hatched. For each site in each year, 11 – 23 nests were used to calculate the average discovery difference, which ranged from 6.9 – 9.9 days. I modeled all covariates as single-effects on flooding and included an intercept-only model, resulting in seven flooding models for each species.

To determine the factors that best predicted sparrow nest predation, I modeled the effect of seven covariates for each species (Table 1). Many of the covariates used in the flooding models also had specific predictions regarding predation, including nest height, high marsh or low marsh cover, year, date, and site. I predicted that nest height and date had a positive relationship with predation because higher nests were more visible and because nest predator populations increased over the breeding season (Greenberg et al. 2006). I included high marsh (Saltmarsh Sparrows) and low marsh (Seaside Sparrows) cover because these vegetation zones may have contained different suites or abundances of predators. Two predation covariates that were not included in the flooding models were nest canopy cover and nest age (Table 1). I predicted that nest canopy cover decreased predation by providing concealment. I modeled nest age as an ordinal covariate that varied within nests (like date) and predicted that age had a positive relationship with predation. I calculated nest age by

estimating the first egg date (above) and subtracting it from the date of the first visit. Nest predation rates have been found to increase in the nestling phase compared to the egg phase, possibly due to chick vocalization and increased adult activity (Dearborn 1999, Burhans et al. 2002, Muchai and du Plessis 2005). I modeled all covariates as single-effects on predation and included an intercept-only model, resulting in eight predation models for each species. Lastly, I included a global model, containing all covariates for flooding and predation, for a total of 57 models for each species.

Results

I monitored 248 Saltmarsh Sparrow and 217 Seaside Sparrow nests from 2011 – 2013. After removing nests with an incomplete set of measurements, I constructed 7-dimensional nest-site hypervolumes from 186 Saltmarsh and 205 Seaside sparrow nests. The Saltmarsh Sparrow hypervolume (516.9 SD^7) was 1.7 times smaller than the Seaside Sparrow hypervolume (859.1 SD^7). Fifty-two percent of the Saltmarsh Sparrow hypervolume was unique (269.6 SD^7) compared to 71% of the Seaside Sparrow hypervolume (611.8 SD^7; Figure 2). Although overlap between species was present in all seven dimensions, inter-specific distinctions were visible in several variables, including nest height, vegetation height, and high marsh cover (Figure 3). Plotted on nest height, vegetation height and high marsh cover, the Saltmarsh Sparrow hypervolume covered a region with below-average nest height and above-average high marsh cover (Figure 4). In contrast, the Seaside Sparrow hypervolume covered a region with above-average nest height and vegetation height, but below-average high marsh cover (Figure 4).

Pair-wise comparisons indicated that Saltmarsh and Seaside sparrow nests differed in all habitat variables, and that all variables had a lower variance and range

for Saltmarsh Sparrows than Seaside Sparrows (Table 2). Saltmarsh Sparrow nests had two times more high marsh cover within 1 m^2 than Seaside Sparrow nests, while the vegetation height at Saltmarsh Sparrow nests was 22% lower than at Seaside Sparrow nests. Seaside Sparrow nest height and canopy cover were 1.6 times greater than Saltmarsh Sparrow nests. Percent cover of water and bare ground within 1 m^2 were 2.7 and 2.0 times greater, respectively, at Seaside Sparrow nests than Saltmarsh Sparrow nests (Table 2).

After censoring nests that had only one active visit and those missing covariate data, I modeled fate for 161 Saltmarsh Sparrow and 170 Seaside Sparrow nests, with an effective sample size of 2,849 exposure days. Of the Saltmarsh Sparrow nests, 43% fledged, 17% flooded, 26% were depredated and 14% failed due to an unknown cause. Of the Seaside Sparrow nests, 58% fledged, 8% flooded, 14% were depredated and 20% failed due to an unknown cause.

I did not find evidence of tradeoffs between flooding and predation. There were three top models for Saltmarsh Sparrow ($\Delta AIC_c < 2.0$; Table 3), while there was a single best model for Seaside Sparrow (Table 4). For Saltmarsh Sparrow, the model-averaged probability of success over the 26-day nesting period (±1 standard error) was 27% lower than Seaside Sparrow (0.19 ± 0.04 versus 0.26 ± 0.07). Both types of nest failure were more likely in Saltmarsh Sparrows than Seaside Sparrows. Saltmarsh Sparrow nest flooding probability was 3.5 times greater than Seaside Sparrow (0.21 ± 0.04 versus 0.06 ± 0.03), and nest predation probability was 1.6 times greater (0.38 ± 0.05 versus 0.24 ± 0.07).

For Saltmarsh Sparrows, days post new moon was the best predictor of nest flooding, but there was less model certainty regarding the cause of nest predation

(Table 3). Days post new moon, which appeared in eight of the top ten models with a cumulative model weight of 0.77, had a negative relationship with flooding probability (Figure 5A). Nests initiated four days after a new moon were four times less likely to flood than nests initiated 20 days after a new moon (Figure 5A). Nest predation was not clearly predicted by any covariates, as one of the three best models had a constant predation rate, and high marsh cover and nest canopy cover appeared in the other best models (Table 3). Predation probability had a positive relationship with high marsh cover (Figure 5B), and a negative relationship with nest canopy cover (Figure 5C). However, high marsh and nest canopy cover were not strong effects because the 95% confidence limits of their parameter estimates crossed zero (Table 5), and the cumulative model weights were relatively low (0.37 and 0.25, respectively).

In contrast to Saltmarsh Sparrow, there was more certainty regarding the importance of covariates for Seaside Sparrow nest failure. A single model with date best predicted Seaside Sparrow nest flooding and study site best predicted Seaside Sparrow nest predation (Table 4). Date had a relatively strong effect on nest flooding probability, as the 95% confidence interval of the parameter estimate did not cross zero (Table 5), and the cumulative model weight was 0.88. Flooding probability was 4.6 times greater for early nests (May 19 – June 19) than later nests (June 19 – July 19; Figure 5D), which corresponded to patterns in tides and rainfall. Although the mean tide height at Atlantic City, NJ was similar across the breeding seasons (2% change between May 19 and August 19, 2011 – 13), the standard deviation of tide height was 23 – 26% greater during May 19 – June 19 than during June 19 – July 19 or July 19 – August 19 (NOAA / National Ocean Service 2013). This increased variation, coupled with increased rainfall during the same period (24% greater during May 19 – June 19

than June 19 – July 19; NJ Weather and Climate Network 2014), may explain why early nests flooded more frequently than later nests. The 26-day predation rate was 1.5 – 4.5 times greater at AT&T (0.39 ± 0.10), which contained the highest amount of non-marsh habitat in the surrounding landscape, than at Oyster Creek (0.24 ± 0.05) and Mullica Wilderness (0.08 ± 0.05). The effect of site on predation was weaker than the effect of date on flooding, as the 95% confidence intervals of the site parameter estimates crossed zero (Table 5), and the cumulative model weight was 0.56.

Discussion

Quantifying nest-site conditions for Saltmarsh and Seaside sparrows as a multi-dimensional niche provided new insights into the ecology of these sympatric and closely related species. Seaside Sparrows selected a greater diversity of nest sites and had a 66% larger nest-site niche than Saltmarsh Sparrows, which translated to lower nest flooding and predation rates. That Seaside Sparrow nests occupied a broader range of conditions than Saltmarsh Sparrows was also indicated by the larger variance and range of the seven nest variables. The range of variables for Seaside Sparrows encompassed the range for Saltmarsh Sparrows in all cases except nest height, possibly indicating a great amount of overlap in nest-site conditions. However, 52% of the Saltmarsh Sparrow hypervolume was unique from Seaside Sparrow, indicating that these taxa select different components of marsh vegetation for nest-sites. Thus, describing nest-site niche as a 7-dimensional hypervolume revealed more distinctions between Saltmarsh and Seaside sparrow nest-site conditions than were evident in one-dimensional analyses. The seven variables incorporated into the hypervolumes have been shown to be important for Saltmarsh and Seaside sparrow nest-site selection and nest success (Marshall and Reinert 1990, Gjerdrum et al. 2005, Humphreys et al.

2007, Shriver et al. 2007), so although other factors likely influenced nest-site niche, the results are representative of nest-site conditions and provide a basis for further examination of the selective forces acting upon nest-site.

Cause-specific nest failure (nest flooding and nest predation) has the potential to be a selective force on nest-site niche. Because flooding and predation potentially act on nest-site selection in opposite ways, a tradeoff has been predicted to exist between them (Greenberg et al. 2006). If nest-site selection for each species evolved in response to this tradeoff, I predicted that each species minimized one cause of nest failure at the expense of the other. However, I found no evidence of this tradeoff as Saltmarsh Sparrows had higher probabilities of both flooding and predation than Seaside Sparrows. Tradeoffs may exist in other populations of tidal-marsh-breeding sparrows in North America, as flooding was negatively correlated with predation across 16 populations of Saltmarsh, Seaside, Nelson's (*A. nelsoni*), Savannah (*A. savannarum*), Song (*Melospiza melodia*), and Swamp (*M. georgiana nigrescens*) sparrows (Greenberg et al. 2006). The tradeoff identified in this previous study could result from a tradeoff at the marsh- and not the nest-site scale because the nest success estimates were from allopatric populations. For sympatric Saltmarsh and Seaside sparrows, however, it appears unlikely that a flooding-predation tradeoff plays a large role in nest-site selection.

Competitive exclusion of Saltmarsh Sparrows by Seaside Sparrows provides an alternative mechanism for nest-site niche partitioning. Larger-bodied birds are typically dominant nest-site competitors over smaller-bodied birds (Leyequien et al. 2007, Zeng and Lu 2009). Seaside Sparrows have 12% greater body mass than Saltmarsh Sparrows (data summarized from Post and Greenlaw 1982, Post and

Greenlaw 1994, Shriver et al. 2005), and behave aggressively towards them. Both sexes chase Saltmarsh Sparrows away from nest-sites and males act aggressively towards Saltmarsh Sparrows that land in their territory (Post and Greenlaw 1975). Nest-site competition between sympatric sparrows has not been widely observed, but one study suggested that the larger White-crowned Sparrow (*Zonotrichia leucophrys*) excluded the smaller Lincoln's Sparrow (*Melospiza lincolnii*) from nest-sites in Colorado grasslands (Beaulieu and Sockman 2012). Dominant competitors usually have fitness benefits over subordinates, as observed between White-rumped (*Montifringilla taczanowskii*) and Rufous-necked (*M. ruficollis*) snowfinches (Zeng and Lu 2009), as well as Great Tits (*Parus major*) and Blue Tits (*P.caeruleus*; Dhondt 1989). In coastal New Jersey, Seaside Sparrows had 37% greater nest success than Saltmarsh Sparrows, providing additional evidence for their status as dominant competitors.

Although their size, behavior, and productivity indicated that Seaside Sparrows may be dominant nest-site competitors, it is difficult to determine that competition shaped nest-site niche without removal or addition experiments (Newton 1998). However, an examination of nest-site niche for Saltmarsh and Seaside sparrows in regions where they do not co-occur would provide a simple test of the role of competitive interactions on nest-site niche. Furthermore, the extent to which Seaside and Saltmarsh sparrows co-evolved on tidal marshes is not known, so nest-site niche may have arisen in response to factors other than competition or tradeoffs. Competition may simply serve to reinforce these previously selected traits (Tokeshi 1999).

The uniqueness of Saltmarsh and Seaside sparrow nest-site niches, indicated by the hypervolume calculations, was further evidenced by inter-specific differences in nest failure probabilities and the best predictors of nest failure. Previous research indicated that the best predictors of nest success differed between the species (Gjerdrum et al. 2005), but this study was the first to compare the variables influencing cause-specific nest failure. Unlike many studies north of New Jersey, which reported that flooding caused the majority of nest losses (Post 1974, Post and Greenlaw 1982, Marshall and Reinert 1990, Gjerdrum et al. 2005, Shriver et al. 2007), this research indicated that predation was the primary cause of failure for both Saltmarsh and Seaside sparrows. The increased predation rates in this study compared to other work may be partially explained by differences in criteria for classifying nests as flooded or depredated. Specifically, I did not consider a nest flooded unless direct evidence was present, such as a wet nest cup or intact eggs outside the nest, while a nest could be classified as depredated without direct evidence if the failure occurred during a period when tides could not have accounted for the loss (i.e. away from the full and new moon tides). Other studies may have required less direct evidence to classify nests as flooded or more direct evidence to classify nests as depredated. However, despite possible methodological differences, it is likely that an actual trend of increasing predation rates with decreasing latitude is present, as many studies south of New Jersey have reported higher losses to predation than to flooding (Post 1981, Post and Greenlaw 1982, Almario et al. 2009, Kern et al. 2012).

Quantifying relative nest-site niche size, as well as nest failure probabilities, can also inform our understanding of avian adaptation to tidal marshes. Saltmarsh and Seaside sparrows are closely related (Zink and Avise 1990, Chan et al. 2006) and

recent molecular analyses (Klicka et al. 2014) place Seaside Sparrows as the sister taxon to the two sharp-tailed sparrows (Saltmarsh Sparrow and Nelson's Sparrow). Given the ephemerality of tidal marshes as an ecosystem (Malamud-Roam et al. 2006) and the estimated divergence times between Saltmarsh and Seaside sparrows and their nearest non-tidal marsh relatives (Nelson's and Le Conte's (*A. lecontii*) sparrows, respectively; Avise and Nelson 1989, Zink and Avise 1990, Rising and Avise 1993), it is reasonable to suppose that Seaside Sparrows have a considerably longer association with the ecosystem. I would predict that Seaside Sparrows, having more time to adapt to the conditions of tidal marshes, would use the habitat in such a way as to have higher fitness than the more recent colonizer. Thus, finding increased Seaside Sparrow nest-site niche space, as well as increased nest survival rates, relative to Saltmarsh Sparrow corroborates the hypothesized evolutionary relationship from molecular analyses. The strength of the relationship between length of time in tidal marshes and niche space or reproductive success could also be examined in other marsh birds, such as Nelson's Sparrow, which co-occurs with Saltmarsh Sparrows in New England (Hodgman et al. 2002, Shriver et al. 2005). This system provides an excellent opportunity to test whether time since colonization can predict the evolutionary niche space of sympatric species.

TABLES

Table 1 Description of covariates included in MCestimate cause-specific failure models for Saltmarsh and Seaside sparrows.

Variable	Description	Models Containing[a] and Predicted Relationship with Nest Failure[b]
Nest height	Distance from marsh surface to bottom of nest cup	Flooding: SA, SE (–) Predation: SA, SE (+)
High marsh cover	Mean percent cover of *Spartina patens* and *Distichlis spicata* within 1 m^2 of nest	Flooding: SA (–) Predation: SA (?)
Low marsh cover	Mean percent cover of *Spartina alterniflora* within 1 m^2 of nest	Flooding: SE (+) Predation: SE (?)
Nest canopy cover	Percentage of nest cup visible through the nest canopy	Predation: SA, SE (–)
Year	2011, 2012, & 2013	Flooding: SA, SE (~) Predation: SA, SE (~)
Date	Julian date of each nest visit	Flooding: SA, SE (–) Predation: SA, SE (+)
Site	3 levels (AT&T, Mullica Wilderness, Oyster Creek).	Flooding: SA, SE (?) Predation: SA, SE (?)
Days post new moon	# days between nest initiation and most recent new moon	Flooding: SA, SE (+)
Nest age	Age of nest (days) at each visit	Predation: SA, SE (+)

[a] SA = Saltmarsh Sparrow; SE = Seaside Sparrow
[b] Positive (+), Negative (–), Random (~) and Unknown (?)

Table 2 Summary statistics (mean ± SE and range) and univariate comparisons (*t* test or Mann-Whitney *U* test) of Saltmarsh and Seaside sparrow nest variables. All comparisons remained significant after using the Holm-Bonferroni correction (indicated by asterisk).

Nest variable	Saltmarsh Sparrow nests (n=186)	Seaside Sparrow nests (n=205)	Saltmarsh Sparrow to Seaside Sparrow comparison
Nest height (cm)	8.58 ± 0.32 (0.00-23.00)	14.12 ± 0.42 (1.50-37.00)	$U = 8553.0$, $P < 0.001$*
Nest canopy cover (%)	22.36 ± 1.87 (0.00-100.00)	36.13 ± 2.20 (0.00-100.00)	$U = 14144.5$, $P < 0.001$*
Thatch depth (cm)	7.58 ± 0.30 (0.00-22.80)	6.45 ± 0.45 (0.00-32.80)	$U = 23469.5$, $P < 0.001$*
Vegetation height (cm)	34.94 ± 0.73 (0.00-61.80)	44.51 ± 0.89 (0.00-83.60)	$t_{379.9} = -8.3$, $P < 0.001$*
High marsh cover (%)	78.53 ± 1.99 (0.00-100.00)	35.55 ± 2.38 (0.00-100.00)	$t_{382.6} = 13.9$, $P < 0.001$*
Bare ground cover (%)	0.76 ± 0.24 (0.00-20.00)	1.48 ± 0.32 (0.00-36.25)	$U = 17631.5$, $P = 0.02$*
Water cover (%)	1.41 ± 0.49 (0.00-52.50)	3.79 ± 0.71 (0.00-57.50)	$U = 17203.5$, $P = 0.001$*

Table 3 Ten best-supported models of Saltmarsh Sparrow nest failure by flooding and predation (2011 – 2013). Nest failure by an unknown cause was held constant in all models.

Model[a]	K	NLL	ΔAIC_c[b]	w_i
m_{flood} (days post new moon)m_{pred} (high marsh)	5	325.42	0.00	0.25
m_{flood} (days post new moon)m_{pred} (nest canopy)	5	325.88	0.92	0.16
m_{flood} (days post new moon)m_{pred} (.)	4	327.16	1.46	0.12
m_{flood} (days post new moon)m_{pred} (age)	5	326.94	3.05	0.05
m_{flood} (days post new moon)m_{pred} (date)	5	326.98	3.12	0.05
m_{flood} (global)m_{pred} (global)[c]	20	311.68	3.16	0.05
m_{flood} (days post new moon)m_{pred} (nest height)	5	327.15	3.46	0.04
m_{flood} (days post new moon)m_{pred} (site)	6	326.55	4.28	0.03
m_{flood} (date)m_{pred} (high marsh)	5	327.67	4.50	0.03
m_{flood} (nest height)m_{pred} (high marsh)	5	327.79	4.74	0.02

[a] m_{flood}(…) indicates models of nest flooding ; m_{pred}(…) indicates models of nest predation.

[b] Lowest AIC_c = 660.88

[c] Global model parameters were: m_{flood}(year+date+site+nest height+high marsh+days post new moon) m_{pred} (year+site+date+nest height+high marsh+nest age+nest canopy cover)

Table 4 Ten best-supported models of Seaside Sparrow nest failure by flooding and predation (2011 – 2013). Nest failure by an unknown cause was held constant in all models.

Model[a]	K	NLL	ΔAIC_c[b]	w_i
m_{flood} (date)m_{pred} (site)	6	281.46	0.00	0.49
m_{flood} (date)m_{pred} (.)	4	285.04	3.12	0.10
m_{flood} (date)m_{pred} (nest age)	5	284.66	4.37	0.05
m_{flood} (date)m_{pred} (low marsh)	5	284.78	4.62	0.05
m_{flood} (date)m_{pred} (date)	5	284.79	4.64	0.05
m_{flood} (date)m_{pred} (nest canopy cover)	5	284.80	4.66	0.05
m_{flood} (date)m_{pred} (year)	6	283.81	4.70	0.05
m_{flood} (date)m_{pred} (nest height)	5	285.03	5.13	0.04
m_{flood} (.)m_{pred} (site)	5	285.48	6.03	0.02
m_{flood} (days post new moon)m_{pred} (site)	6	285.19	7.46	0.01

[a] m_{flood}(…) indicates models of nest flooding ; m_{pred}(…) indicates models of nest predation.
[b] Lowest AIC_c = 574.98

Table 5 Parameter estimates (and 95% confidence intervals) of covariates from best-supported models of Saltmarsh and Seaside sparrow nest failure.

Species	Model	Covariate	Parameter estimate (β)	95% CI of β
Saltmarsh Sparrow	m_{flood} (days post new moon) m_{pred} (high marsh)	Days post new moon	0.09	0.039 – 0.141
		High marsh	0.01	-0.001 – 0.028
	m_{flood} (days post new moon) m_{pred} (nest canopy)	Days post new moon	0.09	0.039 – 0.142
		Nest canopy	-0.01	-0.024 – 0.003
	m_{flood} (days post new moon) m_{pred} (.)	Days post new moon	0.09	0.038 – 0.142
Seaside Sparrow	m_{flood} (date)	Date	-0.05	-0.088 – -0.011
	m_{pred} (site)	Site - AT[1]	-3.57	-4.209 – -2.930
		MW[2]	-1.81	-3.324 – -0.300
		OC[3]	-0.60	-1.404 – 0.211

[1] AT&T (also the intercept)
[2] Mullica Wilderness
[3] Oyster Creek

FIGURES

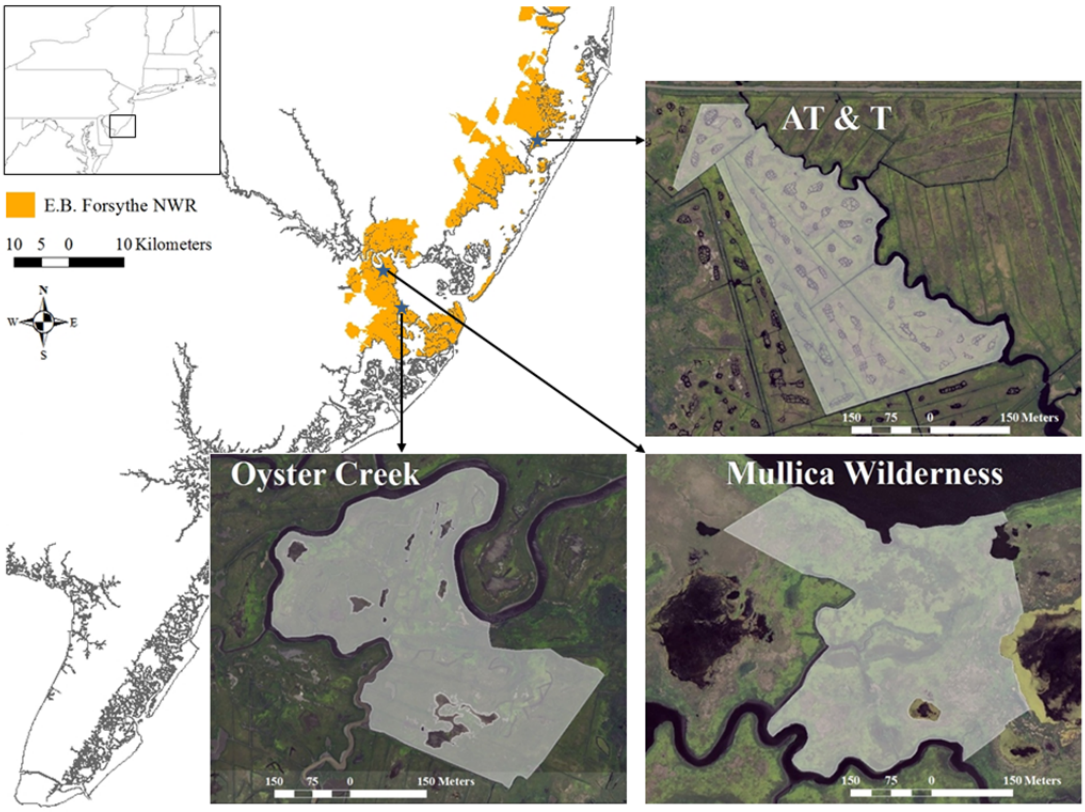

Figure 1 Location of study sites monitored from 2011 – 2013 on Edwin B. Forsythe National Wildlife Refuge, New Jersey, USA.

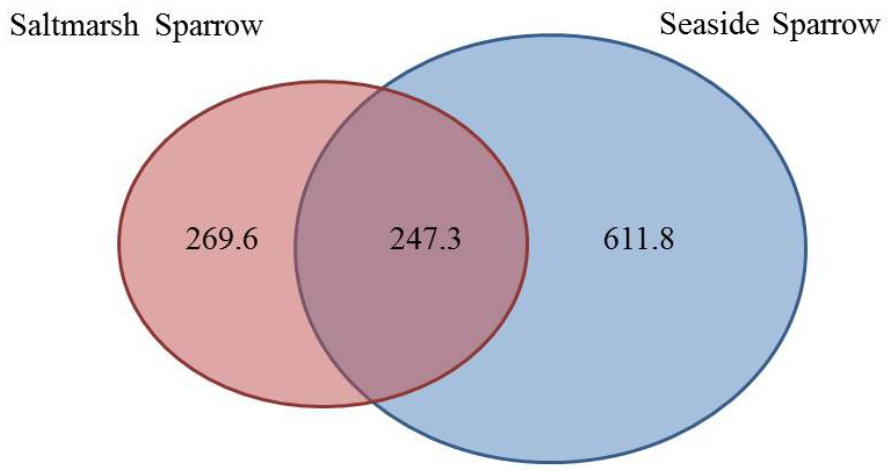

Figure 2 Saltmarsh (red) and Seaside (blue) sparrow nest-site hypervolume intersection and unique features. Nest-site hypervolumes calculated along seven dimensions from nest data collected on Edwin B. Forsythe NWR (2011 – 2013).

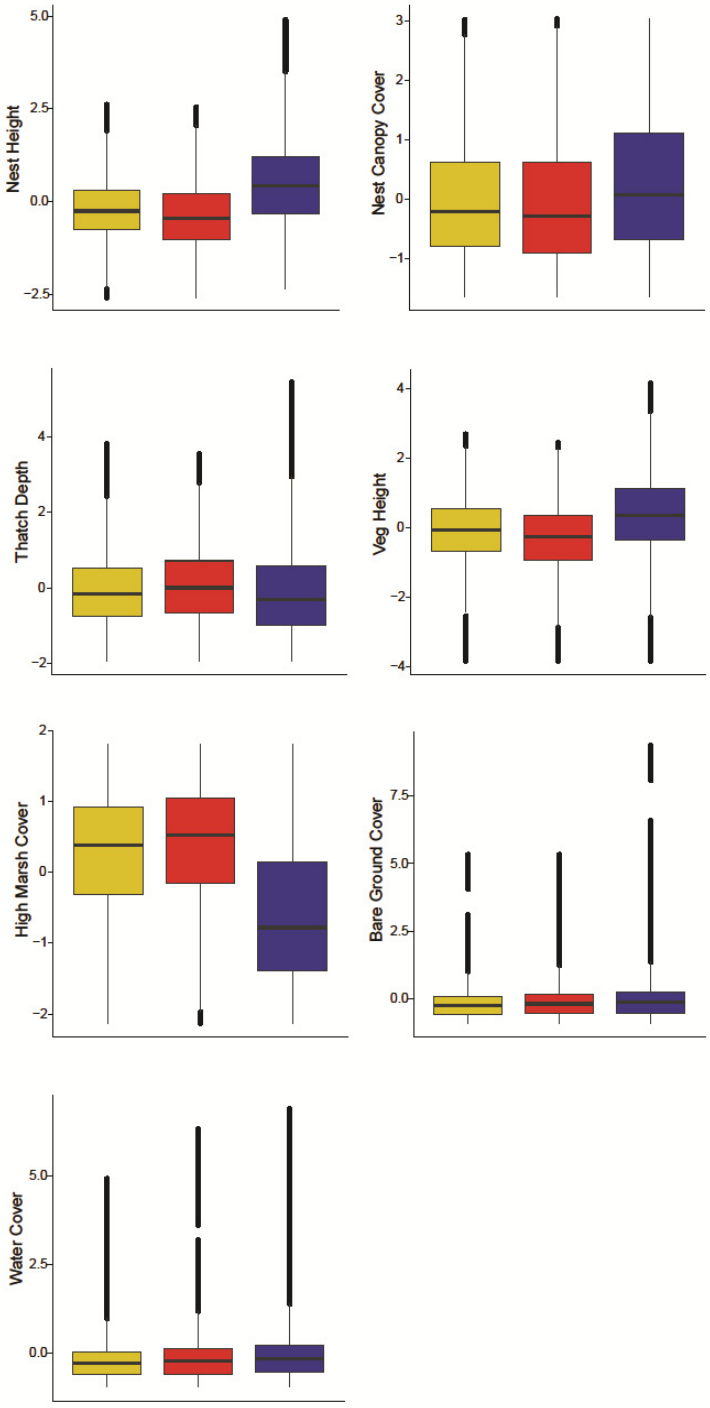
Nest Height
5.0
2.5
0.0
−2.5
Nest Canopy Cover
3
2
1
0
−1
Thatch Depth
4
2
0
−2
Veg Height
4
2
0
−2
−4
High Marsh Cover
2
1
0
−1
−2
Bare Ground Cover
7.5
5.0
2.5
0.0
Water Cover
5.0
2.5
0.0

Figure 3 Distribution of points contained within each dimension of Seaside (blue) and Saltmarsh (red) sparrow hypervolumes, and that appeared in both hypervolumes (yellow). The hypervolumes included data points and random points generated within a hyperbox kernel surrounding each data point. Variables were z-score transformed.

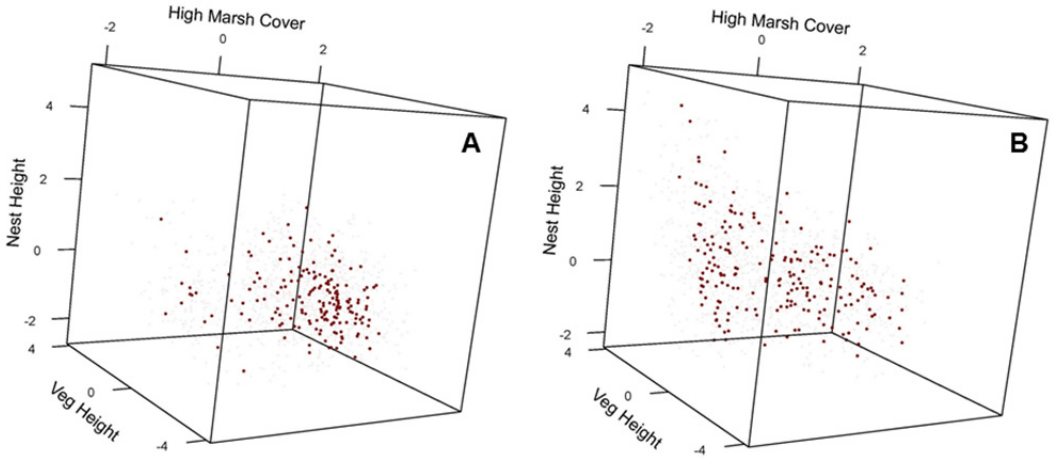

Figure 4 Three axes (high marsh cover, vegetation height and nest height) of Saltmarsh (A) and Seaside (B) sparrow nest-site niches from Forsythe NWR (2011 – 2013).

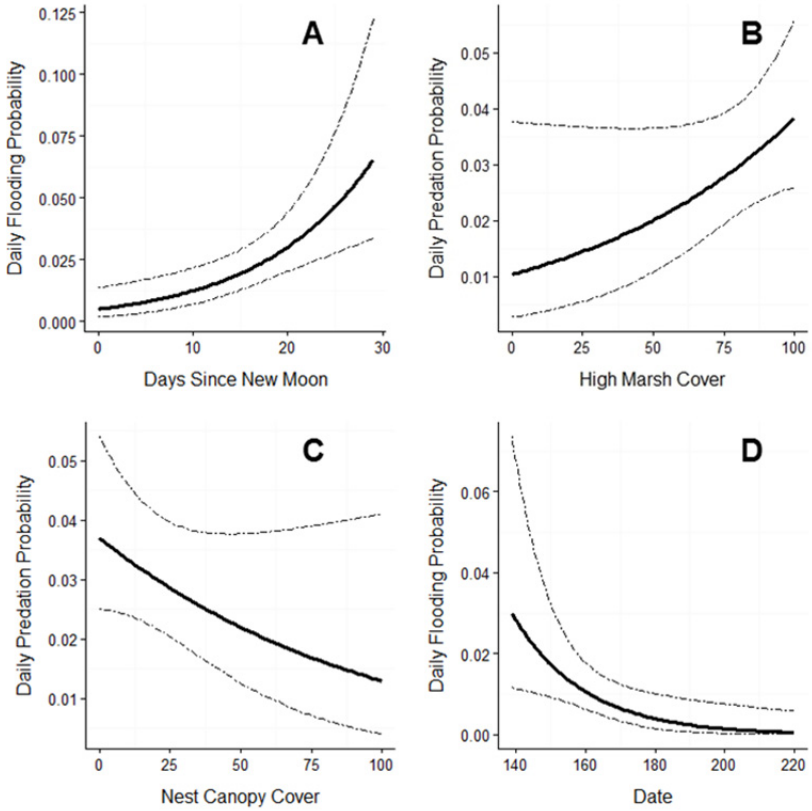

Figure 5 Saltmarsh Sparrow daily flooding probability increased with the number of days between nest initiation and the most recent new moon (A). Saltmarsh Sparrow daily predation probability increased with the percent of high marsh (*Spartina patens* and *Distichlis spicata*) cover within 1 m^2 of the nest (B) and decreased with nest canopy cover (C). Seaside Sparrow daily flooding probability decreased with Julian date (D). Dashed lines are 95% confidence intervals.

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Chapter 2

SHORT-TERM RESILIENCE OF NEW JERSEY TIDAL MARSHES TO HURRICANE SANDY

Introduction

Hurricanes can act as important community-structuring events in many ecosystems, including tidal marshes. Located at the interface of marine and upland environments, tidal marshes absorb hurricane energy and receive both beneficial and detrimental impacts from storms (Michener et al. 1997). Hurricanes can deposit large quantities of sediment, helping marshes grow and accrete in pace with sea-level rise (Rejmánek et al. 1988, Guntenspergen et al. 1995, Nyman et al. 1995, Donnelly et al. 2001), but they can also lower elevations locally through erosion (Morton and Barras 2011). Salinization and wind and wave energy can cause marsh vegetation loss and form new ponds and channels. In some cases, vegetation recolonizes rapidly (Chabreck and Palmisano 1973, Guntenspergen et al. 1995, Courtemanche et al. 1999), while in other locations the altered hydrologic features persist as legacies of the storm event (Morton and Barras 2011). Hurricane impacts on tidal marsh fauna vary based on seasonality, storm severity, and animal mobility. Storm events can reduce population size and growth by direct mortality or destruction of breeding habitat and food resources, and recovery from such effects is a complex process (Marsh and Wilkinson 1991, Michener et al. 1997, Raynor et al. 2013).

On October 29, 2012, Hurricane Sandy made landfall in New Jersey and passed over the marsh on Edwin B. Forsythe National Wildlife Refuge (Forsythe

NWR). The storm had sustained winds of >100 km/hour with over 25 cm of precipitation reported in parts of New Jersey (Blake et al. 2013), but the strongest impacts on terrestrial habitats were caused by storm surge and tides (Hall and Sobel 2013). Hurricane Sandy made a nearly perpendicular approach to the coastline, giving it a large amount of fetch over the open ocean and preventing it from being weakened by previous interactions with land surfaces before reaching New Jersey (Hall and Sobel 2013). This trajectory, coupled with full-moon high tides, produced a peak water level of 2.71 m above mean low tide level at Atlantic City, NJ, ~10 km from Forsythe NWR, causing severe inundation of coastal areas (NOAA / National Ocean Service 2014).

Although Hurricane Sandy caused extensive damage to human-dominated landscapes, its effects on natural ecosystems, like tidal marshes, remain largely unknown. Resilience in ecological systems is often defined as the capacity to persist through a disturbance (Gunderson and Holling 2001) or to undergo disturbance without shifting to an alternate stable state (Holling 1973). In forested habitats, measures of hurricane resilience have included avian community dynamics, abundance, and survival (Johnson and Winker 2010), as well as tree-stand composition, litterfall, and tree growth rates (Imbert and Portecop 2008). Marsh resilience to hurricanes has been most-widely examined in terms of vegetation, but resilience of vertebrates has often been described qualitatively and without formal pre- and post-storm surveys (i.e. Ensminger and Nichols 1958, Gunter and Eleuterius 1971, Gunter and Eleuterius 1971, Cely 1991).

In this study, I evaluated the resilience of tidal marshes to Hurricane Sandy using four metrics: vegetation cover/composition, small mammal abundance, and

Saltmarsh and Seaside sparrow (*Ammodramus caudacutus* and *A. maritimus*) abundance and reproductive success. I defined resilience as a resistance to change or a rapid return to pre-hurricane conditions, measured over a short temporal scale (three to six months pre-storm compared with seven to 11 months post-storm). In the absence of direct habitat destruction, whether hurricanes affect subsequent reproductive success of endemic species is not well-understood, but can have significant implications for population dynamics. Nest success of Saltmarsh and Seaside sparrows is primarily determined by flooding and predation (Greenberg et al. 2006). Hurricanes may increase nest flooding rates by widening channels and creeks and lowering marsh elevation, enabling storm water to inundate the marsh surface more easily, or may decrease nest predation rates by reducing populations of mammalian predators, such as Norway rats (*Rattus norvegicus*; Post et al. 1983, Post and Greenlaw 1994), that cannot survive prolonged storm surge. Quantifying resilience of nest flooding and nest predation rates to Hurricane Sandy will inform our understanding of sparrow vulnerability to large storms and improve our ability to apply appropriate management actions to maintain sparrow reproductive success following these events.

Methods

Study Area

I studied the effects of Hurricane Sandy on tidal marshes at Forsythe NWR, collecting pre-hurricane measurements from May 16 – August 30, 2012 and post-hurricane measurements from May 17 – September 5, 2013. Forsythe NWR includes >12,000 ha of tidal marsh, supports endemic vertebrates of conservation concern, such

as Saltmarsh and Seaside sparrow, and has been designated a Wetland of International Importance under the RAMSAR Convention (U.S. Fish and Wildlife Service 2004, The Ramsar Convention on Wetlands 2014). I collected data at three study sites, which differ in management history and landscape context (Figure 6). The AT&T site (14 ha; 39.697191° N -74.214032° W) and the Oyster Creek site (18 ha; 39.504815° N -74.426283° W) were historically managed with grid-ditching and open marsh water management (OMWM), while the Mullica Wilderness site (17 ha; 39.536166° N -74.438021° W) was within a federally designated wilderness area and contains no ditching or OMWM. Landcover data collected in 2010 by the National Oceanic and Atmospheric Administration's Coastal Change Analysis Program indicates that the AT&T site was closer to vegetated non-marsh, including upland forest and forested wetland, and developed land than Mullica Wilderness and Oyster Creek (National Oceanic and Atmospheric Administration 2014; Table 6).

Field Data Collection

I characterized the vegetation cover and community composition within and around each study site in each year. To quantify the vegetation within a site, I surveyed 1-m^2 quadrats randomly located within the site boundary (28 – 66 points per site per year). I measured thatch (dead vegetation) depth and vegetation height at the center and at the midpoint of each side of the quadrat. I also estimated the percent of dominant cover types, including *Spartina alterniflora* ('low marsh'), *S. patens* and *Distichlis spicata* ('high marsh'), bare ground, and open water, within each quadrat. To quantify the vegetation around a site, I surveyed 10 50-m radius points randomly located outside the site boundary, visiting the same points each year. I constrained the surveys to only tidal marsh habitat, which had a different spatial extent around each

site, so points were located 50 – 4,300 m from the site boundaries. At each point, I ranked six cover classes (low marsh, high marsh, salt-marsh terrestrial border, invasive species, pannes/pools/creeks, and open water) from zero to six (0 = 0% cover, 0.5 < 1%, 1 = 1 – 5%, 2 = 6 – 10%, 3 = 11 – 25%, 4 = 26 – 50%, 5 = 51 – 75%, 6 = 76 – 100%).

I estimated small mammal abundance using live-trapping. At each site, I trapped along two parallel transects that were 180 m in length and separated by 20 m, forming a trapping grid that was 0.36 ha in size (Forys and Dueser 1993, Kruchek 2004, Cameron et al. 2009, Eubanks et al. 2011). The transects were placed at randomly generated locations 100 – 300 m from the study sites. Along each transect, I placed 10 Sherman live traps (8 x 9 x 23 cm), spaced at 20 m intervals. I trapped all sites for three consecutive nights in two rounds per year (round 1 = June 12 – June 21; round 2 = July 24 – August 4), with the exception of round one in 2013 when weather limited trapping to one night at AT&T and two nights at Oyster Creek. I baited traps with a mixture of rolled oats, peanut butter, molasses, and raw apple pieces (Forys and Dueser 1993, Kruchek 2004, Cameron et al. 2009, Eubanks et al. 2011), and placed the bait behind the treadle in the rear of the trap and at the trap entrance. I attached the traps to Styrofoam platforms, secured between two 0.5-m bamboo stakes, to allow flotation during daily tidal changes (Wolfe 1985, DeSa et al. 2012). The duration of each trapping night was 12 hours (1800 to 0600 h) and I did not trap during heavy rainfall, storms, or lunar high tides. All captured animals were identified to species, weighed, and released at the point of capture. The locations of the transects were the same in 2012 and 2013.

I estimated the abundance of Saltmarsh and Seaside sparrows using 5-minute, 50-m-radius point counts (Greenlaw and Rising 1994, Post and Greenlaw 1994, Jobin and Picman 1997, Conway 2011). I randomly located three points within each study site and separated all points by >200 m. I surveyed each point two or three times per year (June 1 – August 6, 2012 and May 31 – July 24, 2013) with at least 10 days between visits. Surveys occurred between sunrise and 1100 h, were not conducted during periods of rain or when wind speeds exceeded 20 km/hr (Conway 2011), and were completed by the same observer. For each survey, I estimated the background noise and sky condition as survey covariates. Background noise was recorded on a scale of zero to four, with zero indicating no noise and four indicating intense noise that prevented the observer from hearing birds >25 m away. The maximum background noise detected was two, indicating moderate noise that likely prevented the observer from hearing birds >100 m away. Sky condition was estimated using the National Weather Service codes (0 = clear, 1 = partly cloudy, 2 = overcast, 4 = fog, 5 = drizzle, 8 = rain).

To estimate nest survival, flooding, and predation probabilities, I monitored sparrow nests on all study sites. Nests were primarily located by observing adults flushing from the nest site or carrying food to the nest. I marked each nest using a GPS and two wire-stake flags, and checked each nest every 2 – 4 days, recording the nest contents (eggs or chicks), female activity, and nest condition on each visit. I assigned each nest one of five possible fates following the methods of Kern et al. (*in review*). Fledged (or successful) nests had at least one live chick leave the nest after reaching ≥10 days of age (Martin and Geupel 1993, Greenlaw and Rising 1994, Post and Greenlaw 1994). Failed nests were placed into one of three categories: flooded,

depredated, or failed by an unknown cause. I assigned a fate of flooded if, following a high tide or heavy rain event, 1) all nest contents were lost and the nest was damp or completely submerged, 2) intact eggs or dead chicks without evidence of external injury were found within a few meters of the nest, or 3) intact cold and dirty eggs were present in the nest and subsequently fail to hatch (Bayard and Elphick 2011). I assigned a fate of depredated if: 1) all nest contents were lost and the nest structure was disturbed, 2) egg fragments or dead chicks with external injuries were present in or near the nest, or 3) all nest contents were lost on a day when tides could not have accounted for the loss. Failed by an unknown cause was assigned if there was conflicting evidence for flooding and predation (e.g., a nest was found empty after a high tide but was not damp or disturbed) or if a nest appeared to be abandoned. In cases where 9-day-old chicks disappeared, I considered nest fate to be unknown because it was unknown whether chicks of this age could have survived after leaving the nest.

At each nest, I measured nest height, nest canopy cover, and percent cover of high marsh and low marsh within 1 m^2. These variables have been found to influence nest fate in other populations of Saltmarsh and Seaside sparrows (Greenberg et al. 2006, Humphreys et al. 2007, Shriver et al. 2007). I determined nest height by measuring the distance from the marsh surface to the bottom of the nest cup. I measured nest canopy cover by placing a white paper disc (6.5 cm in diameter) in the nest cup and estimating the percent of the disc that was visible from directly above. Within one week of nest termination, I centered a 1-m^2 quadrat around the nest and estimated the percent cover of high and low marsh within the quadrat.

Statistical Analyses

I compared the vegetation at each site between years in order to detect hurricane-induced changes. For the within-site vegetation surveys, I used *t*-tests or Kruskal-Wallis rank sum tests when non-normally-distributed data was indicated by D'Agostino's K-squared tests (Zar 1999). I controlled for the experiment-wise error rate using the Holm-Bonferroni correction with $\alpha = 0.05$ and $n = 18$ comparisons (Dean and Voss 1999, Zar 1999). For the around-site vegetation surveys, I used Kruskal-Wallis rank sum tests and controlled for the experiment-wise error rate using the Holm-Bonferroni correction with $\alpha = 0.05$ and $n = 15$ comparisons.

I estimated the abundance of small mammals at each site in each year using binomial *N*-mixture models (function *occuRN*: Royle and Nichols 2003) in the 'unmarked' package (Fiske and Chandler 2011) in Program R (version 3.1.0; R Core Team 2014). This method exploited the underlying relationship between abundance and detection to estimate the abundance of unmarked individuals from repeated presence/absence observations. I compared two candidate models of detection probability, holding abundance constant, using Akaike's information criterion corrected for small sample size (AIC_c) and model weights (w_i). I considered models with $\Delta AIC_c<2.0$ to be equivalent (Burnham and Anderson 2002). I modeled detection as a function of visit number (1, 2, or 3), because each site was trapped for three consecutive nights in each round in each year. I did not have a pre-baiting period before trapping, so detection may have changed across the three visits as the animals changed their responses to the traps and bait. I compared the visit number model to a null model of detection probability. The *N*-mixture models assumed population closure, so I estimated abundance by site for round one and round two of each year using adjusted detection probability.

To estimate abundance of sparrows, I used *N*-mixture models (function *pcount*: Royle 2004) in the 'unmarked' package (Fiske and Chandler 2011) in Program R (version 3.1.0; R Core Team 2014). These models were designed to estimate abundance and detection simultaneously from spatially- and temporally-replicated surveys. I compared seven candidate models of detection probability, including the single predictors Julian date, observer, time, background noise, and sky condition, as well as a null and a global model, using model selection techniques (Burnham and Anderson 2002). Abundance by site and year was subsequently estimated using adjusted detection probability.

To determine the impact of Hurricane Sandy on sparrow nest flooding and nest predation, I used Markov Chain models to estimate nest failure probabilities and compare the importance of nest failure predictors. The Markov Chain algorithms (Program MCestimate; Etterson et al. 2007a, Etterson et al. 2007b) simultaneously estimated the probabilities of flooding and predation, and linked daily flooding and predation probabilities with covariates using a multinomial logit. Prior to analysis, I censored all observations for which the nest was found empty or had chicks that were old enough to fledge (≥10 days) to avoid misclassification of nest fate (Stanley 2004, Etterson et al. 2007a). I used a two-step modeling process for each species (see below). In the first step, I compared 29 candidate models to determine the covariate(s) that best predicted nest flooding and predation probability, considering models with ΔAIC $\leq$ 2.0 to be equivalent (Burnham and Anderson 2002). In the second step, I compared the best model(s) of nest flooding and predation with models that included hurricane effects (year). If Hurricane Sandy altered nest failure probabilities, I would expect a model with year to have equal or greater support, based on ΔAIC and model

weight, than the model(s) that best predicted nest flooding and predation independent of hurricane effects.

In the first modeling step, I compared nine covariates that were the most important predictors of Saltmarsh and Seaside sparrow nest flooding and predation probability in previous work on Forsythe NWR (Kern et al. *in review*). I modeled three flooding covariates (days since new moon, Julian date, and nest height) and six predation covariates (high/low marsh cover, nest canopy cover, nest height, nest age, Julian date, and study site) as single effects. Days since new moon, or the number of days between nest initiation and the most recent new moon, was calculated following the methods of Shriver et al. (2007) and Kern et al. (*in review*). I modeled high marsh as a predation predictor for Saltmarsh Sparrow because it is the primary vegetation community at Saltmarsh Sparrow nests and low marsh cover as a predation predictor for Seaside Sparrow because it is the primary vegetation community at Seaside Sparrow nests. I also included an intercept-only model and a global model, for a total of 29 candidate models for each species.

I then compared the best models from the first step with hurricane effects models. A hurricane effect was modeled using 'year' as a categorical predictor of flooding and/or predation. I included three models with year as a single effect (predicting flooding and predation, predicting flooding only, and predicting predation only), as the hurricane may have impacted flooding and predation singly or simultaneously. I also modeled the effect of year added to the best models from the first step because year may only become important after controlling for the effects of nest characteristics.

Results

Vegetation

The vegetation within the study sites remained largely the same between years, with the exception of five site-specific changes. Low marsh cover at Oyster Creek decreased by 40%, while high marsh cover increased by 135% (Table 1). At AT&T and Mullica Wilderness, bare ground cover was 6 – 14 times greater in 2013, but remained at a relatively low overall percent cover despite the increase (8.50 ± 2.58 and 3.09 ± 1.55, respectively). Average vegetation height decreased by 33% at AT&T (Table 7). I detected no hurricane-induced change of vegetation around the study sites, as cover of low marsh, high marsh, salt-marsh terrestrial border, invasive species, and pannes/pools/creeks within 50 – 4,300 m of the sites did not differ between years (Table 8).

Small Mammal Abundance

In 2012 and 2013, I trapped for 33 nights and had 206 meadow vole (*Microtus pennsylvanicus*) captures, with no other species detected. In both years, 'visit number' was the best-supported model of detection probability (model weight = 1.00) and detection increased across the three visits. Meadow vole abundance within the 0.36 ha trapping grid on each site increased from round one to round two in both years, as new individuals were recruited into the population (Figure 7). In round two of 2012, meadow voles were 1.6 – 2.1 times more abundant at Mullica Wilderness than at AT&T or Oyster Creek (mean ± 1 standard error: 12.59 ± 5.15 versus 7.04 ± 3.10 and 5.78 ± 2.61). However, in round two of 2013, vole abundance was 5.1 – 15.1 times greater at AT&T than at Mullica Wilderness or Oyster Creek (4.56 ± 2.25 versus 0.90 ± 0.35 and 0.30 ± 0.17).

Meadow vole abundance was lower the year after Hurricane Sandy at all sites. I did not detect any voles during round one of 2013 and vole abundance in round two of 2013 was 1.5 – 19.2 times lower than round two of 2012 (Figure 7). In 2013, AT&T had a greater increase in vole abundance from round one to round two than Mullica Wilderness or Oyster Creek, resulting in a final abundance that was 5.1 – 15.1 times greater than the other sites (Figure 7). AT&T had 5 – 78 times more vegetated non-marsh habitat within 1,000 m than Mullica Wilderness or Oyster Creek (Table 6), which may have served as a source for voles to recolonize the marsh (National Oceanic and Atmospheric Administration 2014).

Sparrow Abundance

Saltmarsh and Seaside sparrow abundance did not change between 2012 and 2013. Although Saltmarsh Sparrows were 2.1 – 6.0 times less abundant in Mullica Wilderness and Oyster Creek in 2013, the confidence limits of the estimates were large and overlapping (Figure 8). Saltmarsh Sparrows on AT&T, as well as Seaside Sparrows on all sites, were 1.1 – 5.5 times more abundant in 2013, but the differences were not significant (Figure 8).

Sparrow Nest Survival

I detected differences in Seaside Sparrow nest flooding and predation probabilities pre- and post-Hurricane Sandy, but I did not observe a net change in nest survival probability. There were four top models of Seaside Sparrow nest flooding and predation probability without including hurricane effects (Table 9). When those four models were compared with seven hurricane-effects models, the model in which flooding was predicted by nest height and year, and predation was predicted by date

and year was a top model. This hurricane-effect model indicates that Seaside Sparrow daily nest predation probability (± 1 standard error) was 3.4 times greater in 2013 (0.025 ± 0.008) than in 2012 (0.007 ± 0.004), but that daily flooding probability was 0.7 times lower in 2013 (0.003 ± 0.002) than in 2012 (0.004 ± 0.002). Because the two primary causes of nest failure had opposite directions of change after Hurricane Sandy, there was no net change in Seaside Sparrow nest survival following the storm. Daily nest survival probabilities were similar between years (2012 = 0.97 ± 0.01; 2013 = 0.95 ± 0.01) and the 95% confidence limits of daily nest survival overlapped (2012 = 0.94 – 0.98; 2013 = 0.92 – 0.97).

Additionally, the direction of the changes in Seaside Sparrow nest failure probabilities was counter to observed hurricane impacts, so the mechanism of the changes remains unclear. Based on meadow vole abundance estimates, it was likely that Hurricane Sandy reduced all small mammal nest predator populations, such as Norway rats and rice rats (*Oryzomys palustris*), yet Seaside Sparrow nest predation probability increased. Furthermore, there was a trend of lower vegetation height at all study sites following the hurricane (Table 7) and Seaside Sparrow nest height was 1.3 times lower in 2013 (11.35 cm ± 0.58) than in 2012 (14.33 cm ± 0.60; Welch's *t*-test: $t_{122} = 3.45$, $P < 0.001$), but nest flooding probability decreased.

I did not detect hurricane impacts on Saltmarsh Sparrow nest flooding and predation probabilities. There were six top models of Saltmarsh Sparrow nest failure without including hurricane effects (Table 10). After a comparison with nine hurricane-effects models, these six remained the best models and accounted for 83% of the cumulative model weight. Daily Saltmarsh Sparrow nest survival probability, taken from the model in which year predicted flooding and predation, also was not

impacted by Hurricane Sandy. Although daily nest survival probability (± 1 standard error) increased from 2012 (0.92 ± 0.01) to 2013 (0.93 ± 0.01), the 95% confidence limits of daily nest survival overlapped (2012 = 0.87 – 0.95; 2013 = 0.87 – 0.96), indicating no change between years.

Discussion

Tidal marsh vegetation, small mammal abundance, and Saltmarsh and Seaside sparrow abundance and nest success in New Jersey were resilient to Hurricane Sandy. I detected no changes in sparrow abundance or nest success, and minimal changes in vegetation cover. Although there was a trend of increased bare ground on all sites after the hurricane, indicating that some vegetation may have been removed by wave energy or died from prolonged inundation, it remained at a relatively low total percent cover. Aside from habitat loss, any reduction of sparrow abundance from the hurricane was most likely to come from direct mortality due to wind and rain exposure (Michener et al. 1997), to which they were vulnerable during migration and overwintering. Saltmarsh and Seaside sparrows migrate throughout coastal areas of the northeastern United States during September and October, and overwinter in marshes as far north as Long Island, New York, directly within the path of Hurricane Sandy (Elliott 1962, Robbins 1983, Greenlaw and Woolfenden 2007). These findings indicate, however, that minimal mortality of individuals breeding in New Jersey occurred during the storm.

In contrast, I observed resilience in the meadow vole population through its rapid increase in size following Hurricane Sandy. Inundation from storm surge, high tides, and rainfall was a likely cause of the decline in meadow voles. Other small mammals in North American marshes and beaches, including raccoon (*Procyon lotor*),

beach mouse (*Peromyscus polionotus*), and Eastern harvest mouse (*Reithrodontomys humulis*), have been impacted by storm flooding through either direct mortality or alteration of movement patterns (Gunter and Eleuterius 1971, Swilling et al. 1998, Klinger 2006, Pries et al. 2009). Although meadow voles can swim and dive (Harris 1953), the prolonged flooding during the hurricane likely drowned the majority of individuals on the tidal marsh in New Jersey. Patterns of vole recolonization of the study sites gave further evidence of the impact of storm flooding. AT&T, the site in greatest proximity to upland habitat, was repopulated more quickly than Oyster Creek or Mullica Wilderness, which were farther from upland refugia. Thus, although vole abundance nine months post-hurricane at Oyster Creek and Mullica Wilderness had not reached pre-hurricane levels, they are likely to fully recover with additional time to reproduce and disperse.

Counter to predictions, I detected a decrease in Seaside Sparrow nest flooding probability and an increase in nest predation probability following Hurricane Sandy. However, these changes may simply be due to annual variation because the direction of change cannot be attributed to any measurable hurricane impact. I conclude that the hurricane did not alter marsh structure or hydrology so greatly as to increase nest flooding probability, and did not reduce nest predator populations to a degree that a decrease in nest predation probability was detectable. Given the decrease in meadow vole abundance, it is plausible that other small mammalian nest predators were similarly impacted. However, the absence of a reduction in nest predation probability, as well as the lack of detections of these predator species during the live-trapping surveys, indicates that small mammals likely have little impact on Saltmarsh and Seaside sparrow reproductive success in New Jersey. Other potential nest predators

include mesocarnivores, such as raccoons, red fox (*Vulpes vulpes*), and American mink (*Neovison vison*), avian species, such as gulls (Laridae), crows (Corvidae), and herons/egrets (Ardeidae), and garter snakes (*Thamnophis sirtalis*; Post et al. 1983, Greenlaw and Rising 1994, Post and Greenlaw 1994), but their abundance and frequency of sparrow nest depredation in the mid-Atlantic requires further evaluation. Because mesocarnivores and avian predators are highly mobile, they may have recolonized the marsh rapidly after the hurricane, resulting in no net change in nest predation rates following the storm.

Although our study provided a direct pre- and post-hurricane comparison, informing our understanding of short-term marsh resiliency to Hurricane Sandy, resilience also operates at many other spatial and temporal scales (Carpenter et al. 2001). Further research could evaluate the impact of Sandy on long-term processes, such as population growth rate, in order to better understand how such stochastic disturbances disrupt or are absorbed by decadal trends. I did not observe a change in Saltmarsh or Seaside sparrow nest survival probabilities after the hurricane, but the brief time period of this study did not allow me to distinguish between hurricane impacts and annual variation. A longer time series of nest survival monitoring is needed to better quantify hurricane effects on reproductive success. Tidal marsh resilience could also be examined at different spatial scales, in order to capture the hurricane impact on metapopulations, or measured using other variables, such as annual survival.

Ecosystem resilience may be crucial for maintaining biodiversity and ecological processes in light of global climate change (Mawdsley et al. 2009). Global climate change and sea level rise pose significant threats to the persistence of coastal

wetlands and their endemic species (Erwin et al. 2006, FitzGerald et al. 2008, Woodrey et al. 2012). The intensity of hurricanes in the Atlantic may increase due to global climate change (Emanuel 2005, Webster et al. 2005, IPCC 2014), so quantifying the resilience of tidal marshes to Hurricane Sandy can inform future management and conservation action. These findings show a high level of short-term resilience in four metrics, but a broader understanding is needed by examining different spatial scales and additional variables. Furthermore, although ecosystem resilience is often measured in response to an abrupt disturbance, it is also affected by gradual changes that occur over long time spans (Scheffer et al. 2001). How resilient a tidal marsh can be to a hurricane may be determined by how greatly it has been weakened by small, on-going changes, such as eutrophication or lack of sedimentation (Scheffer et al. 2001). Thus, increasing the likelihood of tidal marsh persistence through global climate change requires managers, policy-makers, and conservationists to address the gradual changes that influence resilience, rather than simply respond to large disturbances.

TABLES

Table 6 Percent of cover types within 500 m and 1000 m of study site boundaries at Edwin B. Forsythe NWR, NJ, based on 2010 National Oceanic and Atmospheric Administration Coastal Change Analysis Program landcover data.

	Percent cover (500 m)				Percent cover (1000 m)			
Study site	Tidal marsh	Veg non-marsh[a]	Water	Dev[b]	Tidal marsh	Veg non-marsh[a]	Water	Dev[b]
AT&T	73.26	20.32	5.08	1.34	55.80	37.35	5.29	1.54
Mullica Wilderness	66.81	0.65	32.55	0.00	74.57	0.48	24.95	0.00
Oyster Creek	92.31	3.62	3.57	0.49	88.24	7.15	4.19	0.32

[a] Vegetated non-marsh
[b] Developed land

Table 7 Vegetation variables (mean ± 1 standard error) collected within each study site at Edwin B. Forsythe NWR, NJ, and univariate comparisons (*t*-test or Kruskal-Wallis test) between years. Comparisons that remained significant following the Holm-Bonferroni correction are designated by an asterisk.

Vegetation variable	Study site	2012 (mean ± 1 SE)	2013 (mean ± 1 SE)	Comparison between years
Low marsh cover (%)	AT	18.98 ± 4.18	15.32 ± 4.79	$\chi^2_{0.05,\,1} = 0.03$, $P = 1.00$
	MW	28.93 ± 4.72	22.72 ± 5.09	$\chi^2_{0.05,\,1} = 0.26$, $P = 1.00$
	OC	77.80 ± 4.73	46.13 ± 5.55	$\chi^2_{0.05,\,1} = 20.45$, $P < 0.01$*
High marsh cover (%)	AT	77.88 ± 4.33	73.86 ± 6.27	$\chi^2_{0.05,\,1} = 1.32$, $P = 1.00$
	MW	70.00 ± 4.81	71.55 ± 6.14	$\chi^2_{0.05,\,1} = 0.01$, $P = 1.00$
	OC	17.98 ± 4.69	40.00 ± 6.18	$\chi^2_{0.05,\,1} = 8.68$, $P = 0.05$*
Bare ground cover (%)	AT	1.44 ± 1.20	8.50 ± 2.58	$\chi^2_{0.05,\,1} = 20.72$, $P < 0.01$*
	MW	0.23 ± 0.22	3.09 ± 1.55	$\chi^2_{0.05,\,1} = 12.85$, $P < 0.01$*
	OC	3.60 ± 1.68	7.84 ± 2.14	$\chi^2_{0.05,\,1} = 7.36$, $P = 0.07$
Water cover (%)	AT	1.01 ± 0.62	1.25 ± 1.25	$\chi^2_{0.05,\,1} = 0.08$, $P = 1.00$
	MW	0.68 ± 0.48	0.00 ± 0.00	$\chi^2_{0.05,\,1} = 1.58$, $P = 1.00$
	OC	0.53 ± 0.52	2.84 ± 2.32	$\chi^2_{0.05,\,1} = 0.66$, $P = 1.00$
Thatch depth (cm)	AT	4.86 ± 0.40	4.06 ± 0.55	$t_{56.0} = 1.18$, $P = 1.00$
	MW	5.23 ± 0.46	7.43 ± 0.67	$t_{57.6} = -1.86$, $P = 0.68$
	OC	1.79 ± 0.41	3.82 ± 0.55	$\chi^2_{0.05,\,1} = 7.68$, $P = 0.07$
Vegetation height (cm)	AT	33.17 ± 1.32	24.85 ± 1.19	$t_{78.9} = 4.66$, $P < 0.01$*
	MW	37.56 ± 2.30	27.12 ± 1.61	$\chi^2_{0.05,\,1} = 7.63$, $P = 0.07$
	OC	35.48 ± 1.44	25.79 ± 1.48	$t_{121.1} = 2.28$, $P = 0.24$

Table 8 Cover class variables (mean ± 1 standard error) collected around each study site at Edwin B. Forsythe NWR, NJ, and univariate comparisons (Kruskal-Wallis test) between years. No comparisons remained significant following the Holms-Bonferroni correction.

Cover class	Study site	2012 (mean ± 1 SE)	2013 (mean ± 1 SE)	Comparison between years
Low marsh	AT	3.00 ± 0.49	3.20 ± 0.48	$\chi^2_{0.05,\,1} = 0.10$, $P = 1.00$
	MW	3.90 ± 0.37	2.70 ± 0.44	$\chi^2_{0.05,\,1} = 3.18$, $P = 1.00$
	OC	3.10 ± 0.50	3.10 ± 0.48	$\chi^2_{0.05,\,1} = 0.01$, $P = 1.00$
High marsh	AT	3.90 ± 0.65	4.20 ± 0.57	$\chi^2_{0.05,\,1} = 0.04$, $P = 1.00$
	MW	4.20 ± 0.46	5.10 ± 0.27	$\chi^2_{0.05,\,1} = 2.64$, $P = 1.00$
	OC	4.10 ± 0.67	3.80 ± 0.67	$\chi^2_{0.05,\,1} = 0.30$, $P = 1.00$
Salt-marsh terrestrial border	AT	0.80 ± 0.31	0.60 ± 0.22	$\chi^2_{0.05,\,1} = 0.08$, $P = 1.00$
	MW	0.70 ± 0.24	0.50 ± 0.25	$\chi^2_{0.05,\,1} = 0.66$, $P = 1.00$
	OC	1.20 ± 0.38	1.10 ± 0.37	$\chi^2_{0.05,\,1} = 0.30$, $P = 1.00$
Invasives	AT	0.35 ± 0.21	0.30 ± 0.11	$\chi^2_{0.05,\,1} = 0.27$, $P = 1.00$
	MW	0.15 ± 0.10	0.10 ± 0.10	$\chi^2_{0.05,\,1} = 0.30$, $P = 1.00$
	OC	0.50 ± 0.29	0.45 ± 0.39	$\chi^2_{0.05,\,1} = 0.71$, $P = 1.00$
Pannes/pools/creeks	AT	3.20 ± 0.41	2.70 ± 0.33	$\chi^2_{0.05,\,1} = 0.68$, $P = 1.00$
	MW	1.25 ± 0.27	1.50 ± 0.34	$\chi^2_{0.05,\,1} = 0.33$, $P = 1.00$
	OC	2.50 ± 0.37	2.10 ± 0.40	$\chi^2_{0.05,\,1} = 0.53$, $P = 1.00$

Table 9 Models examining Hurricane Sandy impacts on Seaside Sparrow nest flooding and nest predation probabilities at Edwin B. Forsythe NWR, NJ (2012 – 13). Models containing 'year' are considered hurricane-effects models. The four models without 'year' were the top models ($\Delta AIC \leq 2.00$) from the set of 29 candidate models that did not include hurricane effects.

Flooding predictor	Predation predictor	*K*	NLL	ΔAIC_c	w_i
Date	Site	6	179.19	0.00	0.23
Year + Date	Year + Nest height	7	178.26	0.17	0.21
Date	Constant (.)	4	181.54	0.66	0.16
Date	Nest height	5	180.76	1.12	0.13
Date	Low marsh cover	5	181.19	1.98	0.09
Year + Date	Year	6	180.29	2.20	0.08
Year + Date	Year + Site	8	178.36	2.40	0.07
Year + Date	Year + Low marsh cover	7	180.05	3.76	0.03
Constant (.)	Year	4	189.80	17.19	0.00
Year	Year	5	188.90	17.41	0.00
Year	Constant (.)	4	190.03	17.64	0.00

Table 10 Models examining Hurricane Sandy impacts on Saltmarsh Sparrow nest flooding and nest predation probabilities at Edwin B. Forsythe NWR, NJ (2012 – 13). Models containing 'year' are considered hurricane-effects models. The six models without 'year' were the top models (ΔAIC ≤ 2.00) from the set of 29 candidate models that did not include hurricane effects.

Flooding predictor	Predation predictor	*K*	NLL	ΔAIC_c	w_i
Date	Date	5	228.29	0.00	0.18
Date	Constant (.)	4	229.32	0.03	0.18
Date	Nest canopy cover	5	228.37	0.16	0.17
Date	Nest height	5	228.74	0.90	0.12
Date	High marsh cover	5	228.77	0.96	0.11
Date	Nest age	5	229.25	1.93	0.07
Year + Date	Year	6	228.83	3.11	0.04
Year + Date	Year + Date	7	227.85	3.20	0.04
Year + Date	Year + Nest canopy cover	7	227.95	3.39	0.03
Year + Date	Year + Nest height	7	228.16	3.82	0.03
Year + Date	Year + High marsh cover	7	228.28	4.06	0.02
Year + Date	Year + Age	7	228.78	5.04	0.01
Year	Constant (.)	4	233.74	8.88	0.00
Year	Year	5	233.69	10.80	0.00
Constant (.)	Year	4	234.98	11.36	0.00

FIGURES

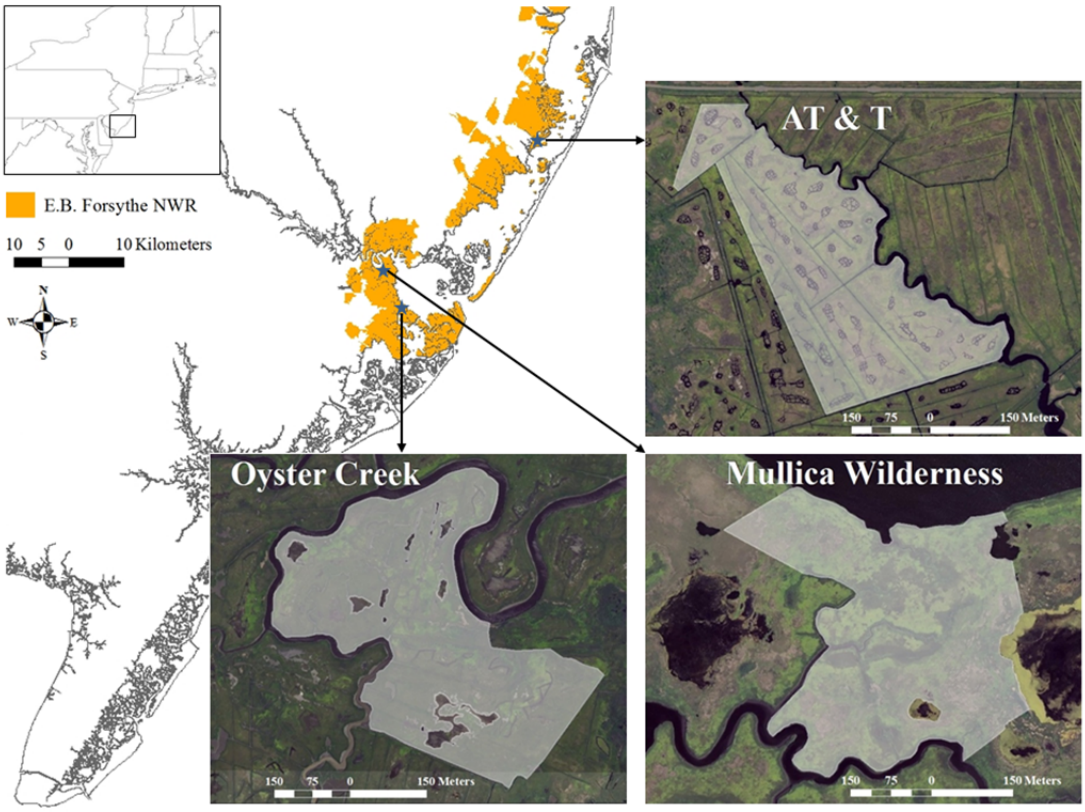

Figure 6 Location of study sites on Edwin B. Forsythe National Wildlife Refuge, NJ, monitored from 2012 – 2013.

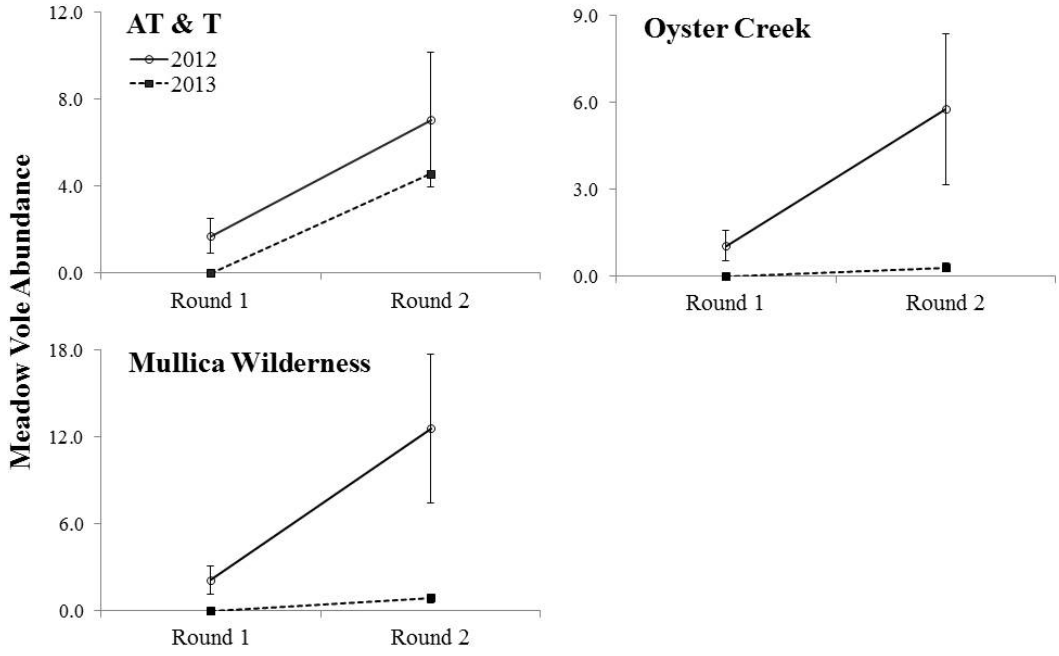

Figure 7 Meadow vole (*Microtus pennsylvanicus*) abundance (mean ± 1 standard error) by study site, year, and round at Edwin B. Forsythe NWR. Round 1 was conducted from June 12 – June 21, and round 2 was conducted from July 24 – August 4.

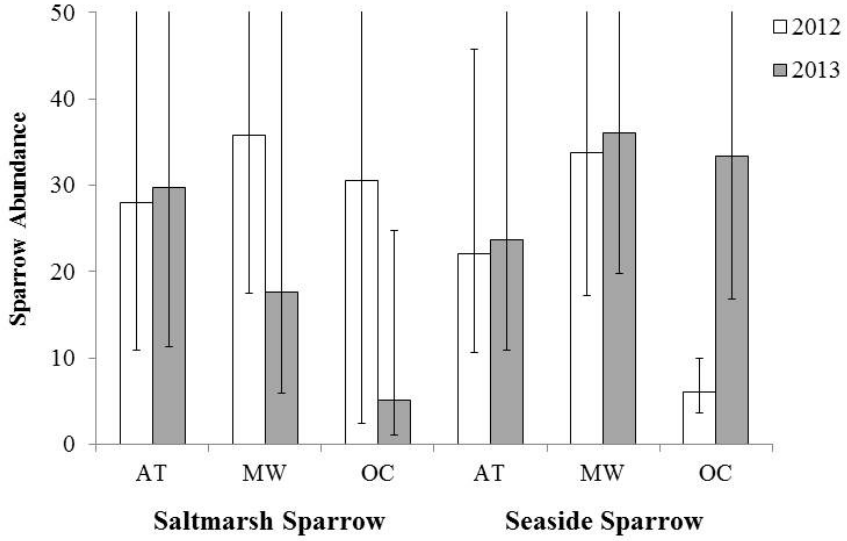

Figure 8 Saltmarsh and Seaside sparrow abundance (±95% confidence limits) at each of three study sites (AT, MW, OC) at Edwin B. Forsythe NWR, NJ, in 2012 and 2013.

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Chapter 3

IMPROVING SEASIDE SPARROW POPULATION VIABILITY IN THE MIDST OF SEA-LEVEL RISE

Introduction

Tidal marshes occupy only ~45,000 km^2 worldwide, but have a value in ecological services and uniqueness that is disproportionately great for their spatial extent (Greenberg et al. 2006, Barbier et al. 2011). Particularly in North America, tidal marshes support a high number of endemic vertebrate species and subspecies, such as Seaside Sparrows (*Ammodramus maritimus*; Greenberg and Maldonado 2006). Seaside Sparrows breed along the Atlantic Coast of the U.S. from Maine to Florida and throughout the Gulf Coast, with as many as nine subspecies described based on plumage, song, and mitochondrial DNA (Post and Greenlaw 1994, Woltmann et al. 2014). Two subspecies (*A. m. nigrescens* and *A. m. pelonota*) became extinct in the 1980s due to habitat destruction and one extant subspecies, Cape Sable Seaside Sparrow (*A. m. mirabilis*), is federally endangered (Post and Greenlaw 1994, Lockwood et al. 1997). The remainder of extant subspecies occur within habitat that is pinched between oceans and human development, putting them at great risk of future declines.

Global climate change and sea-level rise pose the largest and most immediate threat to tidal marshes in North America. Models predicting the extent and rate of sea-level rise (SLR) are continually being refined as processes governing sea levels, such as thermal expansion, changes in salinity and land water storage, and glacier melting,

become better understood (Church et al. 2013). Recent modeling efforts, using historical tide trends (Boon 2012), process-based simulations (Church et al. 2013), or the observed relationship between SLR and global mean surface temperature (Rahmstorf 2007, Vermeer and Rahmstorf 2009) or radiative forcing (Jevrejeva et al. 2012), predict that sea levels will increase 0.37 – 1.6 m by 2100. Most predictions published from 2007 – 2013 also fall within this range (see summary in Church et al. 2013). A 0.37 – 1.6 m increase in sea level will have detrimental impacts on tidal marshes (Wong et al. 2014), putting endemic birds, such as the Seaside Sparrow, at risk.

Because SLR will impact the distribution, abundance, and reproductive success of tidal marsh birds, population viability analysis (PVA) has been used to quantify extinction risk under various SLR scenarios. Population viability analysis is a technique used to estimate the likelihood of population persistence for a specified time period using life-history information and stochastic computer simulations (Boyce 1992, Brook et al. 2000), as well as to evaluate the efficacy of management actions to reduce extinction risk (Reed et al. 1998). Negative impacts of SLR on population size and viability have been predicted for several species of coastal birds, including Snowy Plover (*Charadrius nivosus*; Aiello-Lammens et al. 2011), Eurasian Oystercatcher (*Haematopus ostralegus*; Van De Pol et al. 2010), Bittern (*Botarus stellaris*; Gilbert et al. 2010), Magpie Goose (*Anseranas semipalmata*; Traill et al. 2010), and Seaside Sparrow (Shriver and Gibbs 2004, Kern and Shriver 2014). Although these studies took the important first step of quantifying SLR impacts on population viability, estimates of the relative strength of management actions to reduce negative impacts are lacking, despite the ability of PVA to address such questions (Reed et al. 2002).

To provide managers and conservationists with tools to reduce the negative impacts of SLR on tidal marsh birds, I conducted a PVA of Seaside Sparrows on 12,200 ha of tidal marsh in New Jersey. The first objective of the analysis was to quantify the upper and lower bounds of likely SLR impacts on Seaside Sparrow population viability using the upper and lower bounds of predicted SLR from recent models. After estimating the probable range of SLR effects, the second objective was to compare the relative benefit of management actions designed to reduce SLR impacts by decreasing marsh loss or increasing sparrow nest success.

Methods

Study Site and Scenarios

I modeled Seaside Sparrow population viability on Edwin B. Forsythe National Wildlife Refuge (Forsythe NWR). Forsythe NWR contains 12,200 ha of tidal marsh and spans 64 km of coastline (U.S. Fish and Wildlife Service 2004). To facilitate research and management actions, the tidal marsh on Forsythe NWR was divided into 22 units, ranging in size from 53 – 1862 ha (Figure 9; Table 11). Managers and biologists delineated the units at a scale such that management actions could be applied to the entirety of the unit. Because the PVA objectives were to compare the relative benefit of management actions under different SLR scenarios, I used each marsh unit as a sparrow subpopulation in the models (Table 11). I conducted bird surveys within each marsh unit from 2012 – 2014. I also collected detailed Seaside Sparrow demographic data on three 14 – 18-ha study sites, located within the AT & T, Motts Mullica, and Oyster Creek marsh units from 2011 – 2013 (Figure 9).

I estimated the impact of two SLR scenarios on Seaside Sparrow viability for 42 years (2008 – 2050) using the Sea Level Affecting Marshes Model, version 6 (SLAMM 6). SLAMM simulates the dominant processes involved in wetland creation and maintenance, including inundation, erosion, overwash, saturation, and accretion, and uses a decision tree to convert habitat from one type to another under SLR. First developed in the 1980's (Park et al. 1986), SLAMM has been periodically revised following updates in SLR predictions and in wetland-process modeling. SLAMM has been applied in prospective analyses throughout the U.S. to predict how landcover may change given varying amounts of SLR (Galbraith et al. 2002, Craft et al. 2009), as well as in a retrospective analysis, which agreed with 30 years of field data collected in Florida (Geselbracht et al. 2011). To estimate the effect of SLR on Forsythe NWR, the model used high-resolution LiDAR (Light Detection and Ranging) elevation data and National Wetland Inventory landcover data for initial conditions (2008), and produced a spatially-explicit map of landcover within the refuge at 25 year increments from 2025 – 2100. I used SLAMM to quantify the change in marsh area within each marsh unit under 0.35 m and 0.75 m of SLR by 2050 (Table 11), which align with the upper and lower bounds of SLR predictions from recent studies (e.g. Rahmstorf 2007, Vermeer and Rahmstorf 2009, Boon 2012, Church et al. 2013). I removed the appropriate number of sparrows from each marsh unit based on the area lost each year, assuming a density of three sparrows per ha (see "Initial Abundance, Carrying Capacity, and Dispersal"). I also incorporated the effects of marsh loss by assigning a negative temporal trend in carrying capacity. For each marsh unit, I calculated initial (2008) and final (2050) carrying capacity under 0.35 and 0.75 m of

SLR. I assigned a negative temporal trend to each unit that was the slope of the line between initial and final carrying capacity.

After quantifying the upper and lower bounds of SLR impacts on Seaside Sparrows, I estimated the relative effect of management to increase sparrow fecundity or reduce the rate of marsh loss. I defined two fecundity management scenarios that involved actions to increase sparrow nest survival by decreasing failure due to predation or flooding. In fecundity management scenario one (FM1), I increased nest success by 20% in the five marsh units with the highest sparrow abundance (9 – 22% of the total Seaside Sparrow population; Table 11). Conducting predator and/or flooding control in these units would impact the greatest number of sparrows. In fecundity management scenario two (FM2), nest success was increased by 20% in the five smallest marsh units (Table 11). Due to their size, fecundity management actions in these units would be easiest to conduct and maintain, although they would impact fewer sparrows. I defined one reduction-in-marsh-loss scenario where thin-layer deposition (TL) was implemented on four marsh units (Table 11). Thin-layer deposition is a technique that increases marsh surface elevation and may reduce marsh loss to SLR (Cahoon and Cowan 1988, Ford et al. 1999, Slocum et al. 2005). I assumed that 100% of the areas treated with TL would become marsh, reducing the amount of marsh lost by 20 – 83% in these units and, under 0.35 m of SLR, increasing the area of Barnegat by 26 ha from the initial conditions.

Field Data Collection

I estimated the abundance of Seaside Sparrows using 5-minute, 50-m-radius point counts (Conway 2011). Using package 'spsurvey' in program R (R Core Team 2014), I randomly located 7 – 21 survey points in each marsh unit (W. Wiest,

unpublished). The 'spsurvey' package uses a generalized random tessellation stratified (GRTS) survey design, which emphasizes spatial-balance and mimics the spatial density patterns of surveyed species (Stevens and Olsen 2004). All points were separated by >200 m to maintain independence of counts. I conducted point counts in each marsh unit for one year (May 1 – July 15, 2012, 2013, or 2014), visiting each point three times per year with >10 days between visits. Point counts occurred between sunrise and 1100 h, and were not conducted during periods of rain or when wind speeds exceeded 20 km/hr (Conway 2011).

To parameterize survival and recruitment for the PVA models, I monitored Seaside Sparrows on three demographics study sites. I used capture-mark-recapture methods from May 15 – August 15, 2011 – 2014 to estimate annual survival. I captured adult and fledged juvenile birds using systematic mist-netting, in which each site was divided into three subplots and 3 – 5 mist-netting periods were conducted in each subplot per year. During each mist-netting period, I deployed two arrays of six 12-m nets for 2.5 – 3 hours between sunrise and 1100. Every sparrow received an aluminum USGS band and one color darvic band, and was released within 20 minutes of capture. I also located nests from May 15 – August 30, 2011 – 2013 using regular, systematic searches of the sites. I visited nests every three or four days to determine nest fate, and banded nestlings when they were six or seven days old. From these demographics surveys, I monitored 217 nests, and banded 492 adult and 413 juvenile Seaside Sparrows.

Stages, Survival, and Recruitment

I used two-stage (adult and juvenile), female-based models for Seaside Sparrows in RAMAS GIS version 6.0 (Akcakaya and Root 2013). I estimated adult

apparent survival using Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in package 'RMark' (Laake 2013) in program R (R Core Team 2014). For each bird, I created a capture history that was its presence or absence for four years (2011 – 2014). Previous studies have shown that survival does not differ between sexes (Post and Greenlaw 1982, DiQuinzio et al. 2001), so I combined male and female capture histories. Prior to estimating survival, I tested whether the model fit the assumptions of the CJS model using a goodness-of-fit test in program "Release." Two primary assumptions of the CJS model are: 1) every marked animal present in the population has the same probability of recapture (Test 2), and 2) every marked animal present in the population at a given sampling time has the same probability of survival until the next sampling time (Test 3.SR; Pollock and Alpizar-Jara 2005). The data met these assumptions (Test 2: $\chi^2_{0.05,\,1} = 0.00$, $P = 1.00$; Test 3.SR: $\chi^2_{0.05,\,5} = 8.33$, $P = 0.14$), and the maximum likelihood survival estimate was 0.50 (95% confidence interval = 0.38 – 0.63). I assigned juvenile survival as one-half of adult survival (0.25).

I defined recruitment as the average number of female offspring per female that survive to reproduce the subsequent year. Recruitment is the product of annual survival and annual fecundity (Table 12). Because Seaside Sparrows can have multiple broods each year and I did not identify each nesting attempt by each female in the study sites, I used Markov chain algorithms in program MCnest to simulate annual fecundity given specific population parameters (Etterson et al. 2009). From the nest monitoring data, I determined daily nest failure probability for each site, mean breeding season length, mean clutch size, and mean number of fledglings produced per successful nest (Table 12). Daily nest failure probability was calculated using program MCestimate, which is a generalization of the Mayfield method (Mayfield

1961, Mayfield 1975) using Markov chains (Etterson et al. 2007a, Etterson et al. 2007b). I modeled nest fate as binomial (success or failure) and did not incorporate covariates in predicting nest fate, so the likelihood algorithm was equivalent to that used by other nest-survival methods, such as Program MARK (White and Burnham 1999) and logistic exposure (Shaffer 2004). I also obtained nesting period length and waiting period length following a failed or successful nest from other Seaside Sparrow studies (Table 12; Post et al. 1983, Marshall and Reinert 1990, Greenlaw and Rising 1994, Post and Greenlaw 1994, Shriver et al. 2007). Given these parameters, MCnest simulated the mean fecundity of the average female from 10 populations of 100 sparrows. Because the PVA models were female-based and Seaside Sparrows have a balanced adult sex ratio (Post and Greenlaw 1982, Post and Greenlaw 1994), I divided fecundity by one-half to give the mean number of female fledglings produced per female per year. Using the upper 95% confidence limit of the MCnest fecundity estimates to account for imperfect detection of nestlings that fledged, fecundity was 2.04 female fledglings per female per year. Adult recruitment (survival x fecundity) was 1.02 and juvenile recruitment was 0.51.

Initial Abundance, Carrying Capacity, and Dispersal

I estimated the abundance of adult sparrows from the point count surveys using the 'unmarked' package (Fiske and Chandler 2011) in Program R (version 3.1.0; R Core Team 2014). I fit multinomial-Poisson mixture models (function *multinomPois*) to estimate abundance in each marsh unit with detection probability adjusted by observer and visit number (1, 2, or 3). To obtain adult female abundance estimates, I divided the total abundance estimates by one-half. The initial abundance of juvenile females was the product of initial adult female abundance and adult female

recruitment. To estimate carrying capacity for each subpopulation, I multiplied the subpopulation area with three females per ha (Table 11). While no attempt has been made to directly quantify carrying capacity for tidal marsh sparrows, three females per ha is a reasonable, yet conservative, estimate based on the maximum number of female Seaside Sparrows reported from several studies in the mid-Atlantic and New England (Post and Greenlaw 1975, Post and Greenlaw 1994, Kern et al. 2012).

Juveniles are responsible for dispersal, while adults typically remain site-faithful during the breeding season (Greenlaw and Rising 1994, Post and Greenlaw 1994, Shriver et al. 2010). I assigned a dispersal probability (0.045) to juveniles only and assumed the probability was equal among all subpopulations because little is known about juvenile dispersal distance in these species. Information on juvenile dispersal in tidal marsh sparrows has come primarily from non-migratory Cape Sable Seaside Sparrow (*A. m. mirabilis*) populations (Lockwood et al. 2001, Virzi et al. 2009), but I did not include these estimates in the PVA models because the sparrow populations in New Jersey are migratory.

Density-Dependence, Quasi-Extinction, and Stochasticity

To incorporate the effects of density-dependence on vital rates, I used a ceiling model, in which the populations grew exponentially and stabilized if they reached carrying capacity (Shriver and Gibbs 2004, Kern and Shriver 2014). I also included Allee effects to reduce recruitment by 50% if a subpopulation reached ≤5 females. I set the quasi-extinction threshold to 3,492, or 90% less than the initial abundance of adults and juveniles (34, 923). A decline of that magnitude would trigger significant management concern because small and declining populations are at increased risk of

extinction (O'Grady et al. 2004, Shriver and Gibbs 2004, Fagan and Holmes 2006, Kern and Shriver 2014).

The PVA models included both demographic and environmental stochastities. I incorporated demographic stochasticity such that, at year t, the number of survivors for the ith stage was drawn from a binomial distribution with parameters S_i (survival) and $N_i(t)$, or the population size at year t. The number of offspring produced by the ith stage was then drawn from a Poisson distribution with mean R_i (recruitment) x $N_i(t)$. Because tidal marsh sparrows are influenced by storm events that can change survival and fecundity rates through rain, storm surge, or altered predator abundances (Greenberg et al. 2006, Gjerdrum et al. 2008, Almario et al. 2009, Bayard and Elphick 2011), I also incorporated environmental stochasticity. I estimated the temporal variance of annual survival using a model in which survival was predicted by time in RMark, resulting in a standard deviation of 0.02. The data did not permit estimation of recruitment variance, so I used a standard deviation of 0.17, which is similar to what has been estimated for other small passerines (Akcakaya and Atwood 1997) and was used in other PVA analyses of Seaside Sparrows (Akcakaya and Atwood 1997, Shriver and Gibbs 2004, Kern and Shriver 2014). In each year, the survival and recruitment rates of adults and juveniles were drawn from a lognormal distribution with the assigned mean and standard deviation.

Simulations and Sensitivity Analysis

For each scenario, I ran 1000 simulations over a time period of 42 years (2008 – 2050). I also conducted sensitivity analyses to compare the relative effects of four model parameters (initial abundance, fecundity, carrying capacity, and survival) on the probability of a 70% population decline, the final quasi-extinction probability, and the

number of subpopulations occupied. Sensitivity analyses were performed on the 0.35 m and 0.75 m SLR scenarios, as well as on the management scenario that had the best outcome for the Seaside Sparrow population. During the sensitivity analyses, I varied each parameter individually while holding the others constant. I decreased initial abundance to the lower 95% confidence interval of the estimates for each marsh unit (see "Initial Abundance, Carrying Capacity, and Dispersal"), and examined the effect of reducing fecundity by 20%. I increased carrying capacity by 50% to 4.5 females per ha. Lastly, I evaluated the impact of increased and decreased survival by using the upper and lower 95% confidence limits of the estimate (see "Stages, Survival, and Recruitment").

Results

The Seaside Sparrow population on Forsythe NWR persisted for 42 years under 0.35 m and 0.75 m of SLR, but experienced large declines. Each SLR scenario had a final quasi-extinction probability of 0.00, indicating that the population remained above 3,492 females, and all 22 subpopulations remained occupied. However, large population declines were predicted by both models (Figure 10). Under 0.35 m of SLR, a decline of up to 54% was highly likely (mean likelihood = 0.96; 95% confidence interval = 0.93 – 0.99), while under 0.75 m of SLR, a decline of up to 70% was highly likely (0.96; 0.93 – 0.99). A 70% decline was 32 times more likely under 0.75 m than 0.35 m of SLR (mean likelihood = 0.96 and 0.03, respectively).

Fecundity management actions had a larger impact on the Seaside Sparrow population than thin-layer deposition (Figure 10). Increasing nest survival by 20% on the five units with the greatest Seaside Sparrow abundance (FM1) produced the best

outcome under both sea-level rise scenarios. FM1 under 0.35 m of SLR reduced the likelihood of a 60% population decline by 99% compared to 0.35 m SLR without management (mean likelihood = <0.00 and 0.71, respectively; 95% confidence interval = 0.00 – 0.03, and 0.68 – 0.74, respectively). Under 0.75 m of SLR, FM1 reduced the likelihood of a 70% decline by 93% compared to 0.75 m SLR without management (mean likelihood = 0.06 and 0.96, respectively; 95% confidence interval = 0.04 – 0.09, and 0.93 – 0.99, respectively). FM1 under 0.75 m of SLR also predicted a population decline that was nearly identical to 0.35 m SLR without management (Figure 10). Thus, applying FM1 was equivalent to reducing SLR by 50%.

Sensitivity analyses indicated that the 0.35 m, 0.75m, and 0.35 m + FM1 scenarios were most influenced by changes in fecundity and survival (Table 13). Decreasing fecundity by 20% and survival to the lower 95% confidence interval resulted in a 100% increase in the likelihood of quasi-extinction in all scenarios. For the 0.75 m scenario, which predicted a high likelihood of a 70% population decline, increasing survival to the upper 95% confidence interval resulted in a 99% decrease in the probability of that decline. In all scenarios, reducing abundance and increasing carrying capacity had negligible impacts, indicating that the model results are robust to uncertainty in abundance and carrying capacity estimation.

Discussion

To reduce negative impacts of SLR on Seaside Sparrows over the short-term, managers should employ techniques designed to increase nest survival. Although reducing the amount of marsh loss with thin-layer sediment deposition benefitted Seaside Sparrows, the positive impacts were not as great as improving nest success.

The sensitivity analyses also support this conclusion, as the results were more sensitive to changes in fecundity than changes in abundance or carrying capacity, the parameters affected by thin-layer deposition. Furthermore, the thin-layer scenario assumed that the sediment deposition would create 100% marsh in the treated areas, a best-case outcome of this management. Thin-layer deposition has been found to increase surface elevation, increase above- and below-ground plant production, and improve soil condition (Ford et al. 1999, Slocum et al. 2005, Croft et al. 2006), but efficacy depends on the precision of sediment application. Too much sediment can smother vegetation and prevent treated areas from becoming vegetated marsh (Mendelssohn and Kuhn 2003, Stagg and Mendelssohn 2010). Treating more areas on Forsythe NWR with thin-layer deposition would provide greater benefit for Seaside Sparrows and may be more important to long-term viability (e.g. < 50 years), as sea levels may rise at increased rates, removing habitat more quickly. However, thin-layer applications are costly and logistically challenging due to permitting, locating sediment similar to what is already present on the marsh surface, and dredging and spraying the materials. Thus, in the short-term, management should focus on measures to increase nest success.

Seaside Sparrow nests fail primarily due to depredation or flooding (Marshall and Reinert 1990, Greenberg et al. 2006), so strategies to increase nest success should target these causes. Predator exclusion is one of the most widely used methods of reducing nest depredation in ground-nesting birds and has been shown to improve hatching success (Smith et al. 2011). Wire mesh fencing has been used to exclude mammals from pine savannahs (Derrick et al. 2010, Morris et al. 2011), prairie potholes (LaGrange et al. 1995), beaches (Ivan and Murphy 2005), and marshes in

areas up to 98 ha in size (Jackson 2001). On Forsythe NWR marshes, mammalian nest predators include red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), American mink (*Neovison vison*), Norwary rat (*Rattus norvegicus*), and rice rat (*Oryzomys palustris*; Post et al. 1983, R. Kern, pers. obs.). The abundance of these species in marshes could be reduced with fencing placed along the marsh-upland edge and a trapping program, although it would not affect the abundance of avian nest predators, such as Fish Crows (*Corvus ossifragus*) and gulls (*Larus* spp.). However, reducing mammalian predation would likely improve sparrow nest success, in the absence of compensatory nest failure to flooding, and could also increase juvenile survival.

A more experimental approach to increasing Seaside Sparrow nest success involves mitigating the effects of tidal flooding. Flood control at the scale of a marsh or estuary has been accomplished through dikes (Warren et al. 2002, Cox et al. 2006, Maris et al. 2007), but is known to cause many negative changes, including the invasion of common reed (*Phragmites austalis*), which creates unfavorable conditions for endemic tidal marsh birds (Warren et al. 2002). Therefore, management actions should focus on developing small-scale, temporary, and minimally invasive flooding control for sparrow nests. The majority of nest flooding occurs during lunar high tides and storms (Marshall and Reinert 1990, Shriver et al. 2007, Bayard and Elphick 2011), so protection only needs to occur during brief (2 – 4 day) windows during the breeding season. The most straightforward way to reduce the impacts of tidal flooding is to create elevated habitat for nests, such as building mounds for beach-nesting birds (Koenen et al. 1996, Rounds et al. 2004). However, changing marsh surface elevation would actually remove Seaside Sparrow nesting habitat because *Spartina alterniflora* and *S. patens* only occur within a narrow range of elevation, salinity, and moisture

(Bertness and Ellison 1987). Reducing nest flooding will require creative solutions to lower tidal flooding during lunar high tides and storms without fundamentally altering the marsh hydrology and plant community.

Population viability analyses based on actual demographic data are an effective means of prioritizing management options (Reed et al. 2002). Site-specific demographic data, including survival, fecundity, and abundance, as well as site-specific SLR models, are strengths of this Seaside Sparrow PVA. However, model predictions could be improved by quantifying juvenile dispersal distance and carrying capacity. Also, a more comprehensive inclusion of SLR and global climate change impacts would strengthen the results. In this analysis, SLR affected only habitat availability, but it could also impact demographic parameters through increased nest flooding rate or the occurrence and severity of storms. SLR may also reduce Seaside Sparrow abundance by creating patches of marsh that are too small to be occupied. Seaside Sparrows are area-sensitive and unlikely to breed in patches that are < 15 ha in size (Benoit and Askins 2002), which may increase on Forsythe NWR due to SLR.

This was the first attempt to use PVA to evaluate management actions designed to reduce the impact of SLR on an endemic tidal marsh bird. Although the model only included Seaside Sparrows, management actions applied at the level of a whole marsh will likely benefit the entire suite of obligate tidal marsh breeding birds, such as Saltmarsh Sparrow (*Ammodramus caudacutus*) and Clapper Rail (*Rallus crepitans*). Sea-level rise is the most significant threat to endemic tidal marsh birds in North America (Shriver and Gibbs 2004, Erwin et al. 2006, Bayard and Elphick 2011, Kern and Shriver 2014) and maintaining viable populations requires prompt actions. Short-term measures to improve nest success can offset the negative impacts of SLR

and, if applied to areas with highest bird abundance, may have the same effect as reducing SLR by 50%.

TABLES

Table 11 Location, 2008 area, total percent of marsh loss, temporal trend in carrying capacity, initial abundance, and proposed management actions of 22 subpopulations of Seaside Sparrows on Edwin B. Forsythe NWR, NJ. Marsh units are listed in order of decreasing latitude. Percent of marsh loss and temporal trend in carrying capacity are calculated for 0.35 m and 0.75 m of sea-level rise by 2050. Initial adult abundance was determined through point count surveys and initial juvenile abundance was initial adult abundance x adult recruitment. Management actions include fecundity management (FM) and thin-layer deposition (TL).

Marsh unit (Subpopulation)	Latitude / Longitude	Area (ha)	Total % marsh loss		Temporal trend in carrying capacity		Initial abundance		Management actions
			0.35 m	0.75 m	0.35 m	0.75 m	Adult	Juv	
Metedeconk River	40° 2' 54.0" N 74° 3' 45.4" W	53.51	38.44	62.06	-1.47	-2.37	20	20	FM2, TL
Reedy Creek	40° 1' 55.7" N 74° 4' 39.0" W	147.68	43.59	72.24	-4.60	-7.62	60	62	TL
Kettle Creek	40° 1' 18.4" N 74° 6' 8.3" W	75.03	25.71	62.02	-1.38	-3.32	47	48	FM2
North Barnegat	39° 58' 22.6" N 74° 4' 53.3" W	69.54	16.72	35.40	-0.83	-1.76	68	70	FM2
Good Luck Point	39° 55' 40.6" N 74° 6' 40.7" W	53.39	16.63	31.97	-0.63	-1.22	22	22	FM2
Stouts Creek	39° 51' 6.7" N 74° 9' 1.6" W	179.01	18.11	66.44	-2.06	-3.86	84	86	–

Table 11 continued

Forked River	39° 49' 58.2" N 74° 9' 43.5" W	156.18	16.07	30.19	-1.30	-3.63	80	83	–
Loveladies	39° 45' 17.2" N 74° 8' 2.9" W	129.39	11.69	32.55	-1.64	-3.86	96	99	–
Barnegat	39° 44' 0.1" N 74° 11' 28.8" W	685.00	17.78	41.71	-3.65	-6.87	935	959	TL
AT&T	39° 42' 4.4" N 74° 11' 38.9" W	1094.85	7.45	14.04	-3.89	-10.00	1345	1380	FM1
Cedar Run	39° 39' 19.5" N 74° 14' 29.5" W	529.67	4.98	12.79	-1.51	-5.90	969	994	–
Cedar Bonnet Island	39° 39' 11.7" N 74° 11' 40.9" W	81.20	3.99	15.59	-0.32	-0.64	136	140	FM2
West Creek	39° 38' 18.0" N 74° 16' 16.7" W	1026.28	5.48	10.99	-2.58	-8.01	1216	1248	–
Little Egg South	39° 36' 30.2" N 74° 18' 14.4" W	1077.82	3.53	10.93	-3.19	-8.60	2461	2524	FM1
Little Egg Island	39° 35' 29.9" N 74° 14' 29.5" W	132.91	4.15	11.17	-0.76	-1.29	157	161	–
Bass River	39° 34' 10.4" N 74° 25' 8.7" W	1862.12	8.02	13.59	-1.83	-9.05	3802	3899	FM1
Motts/Mullica	39° 32' 8.9" N 74° 25' 37.4" W	578.45	1.37	6.81	-1.30	-3.77	963	988	–
Nacote Creek	39° 32' 0.9" N 74° 27' 2.0" W	450.74	3.15	9.12	-0.65	-2.32	943	968	–
Nacote Creek West	39° 31' 32.8" N 74° 28' 21.2" W	259.07	2.00	7.21	-0.47	-3.58	116	119	–

Table 11 continued

Oyster Creek	39° 30' 32.8" N 74° 25' 50.5" W	590.66	2.55	19.34	-1.47	-9.58	1490	1528	FM1
Little Beach/Holgate	39° 28' 5.8" N 74° 20' 41.9" W	1458.65	3.49	22.72	-13.49	-29.93	199	204	–
Reeds Bay	39° 28' 18.3" N 74° 24' 49.1" W	1498.06	12.95	28.72	-4.85	-15.87	2030	2082	FM1, TL

Table 12 Input values for Markov chain models of annual fecundity for Seaside Sparrows. Unless otherwise indicated, all values were taken from nest monitoring data collected on Edwin B. Forsythe NWR (2011 – 2013).

Parameter	Value
Daily nest failure probability	0.0433
Breeding season length[1]	May 12 – July 28
Mean clutch size	4
Mean # fledglings per successful nest	3.1356
Eggs laid per day[2]	1
Incubation period (days)[c]	12
Nestling period (days)[2]	10
Waiting period (days) after nest failure[3]	6
Waiting period (days) after nest success[2]	16

[1] Initiation dates taken from nest monitoring data; completion dates estimated by adding mean breeding season length for NY populations (Post and Greenlaw 1994) to initiation dates

[2] Post and Greenlaw 1994

[3] Post et al. 1983; Marshall and Reinert 1990

Table 13 Sensitivity analysis for 0.35 m and 0.75 m sea-level rise scenarios, and 0.35 m + fecundity management 1 (the most favorable scenario for Seaside Sparrows). The effect of changes in survival, fecundity, initial abundance, and carrying capacity on the Seaside Sparrow population are shown. Estimates are the probability that the population declines by 70%, the probability that the populations drops below the quasi-extinction threshold of 3,482 females, and the number of subpopulations (out of 22) occupied after 42 years. Parentheses contain 95% confidence intervals.

Parameter	Effect	Probability of 70% decline	Probability of quasi-extinction	Subpopulation occupancy (±1 SD)
0.35m sea-level rise		**0.03 (0.00 – 0.06)**	**0.00 (0.00 – 0.03)**	**22.00 ± 0.00**
–Survival[1]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	0.00 ± 0.00
+Survival[2]	+	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
–Fecundity[3]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	0.00 ± 0.00
–Abundance[4]	+	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
+Carrying capacity[5]	+	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
0.75m sea-level rise		**0.96 (0.93 – 0.99)**	**0.00 (0.00 – 0.03)**	**22.00 ± 0.00**
–Survival[1]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	0.00 ± 0.00
+Survival[2]	+	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
–Fecundity[3]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	0.00 ± 0.00
–Abundance[4]	+	0.80 (0.78 – 0.83)	0.00 (0.00 – 0.03)	22.00 ± 0.00
+Carrying capacity[5]	+	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
0.35m sea-level rise + FM1		**<0.00 (0.00 – 0.003)**	**0.00 (0.00 – 0.03)**	**22.00 ± 0.00**
–Survival[1]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	0.00 ± 0.00
+Survival[2]	N/A	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
–Fecundity[3]	–	1.00 (0.97 – 1.00)	1.00 (0.97 – 1.00)	2.20 ± 4.00
–Abundance[4]	N/A	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00
+Carrying capacity[5]	N/A	<0.00 (0.00 – 0.003)	0.00 (0.00 – 0.03)	22.00 ± 0.00

[1] Adult survival was the lower 95% confidence interval of the Cormack-Jolly-Seber estimates.
[2] Adult survival was the upper 95% confidence interval of the Cormack-Jolly-Seber estimates.
[3] Adult and juvenile fecundity was decreased by 20%.
[4] Initial adult abundance was the lower 95% confidence interval of the estimated abundance from the callback surveys.
[5] Carrying capacity was increased by 50%.

FIGURES

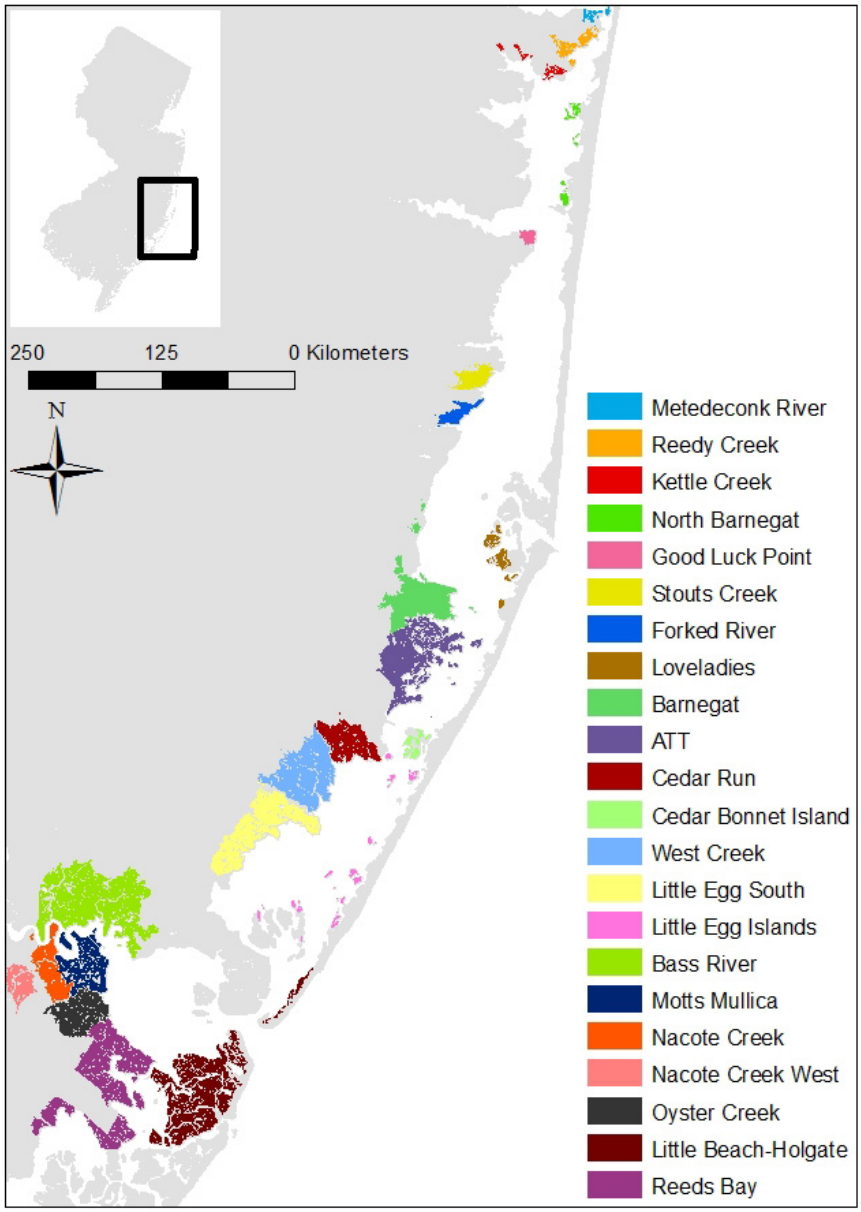

Figure 9 Salt marsh units (north to south) in Edwin B. Forsythe NWR, NJ. Each unit served as a Seaside Sparrow subpopulation in the population viability analysis models.

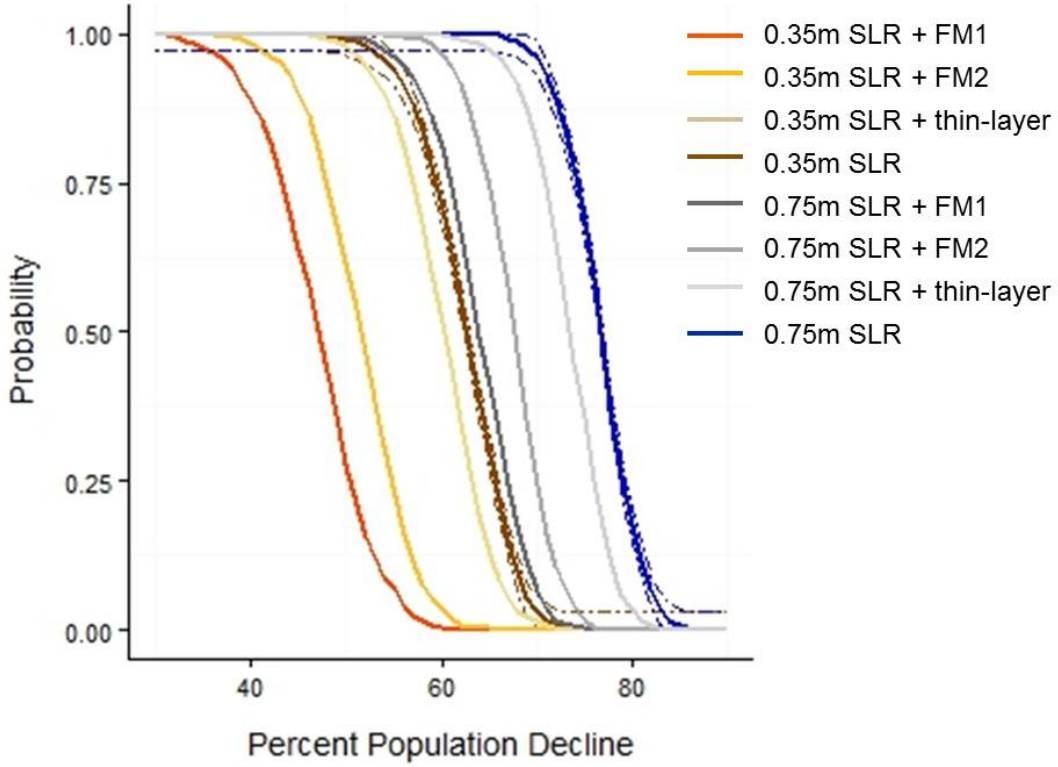

Figure 10 Likelihood of Seaside Sparrow population decline by 2050 under two sea-level rise (SLR) scenarios (0.35 m SLR, 0.75 m SLR) and three management + SLR scenarios (FM1, FM2, and thin-layer). FM1 involved increasing nest survival by 20% on the five units with highest Seaside Sparrow abundance in 2008. FM2 involved increasing nest survival by 20% on the five units with the smallest area in 2008. Thin-layer involved increasing surface elevation with sediment deposition on four marsh units. Dashed lines around the 0.35 m and 0.75 m SLR scenarios are 95% confidence limits.

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Appendix

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE RESEARCH PERMIT

University of Delaware
Institutional Animal Care and Use Committee

Application to Use Animals in Research and Teaching

(Please complete below using Arial, size 12 Font.)

Title of Protocol: Evaluation of the Salt Marsh Small Mammal Community at Edwin B. Forsythe National Wildlife Refuge, NJ

AUP Number: **1231-2012-0** | **← (4 digits only — if new, leave blank)**

Principal Investigator: Dr. Jacob L. Bowman

Common Name: Meadow Vole, White-footed Mouse, Meadow Jumping Mouse, House Mouse, Masked Shrew, Rice Rat, Norway Rat

Genus Species: *Microtus pennsylvanicus*, *Peromyscus leucopus*, *Zapus hudsonicus*, *Mus musculus*, *Sorex cinereus*, *Oryzomys palusris*, and *Rattus norvegicus*.

Pain Category: ***(please mark one)***

USDA PAIN CATEGORY: ***(Note change of categories from previous form)***

Category	Description
☐ **B**	Breeding or holding where NO research is conducted
☒ **C**	Procedure involving momentary or no pain or distress
☐ **D**	Procedure where pain or distress is alleviated by appropriate means (analgesics, tranquilizers, euthanasia etc.)
☐ **E**	Procedure where pain or distress cannot be alleviated, as this would adversely affect the procedures, results or interpretation

Official Use Only

IACUC Approval Signature: _____

Date of Approval: _____