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Intra- and Interspecific Variation in Demographic Rates and Niche Across the Range of a Species, the Saltmarsh Sparrow (Ammodramus caudacutus)

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INTRA- AND INTERSPECIFIC VARIATION IN DEMOGRAPHIC RATES AND NICHE ACROSS THE RANGE OF A SPECIES, THE SALTMARSH SPARROW (*AMMODRAMUS CAUDACUTUS*)

By

Katharine Johanna Ruskin

B.A. Columbia University, 2008

A DISSERTATION
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy
(in Ecology and Environmental Science)

The Graduate School
The University of Maine
August 2015

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DISSERTATION ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Katharine Ruskin I affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

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By Katharine Johanna Ruskin

Dissertation Advisor: Dr. Brian J. Olsen

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
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In this project, we examined various hypotheses that address one of the fundamental questions in ecology and evolution: what determines the range of a species? We used demographic data for saltmarsh sparrows (*Ammodramus caudacutus*) collected over the majority of the global breeding range. Saltmarsh sparrows are considered threatened by climate change, specifically sea level rise, which is predicted to result in loss of the tidal marsh habitat where saltmarsh sparrows live across their entire life cycle. For my dissertation, I investigated the reproductive biology of saltmarsh sparrows both to provide vital information for wildlife managers and to explore broad questions in ecological and evolutionary theory. We examined the spatial variation in risks to fecundity, vital rates, and niches across the global range of a species. We were thus able to investigate some of the most fundamental concepts in ecology, the drivers of species' distributions and spatial and temporal variation in niches. Specifically, I 1) explored competing risks to saltmarsh sparrow fecundity across their global range; 2) quantified

saltmarsh sparrow fecundity across the range and tested whether fecundity decreases from the range center to its periphery; 3) characterized the nesting niche of saltmarsh sparrows across a large spatial scale to determine whether niche conservatism holds in this system; and 4) investigated differences in nesting niches between saltmarsh and sympatric Nelson's sparrows and the fitness consequences of those differences. The results of these chapters suggest that though saltmarsh sparrow fecundity is influenced by large-scale factors such as global predation gradients, the saltmarsh sparrow range is not determined by large-scale trends in demographic rates or habitat marginality with latitude or between sister species.

CHAPTER 1: INTRODUCTION

Though they compose a very small percentage of the global habitat, tidal marshes host an uncommon amount of biodiversity because many are home to endemic species and subspecies (Greenberg et al. 2006). Among these is the saltmarsh sparrow (*Ammodramus caudacutus*), which breeds exclusively in tidal marshes of the northeastern United States (Greenlaw and Rising 1994). Saltmarsh sparrows are uniquely adapted to breeding in tidal marsh environments, which present various challenges such as freshwater limitation and little cover from predators (Greenberg, Maldonado, et al. 2006). Perhaps most importantly, the high marsh habitat in which saltmarsh sparrows breed typically floods at least once per month (during the highest astronomical tides), sometimes more often due to storms (Tiner 2013). Because saltmarsh sparrows nest on the ground, building their nests from tidal marsh grasses, they experience catastrophic nest losses during high marsh flooding events. Studies report that from 25% to over 60% of nest losses annually are caused by flooding (Greenlaw and Rising 1994; Shriver, Vickery, and Hodgman 2007; Gjerdrum, Elphick, and Rubega 2005). However, saltmarsh sparrows are adapted to the harsh disturbance of tidal flooding. Females renest quickly after nest loss and tend to synchronize with high tide events, completing their nesting cycle in as few as 26 days between astronomical high tide events (Greenlaw and Rising 1994; Shriver, Vickery, and Hodgman 2007).

Despite their adaptations to flooding, saltmarsh sparrows are named on the 2014 State of the Birds Watch List of species most in need of conservation action (Rosenberg et al. 2014), largely due to the threat of sea level rise. The population status of saltmarsh sparrows has long been threatened by habitat loss and degradation via environmental contamination from human development along the Atlantic coast. Anthropogenic climate change further threatens saltmarsh sparrow populations, however. Sea level rise is predicted to result in a net loss of high marsh habitat, and recent estimates of observed coastal wetland loss range from 1-2% per year (Pendleton et al. 2012). A predicted rise in storm surge intensity and frequency that could introduce increased disturbance in the tidal marsh flooding regime (Wong et al. 2014) could also threaten saltmarsh sparrow populations by disrupting their distinctive breeding ecology (Greenberg, Maldonado, et al. 2006; Shriver, Vickery, and Hodgman 2007). Specifically, sea level rise threatens to reduce the tidal marsh habitat in which saltmarsh sparrows breed and shorten the interval between tidal events that flood the high marsh zone, an interval that is fundamental to the saltmarsh sparrow nesting cycle.

The persistence of saltmarsh sparrows in the face of climate change is not only important to global biodiversity, but also because the species provides an interesting study system for exploring mating systems. Their mating system is highly promiscuous and “explosive”, with adults of both sexes gathering in high density areas of breeding habitat (S. T. Emlen and Oring 1977; Greenlaw and Rising 1994). Genetic analysis has shown that in a third of nests, each egg was sired by a unique male (Hill, Gjerdrum, and Elphick 2010). Neither males nor females are territorial, and males do not contribute to parental care (Greenlaw and Rising 1994). Among songbirds, promiscuous breeding systems are globally very rare (Gill 2007).

Saltmarsh sparrows also afford a unique opportunity to investigate evolutionary dynamics in the midst of a speciation event. In the northern portion of its breeding range, the saltmarsh sparrow overlaps with its sister species, the Nelson’s sparrow

(*Ammodramus nelsoni*). Though Nelson's sparrow populations on the Atlantic Coast breed in tidal marshes, they also breed in non-tidal marshes found in the interior United States and Canada (Shriver, Hodgman, and Hanson 2011). Until the mid-1990's, saltmarsh and Nelson's sparrows were considered two subspecies of the sharp-tailed sparrows, which refers to both species collectively (Greenlaw and Rising 1994; Rising and Avise 1993). Nelson's sparrows also exhibit a promiscuous mating system, but males have been observed to mate guard females after copulation for 15 minutes to 43 hours (Shriver, Vickery, and Hodgman 2007). Sharp-tailed sparrows hybridize in the zone of contact (Greenlaw and Rising 1994; Shriver, Vickery, and Hodgman 2007), between mid-coast Maine and northern Massachusetts (Jennifer Walsh et al. 2011; Hodgman, Shriver, and Vickery 2002; Jennifer Walsh et al. 2015). There is some evidence that the Nelson's sparrow is expanding southward, but other evidence points to a stable hybrid zone (Hodgman et al. 2002, Walsh et al. 2011, unpublished data). Regardless, sharp-tailed sparrows provide an exemplary study system for examining the ecological and evolutionary dynamics of sympatric sister species that are at some point in a speciation event.

Due to the threats to the unique contributions of saltmarsh sparrows to global biodiversity, researchers joined together to gather information about their population status and ecology. Under the moniker Saltmarsh Habitat and Avian Research Program (SHARP), researchers from five universities, federal and state governmental agencies, non-profit groups, and state wildlife conservation agencies from every coastal state in the northeast joined to study breeding saltmarsh sparrow populations across the northeastern United States (see www.tidalmarshbirds.org).

For my dissertation, I investigated the reproductive biology of saltmarsh sparrows in an ecological and adaptive framework as part of the larger SHARP project. With this research, I hope to inform conservation decisions for tidal marshes and explore the unique breeding ecology of saltmarsh sparrows. More specifically, I 1) explored competing risks to saltmarsh sparrow fecundity across their global range; 2) quantified saltmarsh sparrow fecundity across the range and tested whether fecundity decreases from the range center to its periphery; 3) characterized the nesting niche of saltmarsh sparrows across a large spatial scale to determine whether niche conservatism holds in this system; and 4) investigated differences in nesting niches between saltmarsh and sympatric Nelson's sparrows and the fitness consequences of those differences.

For these analyses, I used demographic data I collected with the help of eight field technicians during the summers of 2011-2013 in Scarborough Marsh, Cumberland County, Maine, U.S.A. Scarborough Marsh is located in southern Maine, at the center of the sharp-tailed sparrow hybrid zone. At four demographic study plots, we captured adults, searched for and monitored nest success, and surveyed surrounding vegetation. I also used demographic data collected with identical protocols in six other states by SHARP collaborators. Members of SHARP implemented the same standardized data collection protocols at nineteen additional study plots, which combined with my demographic study plots in Maine, spans a great circle distance of approximately 575 km (Fig. 1.1). Our survey covered 59% of the saltmarsh sparrow's breeding range (W. Wiest et al. in review) and 89% of the breeding range of the nominate subspecies, *Ammodramus caudacutus caudacutus* (Montagna, 1942).

Across all SHARP study plots, we collected data from 1027 saltmarsh sparrow nests from 2011-2013 (Table 1.1, but see the SHARP 2011-2013 State Wildlife Grant report at www.tidalmarshbirds.org for details on all monitored species). Of these nests, we identified the associated female for 631 nests by capturing the female at the nest with mist nets. We also collected data from 80 Nelson's sparrow nests and 364 sharp-tailed sparrow nests, which include both hybrids and nests for which the female was not trapped and identified within the hybrid zone. We collectively made over 3,100 nest visits, totaling approximately 9,000 exposure days. We recorded approximately 8,400 captures of sharp-tailed sparrows, for a total of approximately 5,000 unique individuals including adults, juveniles, and nestlings.

Using this tremendous dataset, I investigated the reproductive biology of saltmarsh sparrows both to provide vital information for wildlife managers and to explore broad questions in ecological and evolutionary theory. We examined the spatial variation in risks to fecundity, vital rates, and niches across the global range of a species. We were thus able to investigate some of the most fundamental concepts in ecology: drivers of species' distributions and spatial and temporal variation in niches. In the process, we also have provided imperative information to wildlife managers: spatial patterns and predictors of saltmarsh sparrow productivity, locations of habitat patches that should be targeted for conservation, and prioritized threats to saltmarsh sparrow fecundity on both global and local scales. Taken together, the work of my dissertation and the larger SHARP project will help determine how demographic rates vary across a species range and how we can best manage saltmarsh sparrow conservation actions to ensure their persistence.

Figure 1.1. Saltmarsh sparrow breeding range map. Demographic study plots surveyed by SHARP span seven states within the saltmarsh sparrow breeding range (shaded). Within each boxed area, we surveyed one to five study plots. The star indicates the latitudinal center of the saltmarsh sparrow breeding range.

Table 1.1. Location and sample size for demographic study plots. Demographic survey spanned Maine to New Jersey, 2011-2013.

Study plot	State	Latitude (decimal degrees)	Longitude (decimal degrees)	Study Plot Area (ha)	Nest Abundance	Notes
Oyster Creek	NJ	39.5	-74.4	18.5	43	
Mullica Wilderness	NJ	39.5	-74.4	17.4	92	
AT&T	NJ	39.7	-74.2	14.3	111	
	NJ			**50.2**	**246**	
Four Sparrow Marsh	NY	40.6	-73.9	1.2	40	Surveyed 2012-2013 only
Sawmill Creek	NY	40.6	-74.2	3.9	41	Surveyed 2012-2013 only
Marine Nature Park	NY	40.6	-73.6	3.8	22	Surveyed 2012-2013 only
Idlewild	NY	40.7	-73.8	3.1	11	Surveyed 2012-2013 only
	NY			**12.0**	**114**	**Surveyed 2012-2013 only**
Hammonasset	CT	41.3	-72.5	13.2	59	
East River	CT	41.3	-72.7	19.0	69	
Waterford	CT	41.3	-72.1	3.4	1	
Pattagansett	CT	41.3	-72.2	8.4	5	
Barn Island	CT	41.3	-71.9	23.5	40	
	CT			**67.4**	**174**	
John H. Chaffee	RI	41.4	-71.5	12.1	36	
Sachuest Point	RI	41.5	-71.2	3.7	35	
	RI			**15.8**	**71**	
Parker River	MA	42.8	-70.8	27.9	26	
	MA			**27.9**	**26**	
Chapman's Landing	NH	43.0	-70.9	12.0	129	
Lubberland Creek	NH	43.1	-70.9	8.1	25	Surveyed 2012-2013 only
	NH			**20.1**	**154**	
Eldridge Road	ME	43.3	-70.6	11.5	62	
Little River	ME	43.3	-70.5	6.9	2	Surveyed 2011 only
Jones Creek	ME	43.5	-70.4	11.5	79	Surveyed 2012-2013 only
Nonesuch River	ME	43.6	-70.3	13.9	29	
Libby River	ME	43.6	-70.3	13.0	4	Surveyed 2011 only
Scarborough Marsh	ME	43.6	-70.4	9.8	61	
	ME			**66.6**	**237**	

CHAPTER 2: DEMOGRAPHIC ANALYSIS DEMONSTRATES CONTRASTING ABIOTIC AND BIOTIC STRESSORS ACROSS A SPECIES RANGE

2.1. Summary

Sixty-five years ago, Theodosius Dobzhansky suggested that individuals of a species face greater challenges from abiotic stressors at high latitudes and from biotic stressors at their low-latitude range edges. This idea has been expanded to the hypothesis that species' ranges are limited by abiotic and biotic stressors at high and low latitudes, respectively (Asymmetric Abiotic Stress Limitation hypothesis, hereafter AASL). Support has been found in many systems, but this hypothesis has almost never been tested with demographic data. We present an analysis of fecundity across the breeding range of a species as a test of this hypothesis. We monitored saltmarsh sparrow (*Ammodramus caudacutus*) nests at twenty-three sites from Maine to New Jersey, USA. With data from 840 nests, we calculated daily nest failure probabilities due to competing abiotic (flooding) and biotic (depredation) stressors. We observed that abiotic stress (nest flooding probability) was greater than biotic stress (nest depredation probability) at the high-latitude range edge of saltmarsh sparrows, consistent with the AASL hypothesis. Similarly, biotic stress decreased with increasing latitude throughout the range, whereas abiotic stress was not predicted by latitude alone. Instead, nest flooding probability was best predicted by date, maximum high tide, and extremity of rare flooding events. Our results provide support for the AASL hypothesis across the global range of a species. We observed predictable variation in competing biotic and abiotic stressors to saltmarsh sparrow nest survival across the range. However, our results do not indicate a direct

tradeoff between abiotic and biotic stressors along a single gradient. Rather, we found that abiotic and biotic stressors were geographically independent.

2.2. Introduction

Theodosius Dobzhansky (1950) suggested that populations within the same species face systematically different types of stresses across the species range. At high latitudes, he hypothesized that abiotic stressors such as climate pose greater challenges, while biotic stressors such as competition are more limiting for a species near its low-latitude range edge. In the years since its original publication, Dobzhansky’s hypothesis has been expanded by subsequent ecologists to the idea that the range of a species is limited by abiotic stressors at high latitudes and biotic stressors at low latitudes (Brown, Stevens, and Kaufman 1996; Brown 1995; MacArthur 1984). The theory has also grown to include at least two other gradients of abiotic stress, elevation (Diamond 1973) and water depth (Connell 1961). Normand et al. (2009) called this integrated theory the Asymmetric Abiotic Stress Limitation (AASL) hypothesis. Broadly, it postulates that a tradeoff exists between physiological hardiness, which increases fitness in stressful abiotic conditions, and competitive ability, which increases fitness in areas of low abiotic stress.

The AASL hypothesis has been supported by a wide range of tests in a diverse array of species (see Parmesan *et al.*, 2005 for a review). For instance, over half of European alpine plants exhibit range boundaries that correlate with climatic variables at the northern edges of their ranges, but not the southern range edge (Normand et al. 2009); common garden experiments have demonstrated a tradeoff between adaptation to cold hardiness at high latitudes and competitive ability (growth rate) at low latitudes in a variety of temperate tree species (Loehle 1998); and algae species found in low tidal and subtidal depths take longer to recover photosynthetic capabilities following experimental desiccation stress than algae species found in the high tidal zone (Smith and Berry 1986).

Most previous investigations of the AASL hypothesis have provided only indirect support, however. Almost all previous studies have focused on either physiological tolerances of individuals or correlations between species' ranges and climatic parameters (see Brewer & Gaston, 2003 for a notable exception). Absolute empirical support for this hypothesis requires quantifying demographic rates as functions of biotic and abiotic stressors across the range of a species, but the AASL hypothesis has almost never been tested with demographic data.

In this paper, we directly test the AASL hypothesis by investigating patterns of reproduction at sites across the latitudinal range of a species. We quantified nest survival probabilities, a commonly-used measure of avian fecundity, across the majority of the breeding range of the saltmarsh sparrow (*Ammodramus caudacutus*). Using a Markov chain method (Etterson, Nagy, and Robinson 2007; Etterson, Greenberg, and Hollenhorst 2014), we separately estimated the probability of nest loss due to biotic (depredation) and abiotic (flooding) stressors. Finally, we explored how the different failure probabilities vary across the landscape, to test whether biotic stressors become increasingly important moving toward low latitudes and abiotic stressors are more important toward high latitudes, in accordance with the AASL hypothesis.

2.3. Methods

2.3.1. Study system

The geographic range of saltmarsh sparrows is ideally suited for exploring latitudinal trends because of its unique configuration. Saltmarsh sparrows breed exclusively in tidal marshes on the coast of the northeastern United States, from southern Maine to Virginia (Greenlaw and Rising 1994). Thus, the breeding range of Saltmarsh Sparrows is linear, runs roughly north-south, and is clearly bounded on the east and west by absence of tidal marsh habitat. Finally, tidal marshes are a relatively homogenous ecosystems that are defined by a simple structure and species assemblage (Greenberg, Maldonado, et al. 2006), allowing us to rule out many confounding factors associated with more diverse systems (Tiner 2013).

Within the saltmarsh sparrow breeding range, abiotic stressors also follow a roughly north-south gradient. Abiotic stressors include climate, the stressor that formed the basis of the AASL hypothesis, and the magnitude of tidal flooding, which has been identified as the leading cause of saltmarsh sparrow nest failure across a wide geographic range (Gjerdrum, Sullivan-Wiley, and King 2008; Greenlaw and Rising 1994; Gjerdrum, Elphick, and Rubega 2005; Shriver, Vickery, and Hodgman 2007). Saltmarsh sparrows build their nests a few centimeters above the ground in the high marsh zone (Humphreys et al. 2007), which typically floods only during monthly astronomical high tides and some storm events (Tiner 2013). Marshes at the high-latitude edge of the saltmarsh sparrow range experience astronomical high tides that are almost two times greater than those experienced in more southerly marshes (Fig. 2.1).

There is also support for a latitudinal gradient in biotic stressors to saltmarsh sparrow fecundity. In a wide array of other systems, studies have shown that predation and herbivory increase with decreasing latitude (Schemske et al. 2009), providing support for the AASL hypothesis. In tidal marshes across the range of the saltmarsh sparrow, low-latitude wetlands host nest predators that have no high-latitude analog (e.g., rice rats, *Oryzomys palustris* (Post 1981)). Further, in a meta-analysis of all the avian taxa endemic to tidal marshes in North America, nest predation rates decreased with latitude (Greenberg, Elphick, et al. 2006).

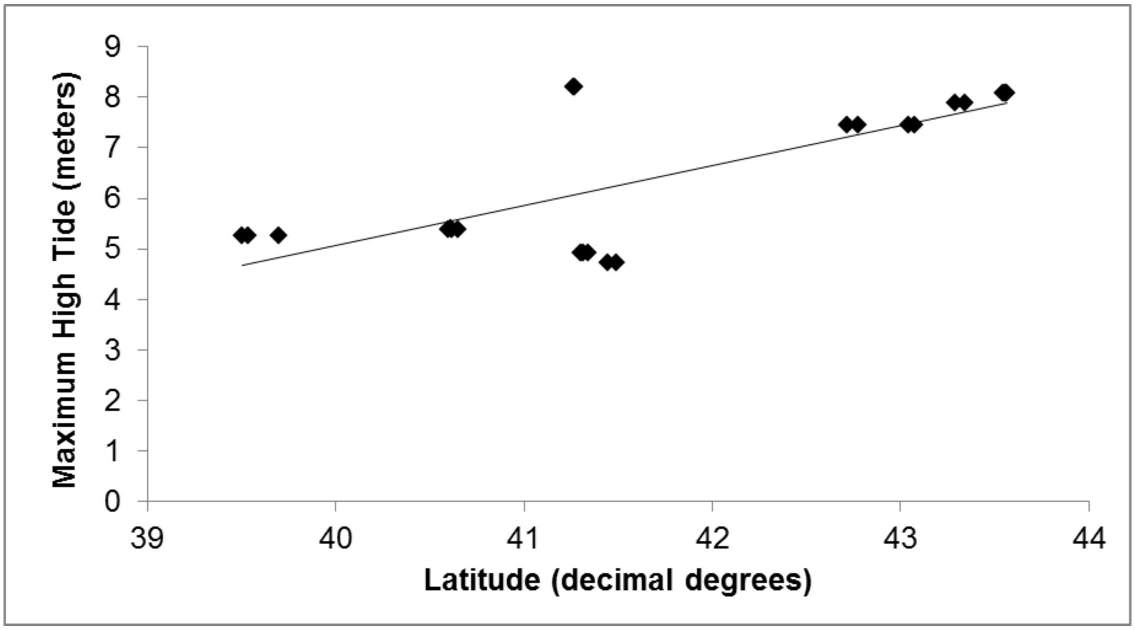


Figure 2.1. Maximum high tide increases with latitude. Maximum high tide height is shown by study plot, as measured by maximum observed water level, May-August in 2011-2013.

2.3.2. Data collection

From 2011 to 2013, we implemented a standardized data collection protocol at twenty-three study plots spanning a great circle distance of approximately 575 km (Fig.

1.1, see Appendix C for protocol). Our survey covered 59% of the saltmarsh sparrow's breeding range (Wiest unpub.) and 89% of the breeding range of the nominate subspecies, *Ammodramus caudacutus caudacutus* (Montagna 1942). Study plots consisted of 5-24 ha areas of tidal marsh in the high-marsh zone. At each study plot, we searched for nests at least once per week throughout the breeding season (May to August). Once we found a nest, we revisited it every 2-5 days to determine success or failure. If a nest failed, we determined the cause of nest failure based on evidence at the nest site (Appendix C).

We assigned depredation (biotic stressor) as the cause of nest failure to nests found with broken or punctured eggs, mangled chicks, or to nests that were empty and dry after nights that did not have tides high enough to flood the high marsh. We assigned flooding (abiotic stressor) as the cause of failure to nests that were wet after nights with tides high enough to inundate the high marsh, contained drowned chicks, or had intact eggs outside the nest (presumably because they floated out). We classified nests as failed for unknown reasons in cases of conflicting evidence (e.g., nest bowl was visibly wet and contained punctured eggs). We considered nests successful if, after survival on all previous visits, they were found empty when at least one nestling would have been 10 days old, the age at which chicks are able to leave the nest (Greenlaw and Rising 1994).

We included two covariates as potential predictors of nest depredation probabilities: latitude and serial date. We recorded the latitude and longitude of each study plot at its approximate center using ArcGIS version 10.1 (Environmental Systems Research Institute, Redlands, USA). Inclusion of latitude in the top model, specifically that nest depredation probability increased with latitude, would provide support for the

AASL hypothesis. We included serial date as a covariate to test an alternative hypothesis. Nest predation increases throughout the breeding season in a variety of avian taxa, perhaps because nest predators increase foraging effort to feed their own growing young (see Verhulst & Nilsson, 2008 for a review). Inclusion of serial date in the top model would demonstrate that biotic stress to saltmarsh sparrow fecundity changed seasonally across the species range.

To measure nest flooding stress, we used three potential predictors to reflect distinct inputs to tidal marsh hydrology: maximum high tide, extremity of rare flooding events, and relative sea-level rise (Appendix A). Tidal marshes are shaped by both regular flooding caused by astronomical tides and irregular flooding caused by weather. Both types of flooding contribute to marsh development and maintenance (Teal 1986). In addition, recent anthropogenic sea-level rise has contributed to higher water levels and increased flooding of tidal marshes (Wong et al. 2014).

We used latitude as a proxy for maximum high tide based on the observed relationship between the two variables in our study region (Fig. 2.1). We also included maximum observed high tide within the study period as a direct measure of tidal height. We obtained water-level data from the National Oceanic and Atmospheric Administration (NOAA) using the observation station with available data that was closest to each demographic study plot (approximately 15-50 km by water). We used NOAA's recorded water levels above the mean daily high tide (mean higher high water datum, hereafter MHHW) for 1% annual exceedance probabilities to reflect the extremity of rare flooding events at a study plot. Exceedance probabilities describe the likelihood that water level will surpass a given level; for example, a 1% annual exceedance probability level of 1.23 m above MHHW means that only once in 100 years will the water level likely reach 1.23 m above MHHW. This datum is corrected for local relative sea level rise. Finally, we collected linear sea-level rise estimates based on 1969-2011 water levels from Boon et al. (2012), using the location nearest to each demographic study plot (approximately 15-55 km by water). Finally, we included serial date as a covariate because monthly high tides decrease in height throughout the breeding season.

Inclusion of latitude or maximum tidal height in the top model, specifically that nest flooding probability increased with either variable, would indicate that regular monthly flooding from astronomical tides posed the greatest abiotic stress to saltmarsh sparrow fecundity, as predicted by the AASL hypothesis. Conversely, inclusion of either exceedance values or sea level rise in the top model, specifically that nest flooding probability increased with either variable, would indicate that irregular, anthropogenic flooding imposed greater stress to saltmarsh sparrow reproduction. Furthermore, because extremity of rare flooding events and rate of sea-level rise are influenced by climate change, their inclusion in the top model would indicate that saltmarsh sparrows face growing abiotic stress under predicted climate change.

2.3.3. Statistical analyses

We used the program MCestimate (Etterson, Nagy, and Robinson 2007; Etterson, Greenberg, and Hollenhorst 2014) to calculate daily probabilities of nest survival and failure from competing risks. MCestimate employs a Markov chain algorithm to estimate daily nest-failure probabilities via a generalization of the Mayfield method (Mayfield 1975). Unlike more traditional logistical exposure models (Rotella, Dinsmore, and

Shaffer 2004; Dinsmore, White, and Knopf 2002; Shaffer 2004), MCestimate separately estimates probabilities of failure due to competing risks, in additional to total daily nest survival probability.

We used MCestimate to generate daily nest survival and failure probabilities as functions of nest- and study plot-level covariates from nest monitoring data (Shaffer 2004; Etterson and Stanley 2008). We adopted a two-stage approach for model selection (see Appendix B for full model lists). First, we separately compared candidate models for biotic and abiotic nest failure probabilities. We compared models containing all additive combinations of potential covariates of nest depredation probability (latitude and serial date) while modeling nest flooding probability as constant, plus an intercept-only null model (4 candidate models total). Similarly, we modeled nest depredation probability as constant while we compared all additive combinations of the potential covariates of nest flooding probability (latitude, maximum high tide, 1% exceedance value, linear sea-level rise rate, and serial date). Again, we also included an intercept-only null model (32 candidate models total). We used second order Akaike's Information Criteria (AIC_c) to compare candidate models in each set while accounting for sample size. We used a difference of 2 or more in AIC_c values to identify which models most parsimoniously described the biotic and abiotic nest failure probabilities (Burnham and Anderson 2002; Akaike 1974). We chose the simplest model within 2 AIC_c values of the top model. For the second stage of model selection, we built a combined model based on the best models for nest depredation and flooding probabilities, and compared the combined model to an intercept-only null model and the best models from the previous stage.

Finally, to report the daily probabilities of nest depredation, nest flooding, and total nest survival by study plot, we created models with study plot as the sole fixed-effect covariate to allow for maximum variation. We created a separate model for each nest depredation probability, nest flooding probability, and total nest survival probability as predicted by study plot.

2.4. Results

We analyzed nest monitoring data from 840 nests found over three years of study. We observed daily nest depredation probabilities that ranged from <0.001 to 0.046 and daily nest flooding probabilities that ranged from 0.016 to 0.116, depending on study plot. Daily nest-survival probabilities ranged widely by study plot, from 0.857 to 0.970 (2% to 48% total nest survival over the 24-day nesting period; Table 2.1).

Despite much local heterogeneity, we observed clear large-scale patterns in nest failure probabilities of saltmarsh sparrows. The model containing only latitude best predicted daily nest depredation probability (w_i=0.57) and performed much better than the null model (ΔAIC_c=23.15, w_i<0.01). Nest depredation probability increased moving toward low latitudes (Table 2.2, Fig. 2.2).

An additive combination of date, maximum high tide, and extremity of rare flooding events best predicted daily nest flooding probability (w_i=0.43) and performed much better than the null model (ΔAIC_c=29.5, w_i<0.01). Nest flooding probability decreased throughout the breeding season, increased with increasing maximum high tide, and increased with increasing extremity of rare flooding events (Table 2, Fig. 2.3). The nest flooding model using latitude as the sole predictive variable performed worse than the null model (ΔAIC_c=30.01, w_i<0.01; Fig. 2.2).

The combined model (nest depredation probability predicted by latitude, nest flooding probability predicted by serial date, maximum high tide, and exceedance value; w_i=1.0) predicted nest failure probabilities better than the top model for nest depredation probability (ΔAIC_c=28.86, w_i<0.01), the top model for nest flooding probability (ΔAIC_c=20.52, w_i=<0.01), and the null model (ΔAIC_c=50.2, w_i<0.01).

Total daily nest survival probability increased toward the high-latitude edge of the saltmarsh sparrow breeding range (Fig. 2.2). Total nest survival probability decreased with increasing exceedance value and increased throughout the breeding season. There was no relationship between maximum high tide and total nest survival probability.

Table 2.1. Global and local probabilities of nest failure and survival. Shown are daily probabilities ± standard error for saltmarsh sparrows by study plot, 2011-2013.

Study Plot	Number of nests	Global Daily Nest Depredation Probability[1]	Local Daily Nest Depredation Probability[2]	Global Daily Nest Flooding Probability[1]	Local Daily Nest Flooding Probability[2]	Global Daily Total Nest Survival Probability[1]	Local Daily Total Nest Survival Probability[2]
Oyster Creek	30	0.034 ± 0.005	0.046 ± 0.015	0.028 ± 0.003	0.029 ± 0.013	0.938 ± 0.006	0.928 ± 0.017
Mullica Wilderness	70	0.034 ± 0.005	0.045 ± 0.009	0.028 ± 0.003	0.021 ± 0.01	0.938 ± 0.006	0.936 ± 0.011
AT&T	68	0.032 ± 0.004	0.033 ± 0.007	0.028 ± 0.003	0.040 ± 0.008	0.940 ± 0.005	0.930 ± 0.011
Four Sparrow Marsh	15	0.025 ± 0.003	0.011 ± 0.008	0.050 ± 0.007	0.022 ± 0.011	0.925 ± 0.007	0.968 ± 0.014
Sawmill Creek	24	0.025 ± 0.003	0.001 ± 0.007	0.036 ± 0.004	0.050 ± 0.015	0.939 ± 0.004	0.940 ± 0.016
Marine Nature Park	10	0.025 ± 0.003	0.000 ± 0.000	0.050 ± 0.007	0.064 ± 0.027	0.925 ± 0.007	0.936 ± 0.028
Idlewild	7	0.024 ± 0.002	0.023 ± 0.023	0.050 ± 0.007	0.093 ± 0.042	0.926 ± 0.007	0.883 ± 0.051
Hammonasset	50	0.020 ± 0.002	0.004 ± 0.003	0.070 ± 0.009	0.062 ± 0.010	0.910 ± 0.009	0.934 ± 0.011
East River	60	0.020 ± 0.002	0.020 ± 0.007	0.056 ± 0.005	0.061 ± 0.011	0.924 ± 0.005	0.921 ± 0.012
Waterford[3]	1	0.021 ± 0.002	NA	0.040 ± 0.005	NA	0.940 ± 0.005	NA
Pattagansett	5	0.021 ± 0.002	0.000 ± 0.001	0.040 ± 0.005	0.057 ± 0.033	0.940 ± 0.005	0.944 ± 0.034
Barn Island	33	0.021 ± 0.002	0.018 ± 0.008	0.040 ± 0.005	0.103 ± 0.020	0.940 ± 0.005	0.885 ± 0.023
John H. Chaffee	29	0.020 ± 0.002	0.016 ± 0.007	0.040 ± 0.005	0.019 ± 0.008	0.940 ± 0.005	0.965 ± 0.011
Sachuest Point	19	0.020 ± 0.002	0.087 ± 0.030	0.040 ± 0.005	0.054 ± 0.03	0.943 ± 0.005	0.857 ± 0.038
Parker River	48	0.014 ± 0.002	0.019 ± 0.006	0.031 ± 0.002	0.031 ± 0.007	0.955 ± 0.003	0.949 ± 0.009
Chapman's Landing	139	0.013 ± 0.002	0.002 ± 0.002	0.031 ± 0.002	0.024 ± 0.004	0.956 ± 0.003	0.970 ± 0.004
Lubberland Creek	24	0.013 ± 0.002	0.000 ± 0.000	0.031 ± 0.002	0.032 ± 0.010	0.956 ± 0.003	0.967 ± 0.010
Eldridge Road	64	0.012 ± 0.002	0.017 ± 0.005	0.034 ± 0.003	0.061 ± 0.010	0.954 ± 0.003	0.923 ± 0.010
Little River	5	0.012 ± 0.002	0.033 ± 0.023	0.034 ± 0.003	0.016 ± 0.017	0.954 ± 0.003	0.951 ± 0.029
Jones Creek	62	0.011 ± 0.002	0.017 ± 0.005	0.038 ± 0.003	0.017 ± 0.006	0.951 ± 0.003	0.964 ± 0.007
Nonesuch River	25	0.011 ± 0.002	0.036 ± 0.012	0.038 ± 0.003	0.032 ± 0.011	0.951 ± 0.003	0.936 ± 0.014
Libby River	3	0.011 ± 0.002	0.002 ± 0.014	0.038 ± 0.003	0.116 ± 0.069	0.951 ± 0.003	0.879 ± 0.068
Scarborough River	49	0.011 ± 0.002	0.015 ± 0.006	0.038 ± 0.003	0.050 ± 0.010	0.951 ± 0.003	0.936 ± 0.012

[1] Global probabilities were calculated using the top-ranked combined model.

[2] Local probabilities were calculated using study plot as the sole predictive variable in models of daily nest depredation, flooding, and survival.

[3] Local probabilities could not be calculated for this study plot because it only had one nest.

Table 2.2. Multinomial logit scale estimates of nest fates. Shown are the estimates from the top-ranked model of variables affecting nest fates of saltmarsh sparrows, 2011-2013.

Nest Fate	Predictor	Effect size	Standard Error	Observed Minimum	Observed Maximum
Depredated	Intercept	7.8233	2.3790	NA	NA
Depredated	Latitude (decimal degrees)	-0.2820	0.0574	39.5056	43.5655
Flooded	Intercept	-3.7056	0.7225	NA	NA
Flooded	Maximum Observed High Tide (m)	0.5910	0.1705	1.4377	2.5021
Flooded	1% Exceedance Value above MHHW (m)	0.9660	0.1993	1.1400	2.0604
Flooded	serial date	-0.0115	0.0031	138	244

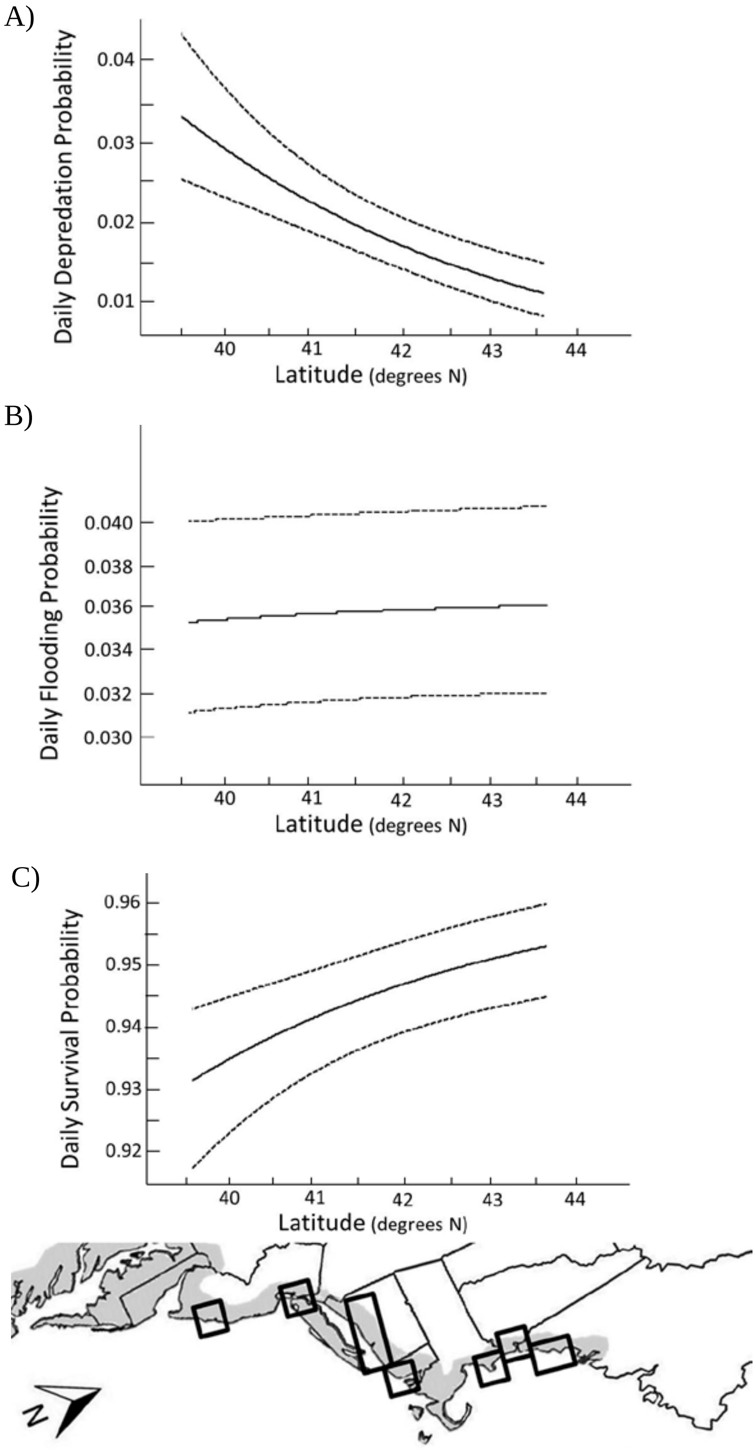


Figure 2.2. Daily nest failure probabilities by latitude. A) Daily nest predation probability for saltmarsh sparrows modeled as a function of latitude (nest depredation probability increased with increasing latitude); B) Daily nest flooding probability modeled as a function of latitude (daily nest flooding probability was not related to latitude); C) Total daily nest survival probability modeled as a function of latitude (total daily nest survival probability increased with increasing latitude).

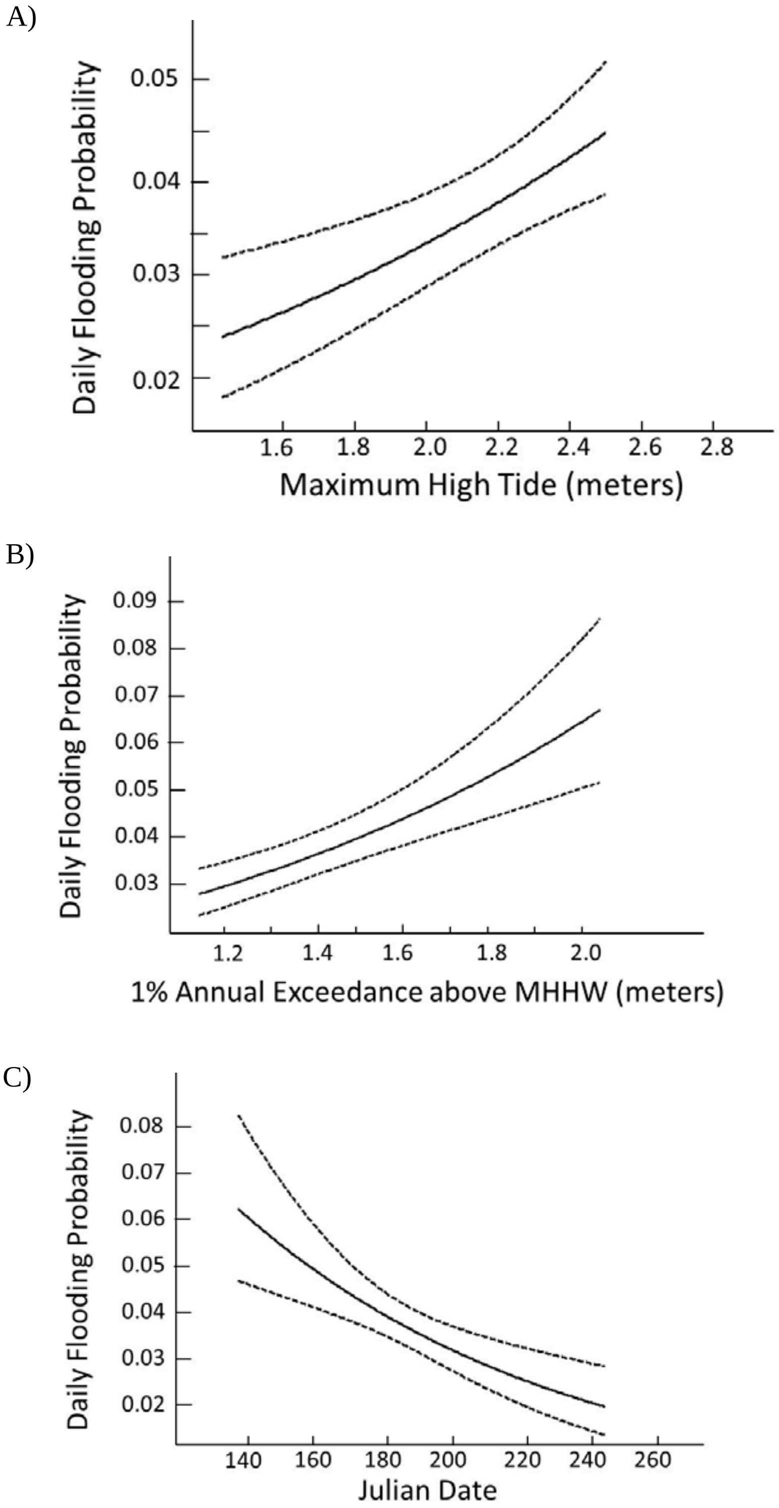


Figure 2.3. Daily nest flooding probability predictors. Daily nest flooding probability of saltmarsh sparrows was best predicted by A) maximum observed high tide during the study period (May-August, 2011-2013); B) meters above mean higher high water (MHHW, the monthly high tide) for the 1% annual exceedance probability; and C) serial date.

2.5. Discussion

Our findings are consistent with the AASL hypothesis that abiotic stressors (flooding) pose greater risks to population growth at high latitudes than biotic stressors (depredation). Further, we found that nest depredation probability varied with latitude, suggesting that biotic stressors become increasingly important moving toward low latitudes. Nest flooding probability did not vary with latitude, however. Instead, nest flooding probability was best predicted by an additive combination of three variables that vary independently from latitude. Therefore, in opposition to modern formulations of the AASL hypothesis, our results suggest that in this system, there is not a direct tradeoff between physiological tolerance and competitive ability. Without experimental manipulation, we cannot be certain that nest flooding and nest depredation probabilities limit saltmarsh sparrow populations where they are highest. We can conclude, however, that the relative importance of each competing stressor changes across the species range and through time.

We found evidence of a latitudinal trend in biotic stress (Fig. 2.2A). Specifically, nest depredation probability increased toward low latitudes. Large-scale patterns in species interactions are likely driving the observed decrease in nest predation with increasing latitude in saltmarsh sparrows. Few data exist for the abundance and diversity of potential nest predators in tidal marshes. However, the species richness of the major groups of nest predators (mammalian, reptilian, and avian) all increase toward low latitudes within the region (Cook 1969; Currie 1991).

The observed increase in nest depredation probability toward low latitudes might also be explained by correlation with some additional metric, such as marsh size. Rates of adverse biotic interactions such as predation and parasitism, particularly well-studied for nests, increase with decreasing distance to the habitat patch edge in many ecosystems and taxa (Paton 1994; Ries and Fagan 2003; Etterson, Greenberg, and Hollenhorst 2014). We observed the highest nest depredation probabilities at the southern end of our study area, however, where marsh size is largest in this region. Thus, we can rule out distance to the marsh perimeter as a confounding influence. For saltmarsh sparrows, therefore, any potential increases in nest predation rate due to upland proximity were overcome by a latitudinal trend in predation risk. Though we found that biotic stress intensified toward low latitudes within the saltmarsh sparrow range, nest flooding probability was still greater than nest depredation probability at one of our three lowest-latitude study plots. We should note, however, that we did not sample sites at the low-latitude margin of this species range.

Consistent with the AASL hypothesis, nest flooding was much more important than nest depredation near the high-latitude margin of the saltmarsh sparrow range. However, we did not observe that abiotic stress varied with latitude across the range (Fig. 2.2B). We observed a variable landscape of competing abiotic and biotic stresses to saltmarsh sparrow fecundity across the species range, but our results suggest that there is not a direct tradeoff between abiotic and biotic stressors. The increased relative importance of flooding among high-latitude populations was due more to the decreases in predation risk than any increase in flooding stress, which was high and variable across the range. Thus, our results do not support the hypothesis that populations face a direct tradeoff between physiological hardiness and competitive ability across this species range.

These results suggest that saltmarsh sparrow reproduction may be shaped by two different gradients of stress that vary independently but act simultaneously. The AASL hypothesis originally cited a single gradient, latitude, which explained both biotic diversity and abiotic stress gradients. Extensions of this hypothesis have similarly used single gradients (e.g., elevation or water depth) to explain the strength of both biotic and abiotic stressors. To our knowledge, multiple gradients have not been examined in the same species. The underlying mechanisms structuring nest predator communities in our system appear to be independent of the controls on nest flooding stress at the scale we examined. Thus, we hypothesize that saltmarsh sparrow population growth probabilities, and hence range edges, are simultaneously limited by biotic and abiotic stressors along two independent gradients: latitude (driving biotic interactions) and water depth, in this case tidal flooding (driving abiotic stress). Latitude is an indirect gradient for abiotic stress (Austin and Smith 1990) that holds within many systems, but evidently not entirely for saltmarsh sparrows. Similar patterns might be expected in other systems in which gradients of abiotic stress vary independently relative to broad latitudinal patterns in biodiversity (e.g., gradients of fire regime, wind damage, or urbanization). Future studies should include comprehensive demographic analyses of species in such ecosystems to test whether a species can be simultaneously limited across multiple gradients of abiotic stress in the manner that the AASL hypothesis predicts. If multiple stress gradients simultaneously affect population growth rates of a species on a large geographic scale, we face complications in attempting to understand range limits.

Our study may have been limited by statistical power, however. Though we sampled a large number of nests (n=840), our covariates were gathered at the level of study plot (n=23). In addition, the resolution of the water level covariates was limited by tidal stations with available data (n=9). In particular, this resolution did not incorporate variation at a small spatial scale that appears important for saltmarsh sparrow fecundity. For example, water level data from the Portland, ME tide station was applied to 4 study plots. Of these, two experience no tidal restrictions (Libby and Nonesuch rivers), one experiences mild restriction (Scarborough River), and one study plot experiences severely restricted tidal flow (Jones Creek). The daily probability of nest flooding at the study plot level varies somewhat concomitantly with the level of tidal restriction (mean daily nest flooding probability for no tidal restriction: 0.07; mild restriction: 0.05; severe restriction: 0.02). Based on our statistical approach, therefore, we cannot definitively say that there was no relationship between flooding (measured by either metric) and nest success, only that the relationship, if present, was of small enough magnitude to prevent detection given the variation in nest success from other sources and our sample size. Given that we were able to detect systematic variation between predation and latitude, however, we argue that a relationship between nest success and flooding, if present, is sufficiently small that variation from other sources is likely more biologically meaningful.

In addition, the lack of a direct tradeoff between biotic and abiotic stress may be an artifact of human modification. The fact that 1% exceedance values demonstrate a strong positive relationship with nest flooding probability is particularly telling. Extreme water levels have increased on a global scale, but these trends are generally driven by sea-level rise (Wong et al. 2014). However, New York and Connecticut host particularly high exceedance values for the region, and these conditions may be due to recent changes that are independent of sea-level rise (Karl and Knight 1998; Menéndez and Woodworth 2010). Urbanization, largely through the increase of runoff caused by impermeable surfaces, has long been known to contribute to ‘flashier’ flooding patterns that result in increased exceedance values (Hollis 1975) and can degrade tidal marshes. Tidal marshes in New York and Connecticut have particularly suffered, experiencing relatively high levels of marsh loss within the region (Tiner 2013; Hartig et al. 2002; Deegan et al. 2012). For example, some islands in Jamaica Bay, New York, USA have lost over 50% of their vegetated area since 1924, and probabilities of erosion have accelerated through time (Hartig et al. 2002).

New York and Connecticut also include the study plots with high nest flooding probabilities relative to the local maxima of high tides. Notably, these areas are the geographic center of the global saltmarsh sparrow population, which is considered imperiled (Greenlaw and Rising 1994; IUCN 2012; Butcher et al. 2007). Latitude alone may have once been a good predictor of nest flooding in saltmarsh sparrows, as maximum high tides do show a latitudinal gradient (Fig. 2.1). Locally heterogeneous responses to climate and landscape changes, however, may have altered any historical tradeoff between biotic and abiotic causes of nest failure. Regardless, modern saltmarsh sparrow populations are affected by an axis of abiotic stress that is independent of latitude, whether heterogeneous flooding has existed throughout the Holocene or is a result of recent patterns of anthropogenic modification of the landscape.

Like nest depredation probability, total nest survival probability was related to latitude (Fig. 2.2C). We observed the highest predicted nest-survival probabilities at the highest latitudes. This result serves as a single empirical example of how reproductive success varies across a species' range. We suggest that more investigations in the same vein are necessary to understand how interactions between niches and environmental heterogeneity produce patterns of population growth through time and across space. Joseph Grinnell (1904) hypothesized that populations toward the center of a range exhibit the highest population growth, because the environmental conditions will be most favorable for a given species there (see Sagarin *et al.*, 2006 for a recent review). Our results do not support Grinnell's hypothesis, though we do not consider this project a direct test of Grinnell's hypothesis because we did not measure total population growth. Further, nest survival probability is commonly used as a proxy for fecundity in the ornithological literature, but it remains several steps removed from annual fecundity (Olsen et al. 2008; Etterson et al. 2011a; H. M. Streby et al. 2014). Variations in life history traits such as clutch size or renesting probability could transform nest failure probabilities across the range into different spatial patterns of annual fecundity. While life history adaptations may show different patterns than those reported here, the spatial pattern for exogenous drivers of fecundity remains clear.

Our study suggests that while different range edges may occur due to different stressors, adaptation to abiotic stressors does not necessarily prevent adaptation to biotic stressors. To understand what, if any, evolutionary consequences exist for the species due to the balance of abiotic and biotic stressors across the range, we must better quantify fecundity. Future studies should include life history parameters such as clutch size or renesting rates and the variation associated with each across the global range of a species. Furthermore, we found that a single vital rate was independently affected by abiotic and biotic stressors across space. However, range-limiting factors could affect multiple vital rates, and future studies should include survivorship and population connectivity. Understanding the demographic and spatial dynamics of species' ranges is an important topic in theoretical ecology, and will become increasingly important for conservation in the face of climate change.

CHAPTER 3: SEASONAL FECUNDITY IS NOT RELATED TO RANGE POSITION ACROSS A SPECIES' GLOBAL RANGE

3.1. Summary

The range of a species is determined by the balance of its demographic rates across space. Population growth rates are widely hypothesized to be highest at the geographic center of the species range, but empirical support has been mixed, and it has rarely been studied with demographic data. Therefore, which processes determine species' ranges remains an open question and one of growing importance in light of climate change. We quantified seasonal fecundity across the global range of a single species, the saltmarsh sparrow (*Ammodramus caudacutus*), which demonstrates a peak of abundance at the geographic center of its range. We compared seasonal fecundity estimates replicated over 3 years of study to latitude. We observed no linear relationships between fecundity and latitude. While fecundity was generally consistent at the study plot scale, it varied greatly within the scale of tens of kilometers. Further, fecundity estimates at study plots near to each other were as different as those from across the range. Our results do not provide support for the hypothesis that demographic rates are highest at the geographic center of a species range. These results instead suggest that local drivers strongly influence saltmarsh sparrow fecundity across their global range and that range edges in this species are likely determined by local environmental characteristics, not gradual declines in suitability.

3.2. Introduction

Identifying the processes that determine species' distributions has long been a central topic of inquiry in ecology. Fundamentally, the range of a species is determined by the balance of demographic rates, specifically birth, death, immigration, and emigration (Pulliam 1988), over space. Grinnell highlighted this principle in his formulation of a hypothesis regarding the pattern and processes governing species' ranges. Grinnell (1904) wrote, "The center of distribution of any animal is where the greatest rate of increase is. The greatest rate of reproduction is presumably where the species finds itself best adapted to its environment." In other words, the core of the species niche is found at the center of the geographic range. Moving away from the range center, population growth rates are thought to decline as habitat becomes increasingly marginal for the species, or toward the periphery of its niche (Pulliam 1988; Guo et al. 2005; Brussard 1984; Saetre et al. 2001; Haldane 1956).

Little is known from empirical studies about how demographic rates vary across species' ranges, however (Sagarin, Gaines, and Gaylord 2006; Gaston 2009). Data on demographic processes of wildlife are difficult to collect, and as a result, few studies have quantified demographic rates across a wide geographic scale. Those that have provide mixed support for Grinnell's hypothesis that demographic rates decline from the geographic center of a species range toward the margins (Purves 2009; Samis and Eckert 2007; Bradford, Taylor, and Allan 1997; Rhainds and Fagan 2010; Brewer and Gaston 2003; Rogers and Randolph 1986). As abundance data are much easier to collect, the majority of investigations of the processes that determine species' ranges have focused on abundance and distribution data. This constitutes a deep body of literature which has also provided mixed support for Grinnell’s hypothesis (Gaston 2003). In some systems, a central peak or broad plateau in abundance has been observed, with gradual declines toward the range margins (Brown 1984; Enquist, Jordan, and Brown 1995; Svensson 1992; Hengeveld and Haeck 1982; J. T. Emlen et al. 1986; Pianka 1970; Rapoport 1982). Other researchers have found a central peak to be more the exception than the rule, instead observing that abundance was either unrelated to latitude or greatest toward range margins (Sagarin and Gaines 2002; Blackburn et al. 1999; Scott et al. 1986; Kluth and Bruelheide 2005). Finally, multiple peaks of greatest abundance or demographic rates have been observed in some systems as well (Scott et al. 1986, Root 1988, Gibbons et al. 1993, Lawton 1993, B. McGill unpublished data). In spite of the mixed empirical evidence for Grinnell’s hypothesis, the idea that population growth rates decline toward range margins remains widespread in the literature.

Grinnell also connected his hypothesis to evolutionary theory, venturing that at the geographic center of a species range where the population growth rate is highest, individuals emigrate to more marginal populations (Grinnell 1904). This idea, in turn, has led to the hypothesis that evolution at range-edge populations is constrained by asymmetrical immigration from populations adapted to conditions at the center of the range (Guo et al. 2005; Haldane 1956; Pulliam 1988; Gaston 2009). Subsequent researchers have advanced these ideas, using the abundant-center or center-marginal hypothesis as the basis for many ecological and evolutionary theories (see box 1 in Sagarin et al. 2006 for a list of examples).

The interaction between ecological and evolutionary processes is important for predicting changes in species’ distributions, particularly in light of global climate change.

In general, species are expected to expand their ranges toward high latitudes and elevations in response to climate change, a pattern that has already been observed globally (Parmesan and Yohe 2003; T. L. Root et al. 2003; Chris D. Thomas and Lennon 1999; Poloczanska et al. 2013). Evolutionary processes at range margins have been shown to be important drivers of the speed and characteristics of range expansions (C D Thomas et al. 2001; Kolbe et al. 2004; Butin, Porter, and Elkinton 2005; Lee 2002). If populations near high-latitude range margins are adaptively constrained by central populations, as Grinnell predicted, we would expect lower adaptive potential and slower expansions in the face of changing climate than for species with population growth rates that do not decline from the geographic center of the range. Therefore, understanding the patterns of variation in demographic rates across space and the processes that govern them is of utmost importance for conserving global biodiversity in the face of climate change.

To address the question of how demographic rates vary across species' ranges, we quantified fecundity for multiple populations of a single species, the saltmarsh sparrow (*Ammodramus caudacutus*), across the majority of its range. Specifically, we tested whether saltmarsh sparrow seasonal fecundity was related to latitude and decreased linearly with increasing distance from the geographic center of the species range.

Saltmarsh sparrows breed exclusively in tidal marshes on the coast of the northeastern United States, from southern Maine to Virginia (Greenlaw and Rising 1994). Therefore, saltmarsh sparrows provide an ideal study system for exploring latitudinal patterns in demography because their geographic range is linear, runs roughly north-south, and is clearly limited to the east and west by the absence of suitable habitat (Tiner

2013). Further, the future distribution of saltmarsh sparrows is imperiled by sea-level rise. Populations in the center of their range are predicted to experience complete reproductive failure by 2050 (C. Field and C. Elphick, unpublished data).

Like many species, saltmarsh sparrows exhibit a peak of abundance at the geographic center of their range (W. Wiest et al. in review). Daily nest survival probability, a commonly used proxy for avian fecundity, increases with latitude for saltmarsh sparrows, however (Ruskin et al. in review). This pattern stands in contrast to Grinnell’s hypothesis, but daily nest survival probability is an imperfect index for fecundity. Daily nest survival probability is several steps removed from and correlates poorly with seasonal fecundity, or the number of young produced by an individual in a given year (Etterson et al. 2011b; Anders and Marshall 2005; Jones et al. 2005; B. C. Thompson et al. 2001; Murray 2000). Seasonal fecundity incorporates several other parameters, such as clutch size, brood size, and renesting rate (Etterson et al. 2011b; Etterson and Bennett 2013). Each of these traits could serve as sites of adaptation, by which populations could alter seasonal fecundity without concomitant changes in nest survival (Peakall 1970). To quantify seasonal fecundity of saltmarsh sparrow in populations across the species range, we used a novel method to incorporate both nest survival probabilities and a suite of life history parameters.

3.3. Methods

3.3.1. Data collection

From 2011 to 2013, we implemented a standardized data collection protocol (Ruskin et al. in review) at twenty-three study plots spanning a great circle distance of approximately 575 km. Our survey covered 59% of the saltmarsh sparrow's global breeding range (Wiest et al. in review) and 89% of the breeding range of the nominate subspecies, *Ammodramus caudacutus caudacutus* (Montagna, 1942). Study plots fall into four subregions (Gulf of Maine, Long Island Sound, New York Harbor, and Coastal New Jersey) based on watersheds and large geographic features (Table 3.1). Each study plot consisted of a 1 to 28 ha area of tidal marsh in the high-marsh zone, the area of the marsh where saltmarsh sparrows nest. In the northeastern United States, the high-marsh zone generally floods once or twice per month and is typically dominated by the grasses *Spartina patens* and *S. alterniflora*.

We searched for nests at least once per week throughout the breeding season (May to August) at each study plot. Once we found a nest, we revisited it every 2-5 days to determine success or failure. We captured females associated with nests using mist nets and individually marked females with uniquely numbered aluminum leg bands to track multiple breeding attempts within the same season. In part of their range (Gulf of Maine), saltmarsh sparrows are sympatric and interbreed with their sister species, the Nelson's sparrow (*Ammodramus nelsoni*). In the hybrid zone, we could only identify a nest as belonging to a saltmarsh sparrow if we successfully caught the female, whereas outside of the hybrid zone (Long Island Sound and south), saltmarsh sparrow nests could be identified by their eggs and location. Species identity within the hybrid zone was assigned using a linear discriminant function analysis developed to predict the genetic species identity using morphometric and plumage characteristics (Jennifer Walsh et al. 2015).

If a nest failed, we determined the cause of nest failure based on evidence at the nest site (e.g. drowned chicks, broken eggs, and whether the nest was wet, for example; see Ruskin et al. in review for full protocol). We considered nests successful if, after survival on all previous visits, they were found empty when at least one nestling would be 10 days old, the age at which chicks are able to leave the nest (Greenlaw and Rising 1994).

Our previous work at these study plots (Ruskin et al. in review) showed that nest survival is best explained by a combination of nest depredation (as a function of latitude) and nest flooding (as a function of both regular tidal flooding and irregular storm events). To model nest survival similarly for this study, we recorded the latitude of each study plot at its approximate center using ArcGIS version 10.1 (Environmental Systems Research Institute, Redlands, CA, USA 2010). To include variability in both regular and irregular flooding, we used the observed daily maximum water levels at the National Oceanic and Atmospheric Administration (NOAA) station nearest to each study plot (approximately 15-50 km by water). We collected data from nine NOAA stations that each served one to five of our study plots.

Table 3.1. Location, sample size, and parameter information for all study plots. Demographic study plots spanned from New Jersey to Maine, USA, 2011-2013.

Study Plot	State	Latitude (decimal degrees)	Longitude (decimal degrees)	Nests Observed	Nests with Identified Females	Observations (visits)	Exposure Days	Nest failure probability transformation	Quitting probability
Oyster Creek	NJ	39.5	-74.4	30	10	80	244	(daily water level)^4	subregional[c]
Mullica Wilderness	NJ	39.5	-74.4	70	40	178	588	(daily water level) ^{4}	subregional[c]
AT&T	NJ	39.7	-74.2	68	36	205	659	(daily water level) ^{4}	subregional[c]
Four Sparrow Marsh[a]	NY	40.6	-73.9	15	12	86	326	(daily water level) ^{4}	subregional[d]
Sawmill Creek	NY	40.6	-74.2	26	21	60	227	$10^{(-\text{daily water level})}$	subregional[d]
Marine Nature Park[a]	NY	40.6	-73.6	10	7	86	326	(daily water level) ^{4}	subregional[d]
Idlewild[a]	NY	40.7	-73.8	6	5	86	326	(daily water level) ^{4}	subregional[d]
East River	CT	41.3	-72.7	60	24	145	511	$10^{(-\text{daily water level})}$	subregional[e]
Hammonasset	CT	41.3	-72.5	50	33	140	486	$2^{(-\text{daily water level})}$	subregional[e]
Pattagansett[b]	CT	41.3	-72.2	5	2	N/A	N/A	N/A	N/A
Waterford[b]	CT	41.3	-72.1	1	0	N/A	N/A	N/A	N/A
Barn Island	CT	41.3	-71.9	33	8	62	238	$1.5^{(-\text{daily water level})}$	subregional[e]
John H. Chaffee	RI	41.4	-71.5	28	4	74	263	(daily water level) ^{4}	subregional[e]
Sachuest Point	RI	41.5	-71.2	20	0	33	126	(daily water level) ^{4}	subregional[e]
Parker River	MA	42.8	-70.8	26	26	106	339	(daily water level) ^{4}	subregional[f]
Chapman's Landing	NH	43.0	-70.9	129	129	700	1648	(daily water level)^2	study plot
Lubberland Creek	NH	43.1	-70.9	25	25	119	327	$10^{(-\text{daily water level})}$	subregional[f]
Eldridge Road	ME	43.3	-70.6	60	60	228	576	$2^{(-\text{daily water level})}$	study plot
Little River[b]	ME	43.3	-70.5	4	2	N/A	N/A	N/A	N/A
Jones Creek	ME	43.5	-70.4	78	78	337	886	$10^{(-\text{daily water level})}$	study plot
Nonesuch River	ME	43.6	-70.3	28	28	124	308	(daily water level) ^{4}	subregional[f]
Libby River[b]	ME	43.6	-70.3	4	4	NA	NA	N/A	N/A
Scarborough Marsh	ME	43.6	-70.4	58	58	235	593	(daily water level) ^{4}	study plot

[a] Combined for ‘Jamaica Bay’ study plot

[b] Did not meet minimum number of observations for any parameter, no MCnest simulations performed

[c] New Jersey coast subregion

[d] New York Harbor subregion

[e] Long Island Sound subregion

[f] Gulf of Maine subregion

3.3.2. Statistical analyses

3.3.2.1. Overall procedure

We used the program MCnest to estimate average seasonal fecundity of females at each study plot via population projections. For full details on MCnest, see Bennett and Etterson (2007) as well as Etterson and Bennett (2013). In short, MCnest creates a compound Markov chain composed of time-varying transition probabilities from one state to another based on daily nest failure probabilities and various life history parameters. Each day of the breeding season is a separate state that falls within seven non-overlapping stages: pre-breeding, rapid follicle growth (beginning of egg formation), egg laying, incubation, nestling brooding, waiting to renest, and post-breeding. The compound Markov chain ultimately describes the probabilities of every transition from one state to another, all of which can vary on each day of the breeding season. For example, females can be more likely to renest early in the breeding season compared to late in the breeding season. Projections then simulate females within this Markov chain and calculate the mean number of successful broods per season across all simulated females, as well as this value multiplied by brood size to calculate the mean number of young fledged per season by each female.

For each study plot, we modeled a population of 100 females to estimate mean seasonal fecundity and its variance. We parameterized the length of each stage and transition probabilities using either field data or values from the literature. We included observed spatial variation in these parameters whenever possible and appropriate. Finally, we explored the relationship between seasonal fecundity and latitude across the saltmarsh sparrow range.

3.3.2.2. Building the Markov Chain – determining the length of each stage

While each state in the Markov chain is precisely one day, the length of each stage varies as a function of life history parameters. We obtained values from the literature for three life history parameters that were outside of the scope of our study. We assumed an egg-formation interval (i.e., rapid follicle growth stage) of 4 days based on the published relationship between egg mass and egg-formation (Alisauskas and Ankney 1992). We assumed females laid one egg per day, a pattern that is observed widely within songbirds (Gill 2007; Perrins 1970) and is consistent with our observations in the field. Finally, we used a nestling interval of 10 days based on previous research on saltmarsh sparrows (Greenlaw and Rising 1994). Again, our observations were consistent with this value, although our 2-5 day visit schedule did not permit precise estimation of this parameter using our data.

We used our field data to calculate the remaining stage lengths: clutch size (contributes to the egg-laying stage length), incubation, wait interval before renesting, and total breeding season length. Wait intervals before renesting were variable in all projections because MCnest randomly draws from the distribution of observed wait intervals for each female that renested. For the remaining parameters as well as brood size, we chose values for each projection by testing for differences in the parameter by study plot using multinomial regressions (R Core Team 2014, base package) and comparing the resultant model to an intercept-only null model. For parameters that did not vary significantly by study plot or for which we had too little data to test for differences among study plots, we used the global mean trait value (across nests at all study plots) in MCnest projections for all study plots and years. For parameters that varied significantly by study plot, we used the mean trait values at the study plot when the number of measurements at a study plot met a required minimum (justification for this minimum below). For parameters that varied significantly by study plot but the number of cases at a study plot did not meet the required minimum in all years, we used the subregional mean trait values for the MCnest projections of that study plot. We did not perform MCnest projections for study plots that failed to meet the minimum number of observations for all parameters, though nests at excluded study plots are included in the subregional and global mean trait value estimates. For those life history parameters that varied by study plot, we used linear regressions to characterize the relationship between latitude and variation of each trait (R Core Team 2014, base package).

We determined the start and end of the breeding season, or the number of states in the entire Markov chain, based on the earliest and latest breeding dates we observed in the field. For all nests, we calculated first egg dates, or the date the first egg of each clutch was laid, in three ways: 1) for nests that were observed in the midst of egg-laying, we back-counted to the date the first egg was laid (assuming 1 egg per day); 2) for nests that hatched, we back-counted based on the estimated age of chicks at the first visit post-hatch, combined with an incubation interval of 12 days (mean and mode of our data, inclusive of the final egg-laying day and hatch day); 3) for nests that were neither observed during egg-laying nor hatched, we used all the nests that were found during egg-laying or hatched from that year and study plot to estimate the average number of days between first egg date and when the nests were discovered. We then subtracted this average from the discovery date for nests that neither were found during egg-laying nor hatched to estimate when the nest likely was initiated, assuming that the local habitat (e.g. height of the vegetation, accessibility of the marsh) and observers (crews included different technicians in each year) were most likely to influence discovery rate of nests. Because our survey spanned three years, our replication was too limited to test for differences in earliest and latest first egg dates by study plot (n=3 for each study plot). Instead, we used linear regressions (R Core Team 2014, base package) to test whether earliest and latest first egg dates varied with latitude to conserve degrees of freedom.

3.3.2.3. Minimum number of cases required for study plot –level parameter values

We set a minimum sample size necessary to estimate parameters for a study plot (instead of using the subregional or global mean) to prevent bias due to low sample sizes at some study plots. Using the most variable life history parameter (clutch size), we compared the mean and standard error for 20 random draws of nests at our largest study plot to the mean and standard error of the full sample at that study plot. If the standard errors for more than one random draw of 20 did not overlap those of the population mean, we increased the size of our random draw and repeated the method. By this process, we determined that 20 observations were sufficient to estimate study plot-level means for our most variable life history parameter. Conservatively, we used this minimum sample size for all our parameters that were approximately normally distributed. Earliest and latest first egg dates are based on maxima and were not normally distributed. To be conservative, we doubled our minimum number of observations required for study plot-level estimates of these traits.

3.3.2.4. Building the Markov Chain – populating the Markov Chain with transition probabilities

To estimate daily initiation probability, or the probability that a female begins breeding on any given day, we calculated the mean number of days each identified female waited until beginning to breed (earliest first egg date of a given identified female at a study plot minus the earliest first egg date for any female at the study plot). We took the inverse of this value as the daily probability of breeding initiation, and calculated the mean daily probability of breeding initiation for females within a study plot and year. We used only nests that had both identified females and first egg dates that were observed during egg-laying or calculating based on hatching (excluding nests for which first egg date was estimated based on study-plot averages of discovery rates). Finally, we averaged the daily probability of breeding initiation for all study plots with at least 10 and at least 20 nests that met these requirements, because no study plot had 40 nests that met this requirement in any year.

At the completion of a female's nesting attempt (success or failure), she was subject to renesting probability. To determine whether to vary renesting probability across the range, we employed two tests; we used a multinomial regression to test whether number of nesting attempts per breeding season varied by study plot and a linear regression to test whether renesting probability was related to latitude (R Core Team 2014, base package). Based on the observed differences in renesting rate across the range, we characterized the daily transition probabilities of renesting throughout the breeding season for four study plots that met the minimum number of observations and for each subregion to use for the remaining study plots. For each of the four study plots and four subregions, we created a logistic regression (R Core Team 2014, base package) to model the relationship between date in the breeding season and whether a female renested following the completion of a nesting attempt. The daily renesting probabilities serve as the transition probabilities in MCnest. If a nesting attempt in our Markov chain model ended, however, after the latest field-observed nest initiation date for that subregion and year, the transition probability to post-breeding was set to one. In this way, we did not model any nesting attempts that began later than our field observations.

Between breeding initiation and post-breeding, females were subject to daily nest failure probabilities except during egg-formation and the wait interval before renesting because during those stages, females do not have nests with contents (presumably they are nest-building during these stages). Daily probabilities of nest failure vary by latitude and in response to water level in our system (Ruskin et al. in review). Based on this knowledge, we generated daily nest failure probabilities for each study plot based on these covariates. We used the program MCestimate, which employs a Markov chain algorithm and a generalization of the Mayfield method, to estimate daily nest flooding and depredation probabilities from our nest monitoring data (Shaffer 2004; Etterson, Nagy, and Robinson 2007; Etterson, Greenberg, and Hollenhorst 2014; Mayfield 1975). Because we have previously found that latitude is the best predictor of nest depredation probability for these study plots and years (and thus we did expect depredation rates at a given site to vary through time; Ruskin et al. in review), we created an intercept-only model of nest depredation probability at each study plot. We have also determined previously that nest flooding probability is best predicted by indices of flooding due to both regular astronomical tides and irregular, weather-related tides (Ruskin et al. in review). We therefore modeled nest flooding probability for each study plot as a function of the observed daily maximum water level at the nearest NOAA station to incorporate both types of flooding. Thus, for each study plot, we used nest depredation probabilities that were constant throughout the breeding season and among years, whereas nest flooding probability varied through time.

For saltmarsh sparrows, nest flooding probability is not a linear function of observed water depth due to the elevation profiles of tidal marshes. Flooding risk is low until water spills over the stream channels of the lower marsh and into the high marsh plain. Further, the steepness of the non-linear relationship between water depth and high marsh flooding probability varies by marsh according to local microtopography. Thus, we tested a variety of transformations (Table 3.1) to model the threshold function of flooding probability in the high marsh zone by study plot. We used second order Akaike's Information Criterion (AIC_c) to compare candidate models while accounting for small sample size, using the criterion that models with $\Delta AIC_C < 2.0$ were equivalent (Burnham and Anderson 2002; Akaike 1974). We used the top model for each study plot as the transformation of water level data for all subsequent steps. At two study plots (Hammonasset and Lubberland Creek), we observed no depredated nests. For those study plots, we modeled overall daily nest failure probability, rather than just the component nest flooding probability, as functions of the observed daily maximum water level data.

3.3.2.5. Latitude versus seasonal fecundity

To test our hypotheses regarding spatial variation in fecundity across the range, we used a linear regression (R Core Team 2014, base package) to compare our predicted seasonal fecundity (as estimated by MCnest population projections for each study plot and year) to study plot latitude. We modeled a quadratic relationship between latitude and seasonal fecundity because we predicted that seasonal fecundity would be highest at the geographic center of the saltmarsh sparrow range and decline linearly toward the range margins. We then quantified variance in seasonal fecundity via pairwise comparisons. For each pair of projections (with separate projections for each plot-year), we calculated the differences in both seasonal fecundity and latitude. We compared variance of seasonal fecundity within and among study plots, as well as within and among subregions with analyses of variance (R Core Team 2014, base package). Finally, we used a linear regression to test whether the difference in latitude between projections predicted the difference in their seasonal fecundity estimates. Because there were many more pairwise comparisons that were geographically close than distant, we controlled for sampling effort through subsampling. We randomly subsampled within each distance band (degree of latitude), drawing the number of pairwise comparisons in the distance band with the fewest comparisons (i.e., the greatest distance). We randomly subsampled the dataset 10 times and ran a linear regression between latitudinal distance and difference in seasonal fecundity for each subset of data.

3.4. Results

3.4.1. Data collection

We collected nest monitoring data from 833 saltmarsh sparrow nests for this analysis. The number of nests monitored at each study plot ranged from one to 129. We found fewer than the minimum 20 nests at six study plots. We did not create MCnest projections for the three study plots that hosted five or fewer nests. The remaining three study plots that did not meet the minimum are all in New York City and are small, fragmented patches of Jamaica Bay. No study plot in Jamaica Bay reached the minimum 20 nests, but they had 30 nests combined. We combined nests from these study plots into an additional "Jamaica Bay" site. We characterized the relationship between latitude and seasonal fecundity both with and without this combined site.

Observations were made between May 17 and September 2 of each year. We made 3,133 nest visits. Only 3,084 of those nest visits were at study plots for which we estimated seasonal fecundity, yielding a total sample size of 8,997 exposure days.

3.4.2. Building the Markov Chain – determining the length of each stage

Clutch size varied by study plot ($p<0.001$ compared to the intercept-only null model) and there was a trend of increasing clutch size with latitude, but it was only marginally significant ($F_{1,815}=3.5$, $p=0.06$, adjusted $R^2=0.003$; Fig. 3.1). The difference in mean clutch size between the study plots at lowest and highest latitudes was less than one egg, however, so we used the global modal clutch size of four eggs in MCnest projections at all study plots. The global mean clutch size (± sd) was 3.66 (±0.74 sd) eggs or nestlings per clutch. Incubation interval did not vary by study plot ($p=0.27$

compared to the intercept-only null model). The global mean incubation interval (± sd) was 12.09 (±0.98 sd) days (inclusive of the final egg-laying day and hatch day) and the mode across all study plots was 12 days. Thus, we used 12 days as the incubation interval in MCnest projections for all study plots. We observed at least 20 wait intervals between nesting attempts at only one study plot, and so we could not test whether wait interval varied by study plot. Instead, we used all of the observed wait intervals for MCnest projections at all study plots. The global mean observed wait interval (± sd) was 10.66 (±9.47) days after we observed the completion of the previous nesting attempt, which due to the nest monitoring schedule, would have been 0-4 days after actual completion.

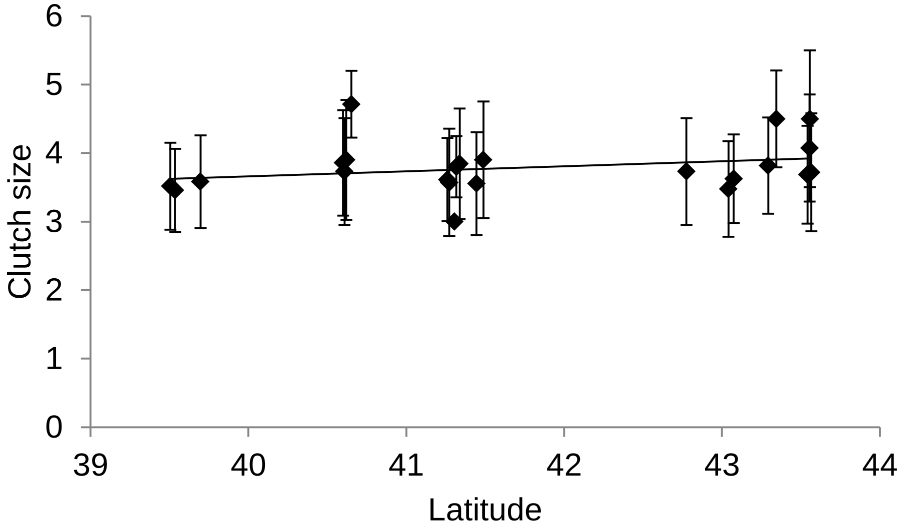


Figure 3.1. Clutch size increased with latitude. Clutch size varied by study plot ($p<0.01$ compared to the intercept-only null model) and we observed a trend of increasing clutch size with latitude, but it was only marginally significant ($F_{1,815}=3.5$, $p=0.06$, adjusted $R^2=0.003$).

3.4.3. Building the Markov Chain – populating the Markov Chain with transition probabilities

Using only study plots with at least 20 nests to estimate breeding initiation probability (N=5), the mean number of days a female waited to begin breeding was 23.7, equaling a daily breeding initiation probability of 0.04. Similarly, using study plots with at least 10 nests (N=24), the mean number of days a female waited to begin breeding was 24.1, also equaling a daily breeding initiation probability of 0.04. Too few study plots met our sample size requirements to test whether breeding initiation probability varied by study plot. We therefore used a daily breeding initiation probability of 0.04 in MCnest projections at all study plots.

Number of nesting attempts varied by study plot (p=0.007 compared to the intercept-only null model) and increased with latitude ($F_{1,494}$=12.2, p<0.001, adjusted R^2=0.02). Only four study plots met the required minimum of observations to characterize number of renesting rate at the study-plot level. Pooled subregional means (± sd) were as follows: NJ Coast = 1.06 ± 0.24 nesting attempts per female; NY Harbor = 1.36 ± 0.60; Long Island Sound = 1.10 ± 0.30; Gulf of Maine = 1.29 ± 0.51. Concomitantly, females showed regional variation in their renesting propensity as the season progressed (Fig. 3.2). Earliest first egg date varied by study plot ($F_{22,30}$=2.0, p=0.04, adjusted R^2=0.29) and increased with latitude ($F_{1,51}$=11.2, p=0.002, adjusted R^2=0.16). Latest first egg date varied by study plot ($F_{22,30}$=2.0, p=0.04, adjusted R^2=0.30) but was not related to latitude ($F_{1,51}$=1.7, p=0.20, R^2=0.01).

Various transformations were selected as the top models (Table 3.1) for the relationship between observed daily maximum water level and nest flooding probability at each study plot. For two study plots, the null model was better than the daily observed water level models. For those two sites, daily flooding probability was held constant and therefore did not vary throughout the breeding season or among years.

3.4.4. Latitude versus seasonal fecundity

Brood size did not vary by study plot ($p=0.13$ compared to the intercept-only null model). As a result, the global mean brood size (± sd) of 2.73 (±1.05 sd) was used in all MCnest projections for all study plots, and we present seasonal fecundity estimates as measured by mean number of successful broods per season for each female. We observed a wide range of estimated seasonal fecundity (95% confidence interval) across study plots, from 0.09 (0.05-0.13) and 0.78 (0.61-0.94) successful broods per season for each female. Combined with the global mean brood size, this equates to means of 0.26 (0.14-0.35) and 2.29 (1.67-2.57) fledged young per season for each female in a population. The mean seasonal fecundity (± sd) across all populations and years was 0.46 ± 0.16 successful broods per female per season, or 1.26 ± 0.45 young per female per season. Within a single year, the maximum variation in seasonal fecundity among study plots was between 0.09 and 0.25 broods per season for each female at a single study plot.

Seasonal fecundity did not vary with latitude across the saltmarsh sparrow range, both with ($F_{2,44}=1.5$, $p=0.23$ (overall model), $p=0.09$ (linear term), $p=0.09$ (quadratic term), adjusted $R^2=0.02$; Fig. 3.3) and without the combined Jamaica Bay site ($F_{2,42}=1.8$, $p=0.18$ (overall model), $p=0.06$ (linear term), $p=0.06$ (quadratic term), adjusted $R^2=0.04$). We observed significantly more variance in seasonal fecundity estimates among study plots than within them ($F_{1,1079}=40.8$, $p<0.001$, adjusted $R^2=0.04$; Fig. 3.4A). The variance in seasonal fecundity estimates among subregions did not differ from variance within subregions ($F_{1,1036}$=0.2, p=0.66, adjusted R^2=<0.001; Fig.3.4B). Similarity in seasonal fecundity estimates increased with the latitudinal distance between projections ($F_{1,1036}$=17.9, p<0.001, R^2=0.02; Fig. 3.4C). This pattern was consistent in 9 of 10 subsamples used to control for the effect of sampling size across different distance bands. However, when we removed study plots in Long Island Sound, which exhibited more variable seasonal fecundity estimates than the other subregions, there was no relationship between latitudinal distance and seasonal fecundity difference between projections ($F_{1,494}$=0.2, p=0.63, adjusted R^2<0.001; Fig. 3.4D). This pattern was consistent in 10 of 10 subsamples.

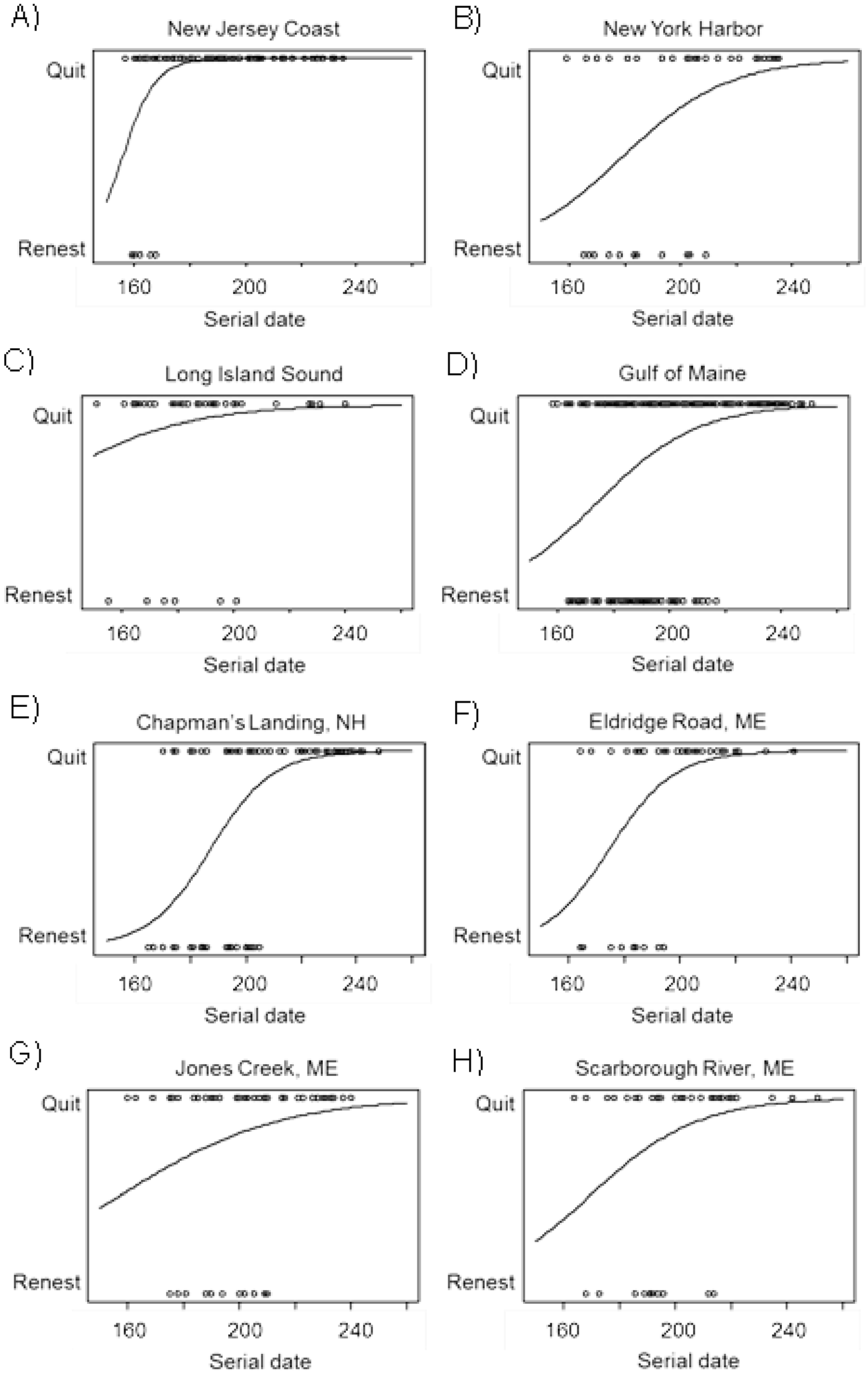


Figure 3.2. Observed cases and modeled probabilities of renesting. Observed cases of females quitting their breeding attempt for the season versus renesting (circles) were used to model daily renesting probabilities (lines) within the four subregions (A-D) and at four study plots that met the required number of observations (E-H).

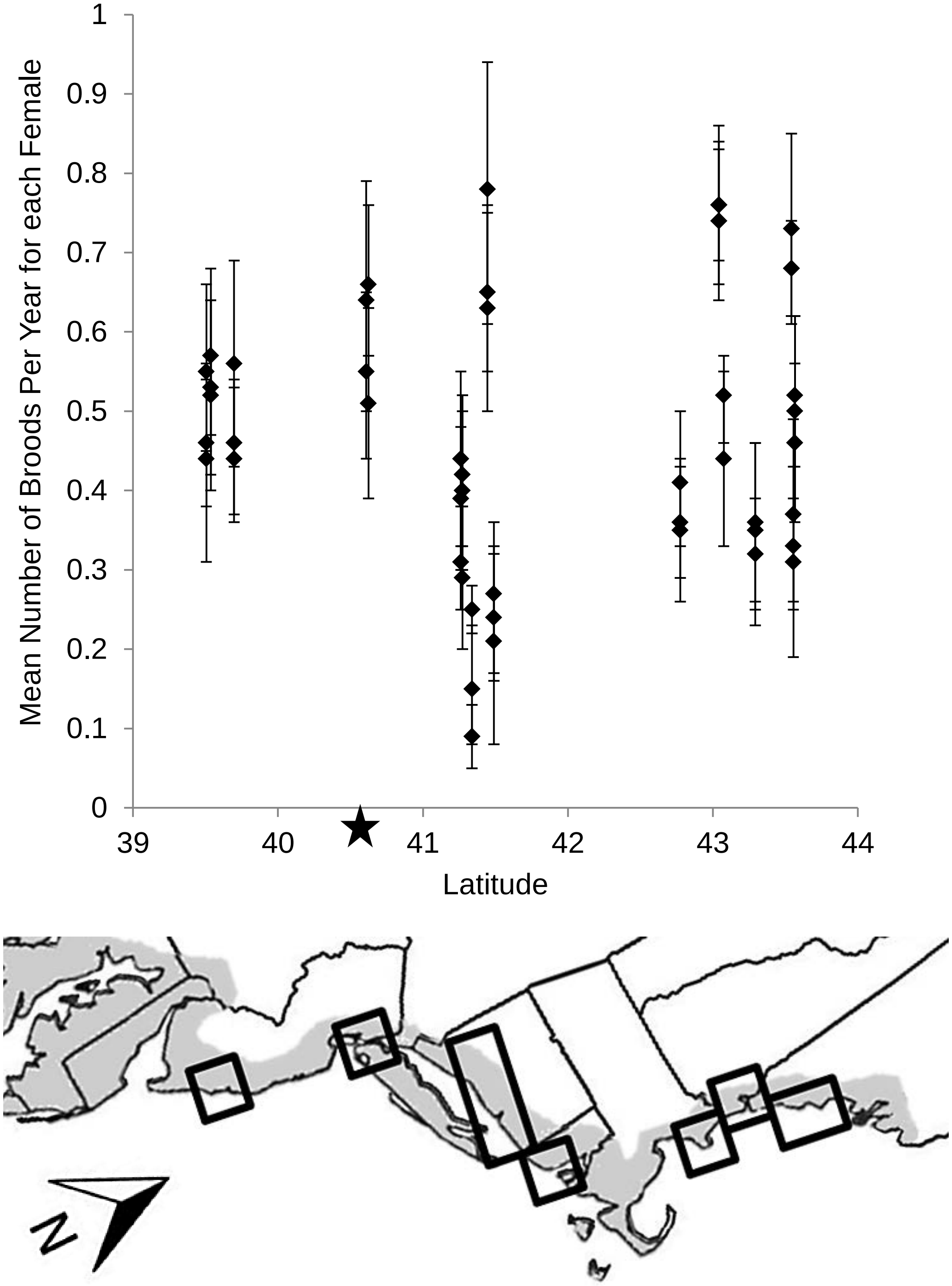


Figure 3.3. Seasonal (annual) fecundity by study plot. The star denotes the geographic center of the saltmarsh sparrow's latitudinal range. The map below the figure is aligned to show the approximate locations of the estimates above. Study plots were within the boxes and the breeding range of the Saltmarsh Sparrow is shaded.

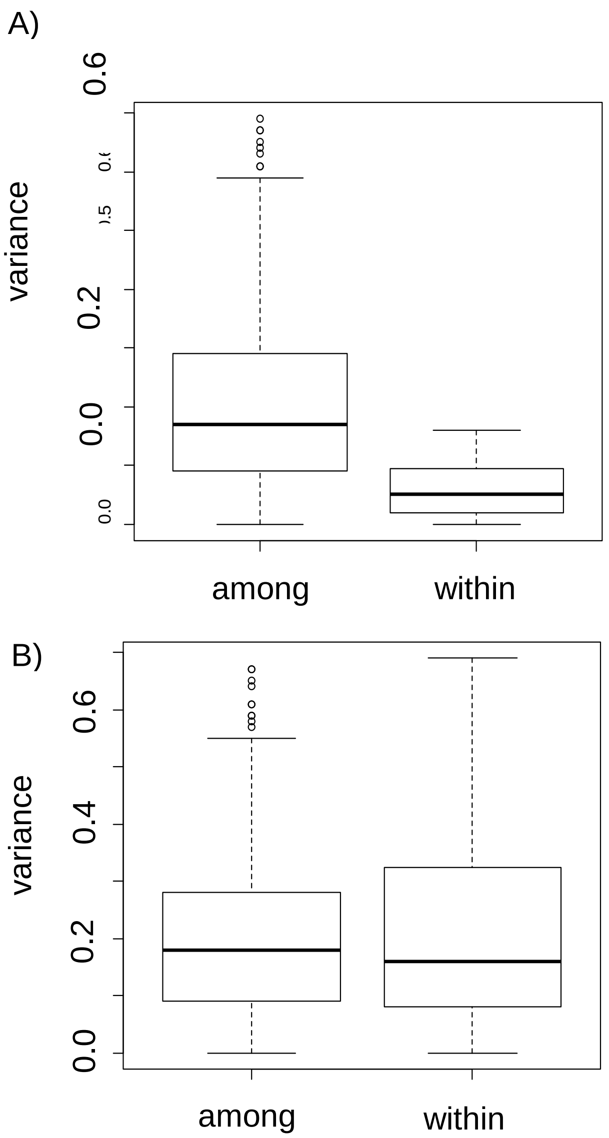
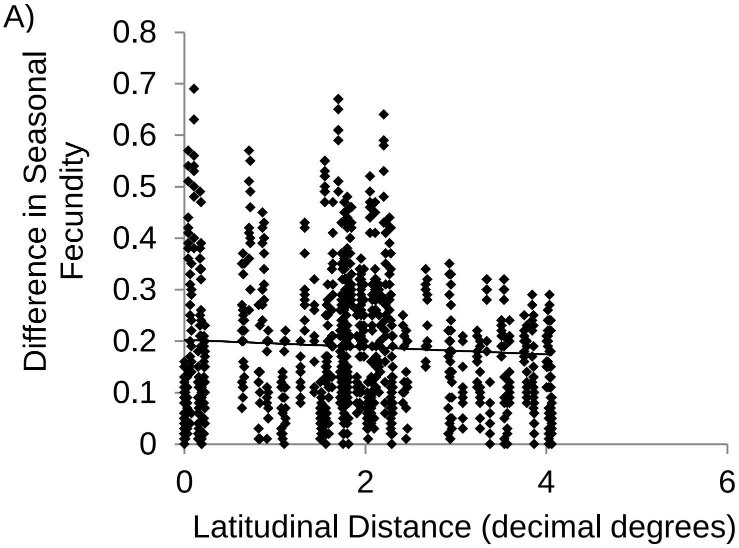


Figure 3.4. Variation in seasonal fecundity. A) Variation in seasonal fecundity among study plots was greater than variation within study plots ($F_{1,1079}$=40.8, p<0.001, adjusted R^2=0.04). B) Variation among subregions was equivalent to variation within subregions ($F_{1,1036}$=0.2, p=0.66, adjusted R^2<0.001).

A)



B)

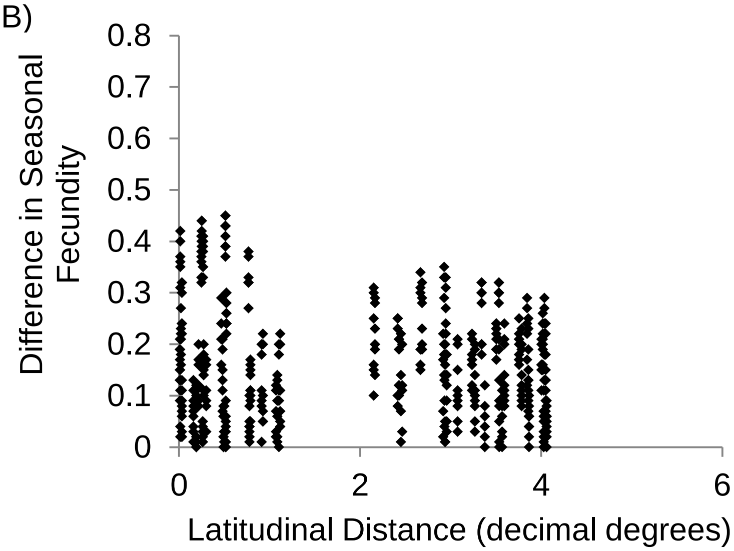


Figure 3.5. Seasonal fecundity estimate differences relative to distance. A) Seasonal fecundity estimates were increasingly similar at greater distances in the entire sample ($F_{1,1036}$=17.9, p<0.001, R^2=0.02). B) This trend did not persist when Long Island Sound study plots, which experienced particularly variable seasonal fecundity estimates, were removed ($F_{1,494}$=0.2, p=0.63, adjusted R^2=0.001).

3.5. Discussion

Though saltmarsh sparrow abundance peaks at the geographic center of their range (W. Wiest et al. in review), fecundity did not vary linearly throughout the range. Instead, seasonal fecundity estimates were relatively consistent within each study plot but varied widely even among nearby study plots. These results suggest that local drivers, whether plasticity, adaptation, or exogenous factors related to local habitat, strongly influence saltmarsh sparrow fecundity across their global range.

Species ranges, which are the product of demographic rates, are often thought to be governed by large-scale processes. For example, abiotic stressors are thought to limit the distribution of species toward high latitudes while biotic stressors limit species toward low latitudes (Dobzhansky 1950; MacArthur 1984; Brown, Stevens, and Kaufman 1996). This theory has been supported in a wide array of systems (Loehle 1998; Normand et al. 2009; Pianka 1970; Brown 1995), including saltmarsh sparrows (Ruskin et al. in review). Specifically, saltmarsh sparrow nest depredation probability increases with decreasing latitude, while probabilities of nest flooding outweigh probabilities of depredation for populations near the high-latitude range margin.

Despite these large scale and latitudinal trends in the exogenous drivers of fecundity, female behavior appears to ameliorate macroecological patterns of nest success. Our results thus do not support the hypothesis that populations at the geographical periphery of a species range are constrained by adaptations of populations at the center of the range. Further, we find no evidence that range expansion due to climate change would be hindered by the demographic influence of central or peripheral populations in this species. Our results instead point to the importance of local factors in shaping seasonal fecundity. We observed a mosaic of source and sink habitats throughout the range, rather than central source populations that transition to sinks toward the range margins. These results are consistent with previous research that inferred both source and sink habitat patches at nine sites inhabited by saltmarsh sparrows using genetic data (J Walsh et al. 2012). Walsh et al. also observed that saltmarsh sparrows exhibited relatively strong spatial patterns in population genetic structure, particularly compared to other migratory birds which are generally considered too mobile to exhibit strong spatial structure in populations (Crochet 2000).

Habitat patchiness has been hypothesized as a potential disruptor of range-center peak fecundity. One of the assumptions of Brown's influential hypothesis on range-center peak abundance is that environmental variables which affect the population growth rate of a species are autocorrelated (Brown 1995; Brown 1984; Brown, Mehlman, and Stevens 1997). Patchy habitats like tidal marshes may violate this assumption, resulting in the variable mosaic of fecundity we observed (J. A. Wiens 1989; Brown 1995). Future studies should characterize the variability of habitat among tidal marshes, test whether tidal marshes are more patchy and heterogeneous than other habitat types, and correlate habitat variables with saltmarsh sparrow seasonal fecundity. Future studies should also test whether local adaptation or plasticity is shaping the observed heterogeneity in saltmarsh sparrow fecundity by examining saltmarsh sparrow fecundity at an individual, rather than population, level. Local adaptation or plasticity might increase the capacity of saltmarsh sparrow populations to specialize on a small spatial scale in expanded or changing habitat.

Future studies should also examine individual fitness to expand the sample size from what is presented here. Though we observed no large-scale trend in mean seasonal fecundity relative to latitude, perhaps instead we would expect to observe a filled curve of constraint where a peak in fecundity is only detectable among the top quantile of individuals within each population. Such a pattern would indicate that the maximum fecundity is possible near the geographic range center of a species, but local processes can diminish the fecundity to zero at all sites. In fact, the observed patterns of many studies of abundance over space suggest this pattern (Samis and Eckert 2007; Sagarin and Gaines 2002; Brown 1995; Gaston 2003). Our sample size was likely too small to detect the pattern of a filled curve, as we observed only 19 study plots, but the study plot with highest estimated fecundity was indeed near the range center (Fig. 3.3).

While this study is an empirical step forward in documenting range-wide variation in fecundity, seasonal fecundity is only part of the demographic equation. It is possible that variation in adult survival and dispersal would cause population growth rates of saltmarsh sparrows to vary systematically across their geographic range. Preliminary analyses of adult survival at these same study locations, however, reveal no geographically systematic differences (C. Field unpublished data). Further, fewer than <2% of individuals were observed to move among study plots, which were as little as <0.5 km apart (K. Ruskin unpublished data). Therefore, it seems unlikely that either adult survival or movement is likely to produce rates of population growth that are fundamentally different from the pattern of seasonal fecundity.

Regardless of the patterns of survival and movement, however, it remains interesting that seasonal fecundity shows no relationship with latitude though saltmarsh sparrows reach peak abundance at the geographic center of their range. Our results stand in contrast to a long history of theory and assumptions within the ecological literature and joins a growing body of evidence that fecundity does not decline linearly with distance from the geographic center of the range and peak abundance for many species. Our results suggest that local drivers strongly influence large-scale patterns of fecundity in saltmarsh sparrows, and that range edges in this species are likely determined by local environmental characteristics, rather than declines in habitat suitability across a large spatial scale.

CHAPTER 4: INTRASPECIFIC NICHE BREADTH, BUT NOT POSITION, IS CONSTANT ACROSS A SPECIES RANGE

4.1. Summary

In the half-century since Hutchinson proposed the model of an n-dimensional hypervolume to describe a species' niche, evidence suggests that niches, like any other phenotypic character, vary intraspecifically across a species' geographic range. Intraspecific niche variation challenges the widely-held paradigm of niche conservatism, which predicts that niches are constant within a species or vary minimally, in concert with range position. To explore the patterns, causes, and fitness consequences of intraspecific niche variation, we characterized the habitat selection of a single species, the saltmarsh sparrow (*Ammodramus caudacutus*). We created 8-dimensional hypervolumes to describe the niche space of nest sites and available environmental space at 17 study plots spanning 59% of the global breeding range of saltmarsh sparrows. We found that position of both nesting niche and available environmental space, as well as the similarity between locally available and selected habitat, differed over the range but were not related to range position. Some, but not all, of the intraspecific niche variation we observed was related to local habitat availability. The similarity between nesting niche and available habitat did not appear to have fitness consequences, and thus we observed no signs of habitat marginality near the range margin of saltmarsh sparrows. Our results point to high levels of habitat heterogeneity and the importance of local drivers in shaping intraspecific niche variation. The high-latitude range margin of saltmarsh

sparrows is not likely limited by available niche space at the spatial scales we examined, but rather may be governed by other axes of the niche at larger spatial scales.

4.2. Introduction

In the half-century since Hutchinson (1957) proposed the model of an n-dimensional hypervolume to describe a species' niche, multiple lines of evidence have suggested that niches, like any other phenotypic character, are not constant across a species' geographic range. For example, habitat preferences of a species may differ within its range (R. B. Root 1967; Pfenninger, Nowak, and Magnin 2007; Lennon and Martiny 2008); common garden experiments show that lineages from different regions of the geographic range of a species persist differently or not at all when displaced to another region (Svanbäck and Schluter 2012; Rehfeldt et al. 1999; Ying 1991); and in a wide range of systems, species do not occupy habitats that appear suitable as predicted by environmental variables shown to influence distribution (De Moraes Weber et al. 2014; Svenning and Skov 2004; Murphy and Lovett-Doust 2007; Ryan Shipley et al. 2013).

Though intraspecific niche variation has been observed *in situ*, experimentally increased in the lab (Agashe and Bolnick 2010; D I Bolnick 2001; Daniel I Bolnick 2004; Parent, Agashe, and Bolnick 2014), and is thought to contribute to the most promising examples of sympatric speciation (Coyne and Orr), its existence challenges the widely-held paradigm of niche conservatism. The niche of a species is predicted to be constant over space or at most, vary minimally if niche is a conserved trait (J. J. Wiens and Graham 2005). Grinnell (1904) postulated that populations at the geographic center of a species range exhibit the highest rates of increase, where the combination of environmental variables is most favorable. Moving away from the geographic center of the range, the habitat is thought to become more marginal (i.e., less of the available environmental space overlaps the species niche), supporting fewer individuals with lower rates of increase. Thus, under a paradigm of niche conservatism, we would expect to see changes in both niche position (i.e., the values of the hyperdimensional centroid or boundaries) and niche breadth (i.e. the hypervolume of the niche) that parallel changes in available environmental space along species-relevant axes. Niche conservatism also predicts that if a niche varies intraspecifically across space, it varies minimally, and in concert with genetic isolation. Alternatively, intraspecific niche evolution would allow for different spatial patterns of variation, caused by evolution in response to local differences in habitat, predation pressure, or climate, for example.

The first step to understanding intraspecific niche evolution is to describe the pattern of niche variation across a species' range. We present a characterization of the habitat selection of a single species, the saltmarsh sparrow (*Ammodramus caudacutus*), across the majority of its global breeding range. We tested whether niche is conserved across the geographic range of a species and whether intraspecific niche variation is related to available environmental space and fitness. While one can view the species niche as a whole, it is also possible to discretely quantify niche in a modular fashion, focusing on diet (Hindmarch and Elliott 2014; Bearhop et al. 2013; Ferreira and Absy 2015), habitat (Ciechanowski 2015; Rehfeldt et al. 1999; Thuiller et al. 2005), ontogenetic variation (Olson 1996; Lima and Moreira 993; Scharf et al. 2000), or functional traits (Lamanna et al. 2014; Roscher et al. 2015; Van Valen 1965), for example. In this paper, we characterized the nesting niches of saltmarsh sparrows, a module of the species niche, using habitat characteristics associated with nest sites.

We quantified nesting niche position and breadth with 8 habitat characteristics and tested whether the nesting niche of saltmarsh sparrows varies intraspecifically across the species range. Under the paradigm of niche conservatism, we predicted that nesting niche position and breadth was conserved across the saltmarsh sparrow range, or varied minimally and in concert with distance as a proxy for genetic isolation (Table 4.1). We also characterized available environmental space along the same 8 axes to test whether local habitat availability predicted local nesting niche. We compared nesting niches and available environmental space across the species range to test whether saltmarsh sparrow habitat selection varies intraspecifically. Finally, we tested whether intraspecific variation in nesting niche position and breadth correlated with fecundity to test whether intraspecific niche variation affects fitness.

Table 4.1. Predicted and observed patterns of intraspecific niche variation.

	Empirical Test	**Predicted Outcomes**		**Empirical Result**
		Niche Conservatism	*Intraspecific Niche Variation*	
1	Variation in Niche Position and Breadth	Nesting niche does not vary, or varies minimally in concert with latitudinal distance or range position (distance from center)	Nesting niche varies independently of latitudinal distance or range position (distance from center)	Nesting niche position varies, independently of distance or range position, niche breadth is constant
2	Available environmental space	If available environmental space varies, niche position and breadth show signs of marginality; if it does not vary, neither does nesting niche	Niche position and breadth vary either in concert with variation in available environment, or independently	Available environmental space position varies and is not related to distance or range position, breadth increases with latitude
3	Habitat Selection	Evidence for similar preferences across range	Evidence for some variable preferences across range	Evidence for some variable preferences across range
4	Niche Position vs. Fecundity	More similar niches have more similar fecundity	Fecundity is independent of niche position	Fecundity is independent of niche position

4.3. Methods

4.3.1. Study species and site descriptions

The distribution of saltmarsh sparrows presents a number of characteristics that simplify niche variation comparisons. First, saltmarsh sparrows breed exclusively in tidal marshes on the Atlantic coast of the United States, and thus the range is roughly linear in a north-south orientation (Greenlaw and Rising 1994, W. Wiest et al. in review; Fig. 1.1). Therefore, we expect linear trends in various environmental factors such as available habitat and predation pressure on nest sites, which has been shown to vary with latitude in a variety of systems (Schemske et al. 2009), including saltmarsh sparrows (Ruskin et al. in review). Second, saltmarsh sparrows are thought to have colonized this range following the most recent glacial retreat (Rising and Avise 1993). As a result, genetic isolation likely follows a linear gradient within the range, with the populations south of New York representing the ancestral population from which more northern populations became isolated and possibly evolved gradually as they colonized new areas of the current range. In support of this hypothesis, the genetic structure of saltmarsh sparrow populations generally follows the pattern of isolation by distance (J Walsh et al. 2012). Third, tidal marshes possess a relatively simple species assemblage and community structure across this range (Tiner 2013), limiting the number of environmental axes that are relevant to the species.

Saltmarsh sparrows exhibit a unique breeding system that further distills the number of dimensions relevant to their nesting niche. Saltmarsh sparrows are promiscuous (individuals do not form pair bonds) and both sexes are non-territorial (Greenlaw and Rising 1994; Hill, Gjerdrum, and Elphick 2010). Bayard and Elphick

(2010) found that saltmarsh sparrow nests were distributed randomly in space, showing no signs of intraspecific competition for nest sites. Due to the high abundance of insects in tidal marshes, it is also thought that saltmarsh sparrows experience no competition for food (Greenlaw and Rising 1994). Therefore, saltmarsh sparrows provide a unique opportunity to study habitat selection that is not likely influenced by territories, dominance hierarchies, or density-dependent factors common in other avian systems.

In 2012 and 2013, we monitored saltmarsh sparrow nests throughout the breeding season (May to early September) at 17 study plots. Each study plot included high marsh habitat (areas with regular tidal flooding every two to four weeks), and ranged in size from 1 to 28 hectares. Our study plots were between Maine and New Jersey and spanned 4.1° latitude, which covers 59% of the global breeding range of saltmarsh sparrows and 89% of the breeding range of the subspecies *A. caudacutus caudacutus* (Montagna 1942, W. Wiest et al. in review). Our study plots included the geographic and abundance centers of the species (approximately 40.7°N and southern New England, respectively; W. Wiest unpublished data) and spanned to within 0.5° latitude (125 km) of the high latitude margin of the species range.

In a portion of their range (Gulf of Maine), saltmarsh sparrows are sympatric and interbreed with their sister species, the Nelson’s sparrow (*Ammodramus nelsoni*). We could only identify a nest as belonging to a saltmarsh sparrow in the hybrid zone if we successfully captured the female via mist nets, whereas we could identify saltmarsh sparrow nests by their eggs and location outside of the hybrid zone (Long Island Sound and south). We assigned species identity within the hybrid zone using a linear discriminant function analysis developed to predict the genetic species identity using morphometric and plumage characteristics (Jennifer Walsh et al. 2015). We included only pure and back-crossed saltmarsh sparrows in these analyses, excluding Nelson's sparrows and both first and second generation hybrids (F1 and F2).

4.3.2. Field data collection

We conducted vegetation surveys at nests within a week of the nest completion to minimize disturbance to females. For each study plot, we generated randomly selected points using the "Create Random Points" tool in the "Data Management" toolbox of ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, CA 2010). We surveyed a randomly selected point for each nest within a week of its completion to control for plant phenology over the course of the breeding season. Because we also surveyed randomly selected points in association with the nests of other species (not included in this study), we surveyed more random points than saltmarsh sparrow nests at most study plots. We excluded randomly selected points which were in standing water during field surveys.

At both nest and randomly selected points, we collected various vegetation measurements within a 1-m^2 quadrat surrounding each point. We measured the depth of thatch (dead vegetation from previous years' growth) and estimated the average vegetation height at five points: the center of the quadrat (immediately adjacent to the nest for nest sites) and at each midpoint of the quadrat sides. We then averaged the five measurements for each 1-m^2 plot. Finally, we visually estimated the percent cover of the following dominant types: wrack (unattached dead vegetation, usually floated to the site), bare ground (usually mud), standing water, *Spartina patens*, *S. alterniflora*, *Distichlis* *spicata*, and *Juncus gerardii*. We grouped all other cover types (typically rare species) in a single “other species” cover category.

4.3.3. Statistical analyses

We performed all statistical analyses in R (R Core Team 2014). We excluded the percent cover of wrack and bare ground categories from statistical analyses to eliminate non-independence among cover categories and because they were rare on the landscape. Thus, we used two structural (average thatch depth and vegetation height) and six percent cover measurements for all of the following statistical analyses.

4.3.3.1. Does niche position and breadth vary over the geographic range of a species?

Using scaled data of these eight vegetation characteristics, we created 8-dimensional hypervolumes to describe the niche space for points chosen as nest sites at each study plot using the “hypervolume” package in R (Blonder et al. 2014a; Blonder et al. 2014b), with years pooled. The package infers the shape and volume of n-dimensional objects through kernel density estimation. We used a bandwidth for the kernel density estimation identified by the Silverman estimator and a quantile threshold of zero. The estimated hypervolume thus included all observed points, rather than some percentage (e.g. 95%) of observed niche positions. We then calculated the volume of the nesting niche at each study plot.

To test whether nesting niche position varied across the geographic range of saltmarsh sparrows, we calculated the Sørensen overlap index for all pairwise comparisons of nesting niches among study plots. The Sørensen overlap index is the volume of overlapping space between two hypervolumes, divided by the mean volume of the two hypervolumes (Blonder et al. 2014b). We then used a linear regression (R Core Team 2014, base package) to test whether the differences in overlap of nesting niches between study plots predicted the latitudinal distance between them.

To describe variation in nesting niche breadth, we first created a linear regression to test whether niche volume was related to the number of observations that contributed to its estimation. We then calculated the proportional volume of each hypervolume, which we define as the volume of the hypervolume divided by the number of observations used in its estimation (to control for the effect of sampling frequency). Finally, we created a linear regression to test whether niche breadth of selected habitat (proportional volume of the nesting niche hypervolume) varied with latitude.

4.3.3.2. Does available habitat vary across the range of the species?

We created 8-dimensional hypervolumes to describe the available environmental space using the scaled data from the randomly selected, non-nest points at each study plot, with both years pooled. We then calculated the breadth of the available environmental space in the same way as the nesting niche. To test whether the position and breadth of available environmental space varied across the range of saltmarsh sparrows, we calculated the Sørensen overlap index for the hypervolumes of available environmental space for all pairwise comparisons of study plots. We then used a linear regression to test whether the differences in available environmental space between study plots predicted their latitudinal distances. As with the nesting niche hypervolumes, we created a linear regression to test whether the proportional volume of environmental space varied with latitude.

4.3.3.3. Does habitat selection vary across the range of a species?

We characterized patterns of habitat use relative to habitat availability across the geographic range of saltmarsh sparrows in three ways. First, we used a multivariate logistic regression to model point type (nest or random) as a function of the eight vegetation characteristics, each nested within study plot (R Core Team 2014, base package). We thus allowed both the intercepts and slopes of the fixed effects to vary with study plot. As such, we controlled for local differences in available environmental space and the responses of saltmarsh sparrow habitat selection in response to the possibly heterogeneous habitat.

Second, we characterized variation in habitat selection by quantifying the similarity between hypervolumes for nests and randomly selected points at each study plot using the Sørensen overlap index. We then used a linear regression to test whether the similarity between available and selected habitat varied with latitude. Arguably, both high and low levels of similarity between available and selected habitat could be signs of marginality for a species. At sites with poor quality habitat for a species, individuals may choose very specific nest locations, resulting in a narrow nesting niche that is highly dissimilar to the available habitat. Alternatively, they may be without the option to choose their preferred habitat and select broadly from the available habitat, resulting in a wide nesting niche that is similar to the available habitat.

Third, we tested whether available environmental space predicted selected habitat. We used a linear regression to test whether the similarity of available environmental space predicted the similarity between nesting niches (both as measured by the Sørensen overlap index) between study plot pairs. Combined with previous analyses, this comparison allowed us to identify pairs of study plots where the environmental spaces were similar, but the nesting niches were not. Such a scenario would be predicted where nesting niche preferences vary across a range.

4.3.3.4. What are the fitness consequences of differences in niche across the range of a species?

Finally, we tested whether the similarity between selected and available habitat at each site was related to seasonal fecundity, as measured by the average number of successful nests per year for each female. We obtained average seasonal fecundity estimates that were calculated for populations at each study plot within overlapping years of study (2011-2013) by Ruskin et al. (in review). We used a linear regression to test whether the Sørensen overlap index between nesting niche and random-point hypervolumes predicted seasonal fecundity by study plot. We predicted that if the nesting niche were conserved across the range, but available environmental space varied, we would observe a relationship between habitat marginality (similarity of available and selected habitat) with seasonal fecundity. Though high or low degrees of similarity between available and selected habitat could be signals of marginality, we expect a relationship between habitat similarity and seasonal fecundity if niche is conserved either way. Alternatively, similar fecundity despite variations in habitat selection would be consistent with variable niches across the range. Further, we created a linear regression to test whether the Sørensen overlap between study plots (pairwise comparisons) predicted the difference in observed seasonal fecundity between them.

4.4. Results

4.4.1. Summary

We used vegetation measurements from 658 nests and 1292 randomly selected points. We observed between 11 and 88 nests, and 10 and 147 randomly selected points by study plot (Table 4.2). All points were surveyed between May 17th and September 10th of each year.

4.4.2. Does niche position and breadth vary over the geographic range of a species?

The units of all hypervolumes are standard deviations to the power of the number of trait dimensions used (Blonder et al. 2014a). The breadths of nesting niches (volume of nest site hypervolumes) varied between 2.2 SD sd^8 and 10.1 SD sd^8 by study plot (n=17; Table 4.2). Mean volume of nesting niche (±sd) was 5.4±2.2 SD sd^8. Sørensen overlap indices of nesting niches between study plots pairs varied from <0.0001 to 0.44, with a mean overlap (±sd) index of 0.16±0.09 (n=17). Similarity among nesting niches between study plots did not predict latitudinal distance ($F_{1,134}$=0.6, p=0.43, adjusted R^2<0.001; Fig. 4.1A). Number of observations significantly predicted the breadth of nesting niche ($F_{1,15}$=84.8, p<0.0001, adjusted R^2=0.84) for nests (Fig. 4.2). Proportional volumes of nesting niches ranged between 0.10 SD sd^8 and 0.20 SD sd^8 by study plot, with a mean (±sd) of 0.15±0.03 SD sd^8. Proportional volume of nesting niches by study plot did not vary with latitude ($F_{1,15}$=0.005, p=0.94, adjusted R^2<0.0001; Fig. 4.3).

4.4.3. Does available habitat vary across the range of the species?

The breadths of available environmental spaces (random-point hypervolumes) varied between 15.1 SD sd^8 and 196.7 SD sd^8 by study plot (n=17; Table 4.3). Mean volume of available environmental space (±sd) was 94.4±46.0 SD sd^8. Sørensen overlap indices of available environmental spaces between study plots pairs varied from 0.03 to 0.52, with a mean overlap index (±sd) of 0.20±0.10 (n=17). Similarity among available environmental space between study plots did not predict latitudinal distance (F= $1.6_{1,134}$, p=0.20, adjusted R^2=0.005; Fig. 4.1B). Number of observations also significantly predicted the breadth of available environmental space (F=$60.4_{1,15}$, p<0.0001, adjusted R^2=0.79), although this relationship was much steeper than the one for nesting niches (Fig. 4.2). Proportional volumes of available environmental spaces ranged between 0.71 SD sd^8 and 1.71 SD sd^8 by study plot, with a mean (±sd) of 1.27±0.25 SD sd^8. Proportional volume of available environmental spaces by study plot varied with latitude (F=$6.4_{1,15}$, p=0.02, adjusted R^2=0.25; Fig. 4.3).

Table 4.2. Hypervolume summary. Comparison of hypervolumes for randomly selected points and saltmarsh sparrow nest sites by study plot from New Jersey to Maine, U.S.A., 2012-2013.

				Random points			Nest sites				
Study plot	State	Latitude (decimal degrees)	Longitude (decimal degrees)	N	Niche breadth	Proportional volume	N	Niche breadth	Proportional volume	Sørensen overlap, nesting niches vs. available environment	Seasonal fecundity (successful nests per female)
Oyster Creek	NJ	39.5	-74.4	100	71.3	0.7	18	3.09	0.2	0.05	0.48
Mullica Wilderness	NJ	39.5	-74.4	100	93.1	0.9	54	5.70	0.1	0.09	0.54
AT&T	NJ	39.7	-74.2	87	86.3	1.0	59	5.97	0.1	0.09	0.49
Four Sparrow Marsh	NY	40.6	-73.9	68	101.3	1.5	37	5.87	0.2	0.03	0.59
Sawmill Creek	NY	40.6	-74.2	75	104.7	1.4	33	6.31	0.2	0.05	0.60
Marine Nature Park	NY	40.6	-73.6	51	56.2	1.1	19	2.95	0.2	0.04	0.59
Idlewild	NY	40.7	-73.8	80	118.8	1.5	11	2.19	0.2	0.01	0.59
Hammonasset	CT	41.3	-72.5	61	83.9	1.4	44	6.90	0.2	0.07	0.38
East River	CT	41.3	-72.7	76	84.3	1.1	48	6.53	0.1	0.05	0.37
Barn Island	CT	41.3	-71.9	47	65.5	1.4	30	5.41	0.2	0.05	0.16
Parker River	MA	42.8	-70.8	10	15.1	1.5	20	3.17	0.2	0.10	0.37
Chapman’s Landing	NH	43.0	-70.9	108	151.9	1.4	88	9.42	0.1	0.05	0.75
Lubberland Creek	NH	43.1	-70.9	35	37.9	1.1	25	3.82	0.2	0.06	0.48
Eldridge Road	ME	43.3	-70.6	53	74.6	1.4	35	5.01	0.1	0.05	0.34
Jones Creek	ME	43.5	-70.4	147	173.5	1.2	78	10.08	0.1	0.07	0.71
Nonesuch River	ME	43.6	-70.3	53	90.5	1.7	21	3.22	0.2	0.04	0.34
Scarborough River	ME	43.6	-70.4	141	196.7	1.4	38	6.65	0.2	0.03	0.49

Table 4.3. Habitat selection by study plot.

Study plot	Thatch height (cm)	Average height (cm)	Water (% cover)	*Spartina patens* (% cover)	*Spartina alterniflora* (% cover)	*Distichlis spicata* (% cover)	*Juncus gerardii* (% cover)	Other species (% cover)
Oyster Creek	+	+++	+++	+++	-	-	N/A	-
Mullica Wilderness	++	-	-	+++	- - -	- - -	N/A	+
AT&T	+	+	N/A	+++	- - -	-	N/A	+++
Four Sparrow Marsh	++	+	++	-	+++	-	N/A	-
Sawmill Creek	+++	++	++	+	-	++	N/A	+
Marine Nature Park	+++	+	- - -	+++	-	+++	N/A	-
Idlewild	+	-	-	+++	-	+++	N/A	-
Hammonasset	++	+++	+	+++	-	+	-	-
East River	+++	+++	-	+++	-	+	+	-
Barn Island	+	+++	-	+	-	+	+	-
Parker River	+	+	+	-	+++	+	-	+
Chapman's Landing	+++	- - -	-	+++	+++	- - -	-	-
Lubberland Creek	+++	- -	- - -	- - -	+++	-	+	-
Eldridge Road	+++	+++	-	- - -	+++	-	-	- - -
Jones Creek	+++	+	-	+++	- - -	-	N/A	-
Nonesuch River	+	+	+++	+++	+	-	-	-
Scarborough River	+++	+	-	+++	+++	-	-	-

Results from the nested multiple logistic regressions used to test whether means for vegetation characteristics of nest sites differed from randomly selected points at each study plot. Plus signs indicate that nest sites exhibited higher means than randomly selected points (+++ when $p<0.05$, ++ when $p<0.10$, + when non-significant), while minus signs indicate that nests exhibited lower means than randomly selected points (- - - when $p<0.05$, - - when $p<0.10$, - when non-significant). N/A indicates that there were no observations of the vegetation characteristic for either nest sites or randomly selected points at a study plot.

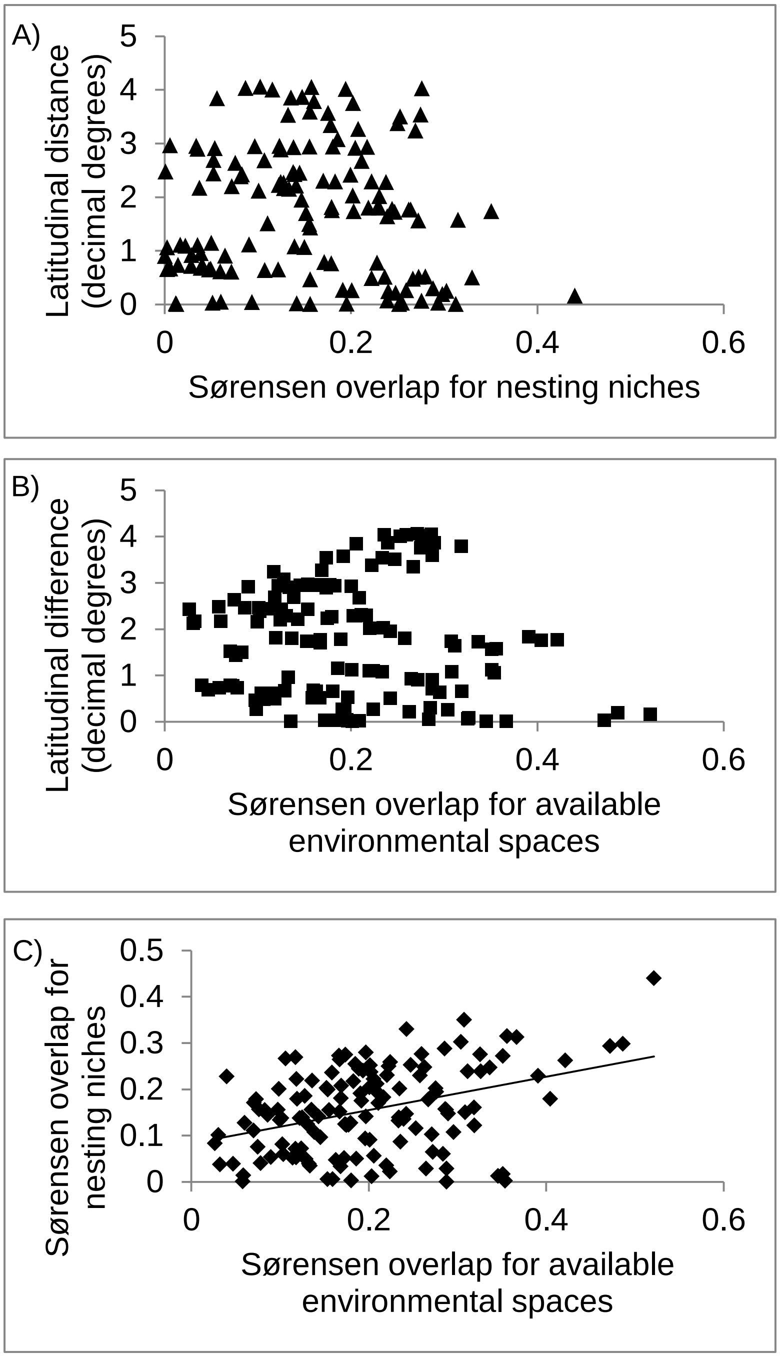


Figure 4.1. Similarity between nesting niches and available environmental space. A) nesting niches of saltmarsh sparrows and B) available environmental space was not related to latitudinal distance for all pairwise comparisons of study plots from New Jersey to Maine, U.S.A., 2012-2013. C) Similarity between nesting niches increased with similarity of available environmental space for pairwise comparisons of study plots, though variability was high.

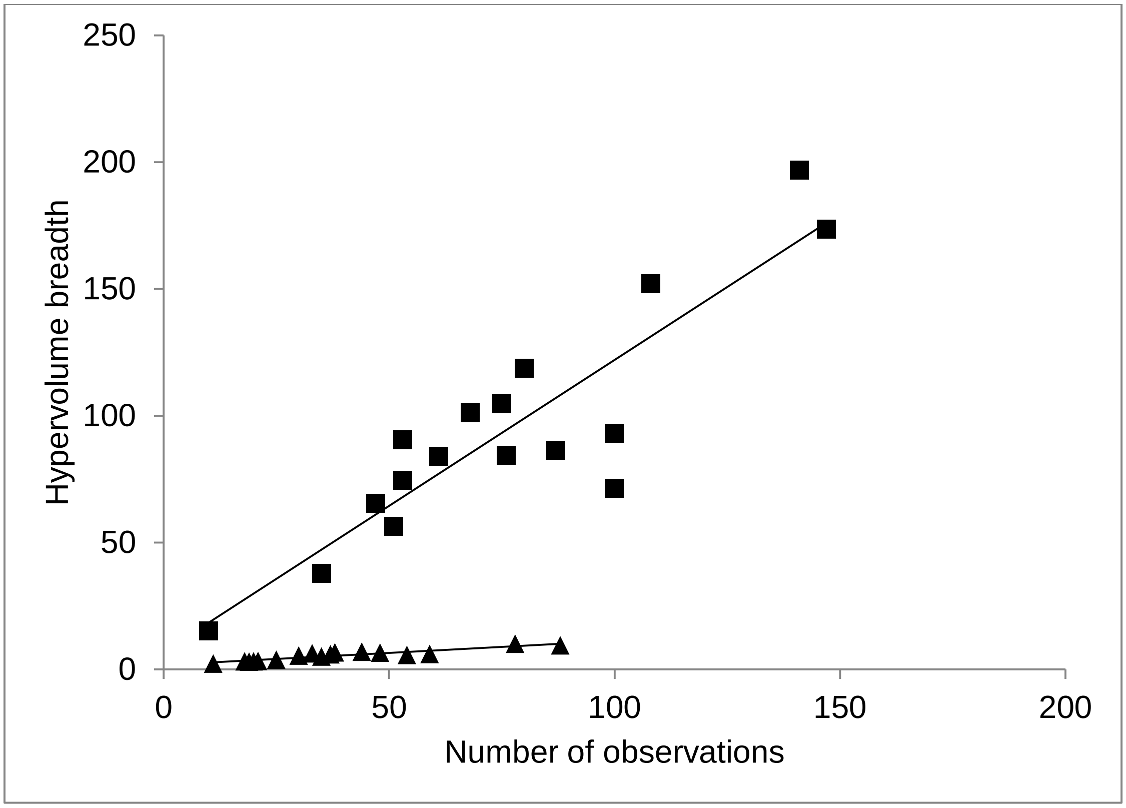


Figure 4.2. Hypervolume breadth increased with number of observations. Niche breadth (volume of the 8-dimensional hypervolume) increased with number of observations for both available habitat (randomly selected points, shown with squares; $F=60.4_{1,15}$, $p<0.0001$, adjusted $R^2=0.79$) and saltmarsh sparrow nest points (shown with triangles; $F_{1,15}=84.8$, $p<0.0001$, adjusted $R^2=0.84$). Nesting niche breadth increased with number of observations at a lesser rate for nests, however, indicating that female saltmarsh sparrows are exhibiting a habitat selection throughout all study plots.

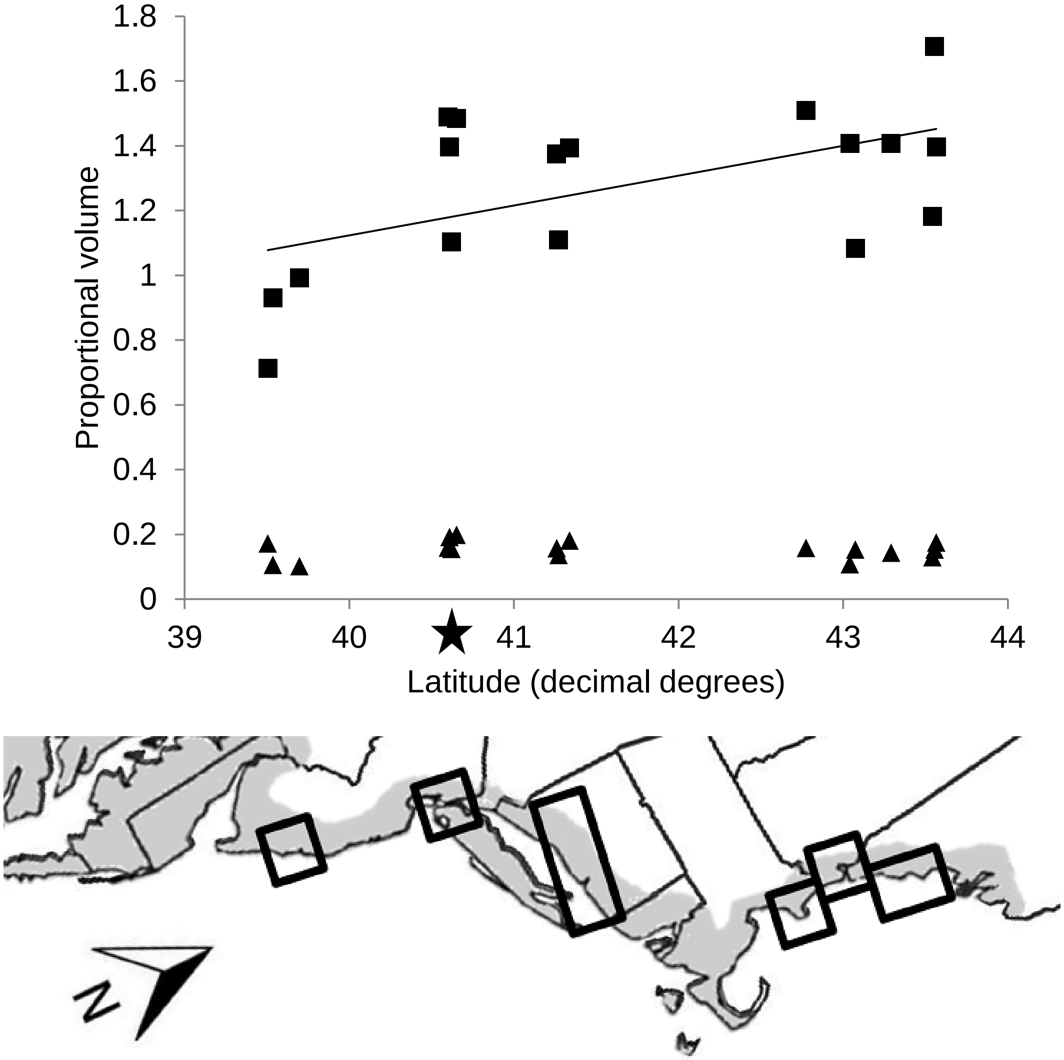


Figure 4.3. Hypervolume breadth by latitude. Niche breadth of available habitat (randomly selected points, shown with squares) increased with latitude (proportional volume; $F=6.4_{1,15}$, $p=0.02$, adjusted $R^2=0.25$), while nesting niche breadth of saltmarsh sparrows (shown with triangles) was not related to latitude or distance from the range center (proportional volume; $F_{1,15}=0.005$, $p=0.94$, adjusted $R^2<0.0001$). Instead, nesting niche breadth was remarkably consistent throughout the range. The star indicates the latitudinal center of the global saltmarsh sparrow breeding range.

4.4.4. Does habitat selection vary across the range of a species?

The multivariate logistic regression demonstrated both that saltmarsh sparrows exhibit small scale habitat selection across their geographic range, and that their selection does not vary for some vegetation characteristics but does for others by study plot (Table 4.3). For example, nests were associated with a thicker thatch layer than randomly selected points at all study plots (p-values ranging from <0.0001 to 0.008 for the 8 of 17 study plots where the effect was significant). For other characteristics, such as the average vegetation height, nests were associated with both significantly higher and significantly lower vegetation than randomly selected points, depending on study plot. Sørensen overlap indices between nesting niches and available environmental space at each study plot ranged between 0.01 and 0.10, with a mean overlap index (±sd) between selected and available habitat of 0.06 ±0.02 (n=17). The similarity between available and selected environmental space at each study plot was not related to latitude ($F=0.2_{1,15}$, $p=0.65$, adjusted $R^2<0.0001$; Fig. 4.4). The proportional volume of available environmental space was greater than the proportional volume of nesting niche at every study plot (n=17; Table 4.2). Finally, the similarity between nesting niches increased with similarity between available environmental spaces for study plot pairs ($F=23.4_{1,134}$, $p<0.0001$, adjusted $R^2=0.14$; Fig. 4.1C).

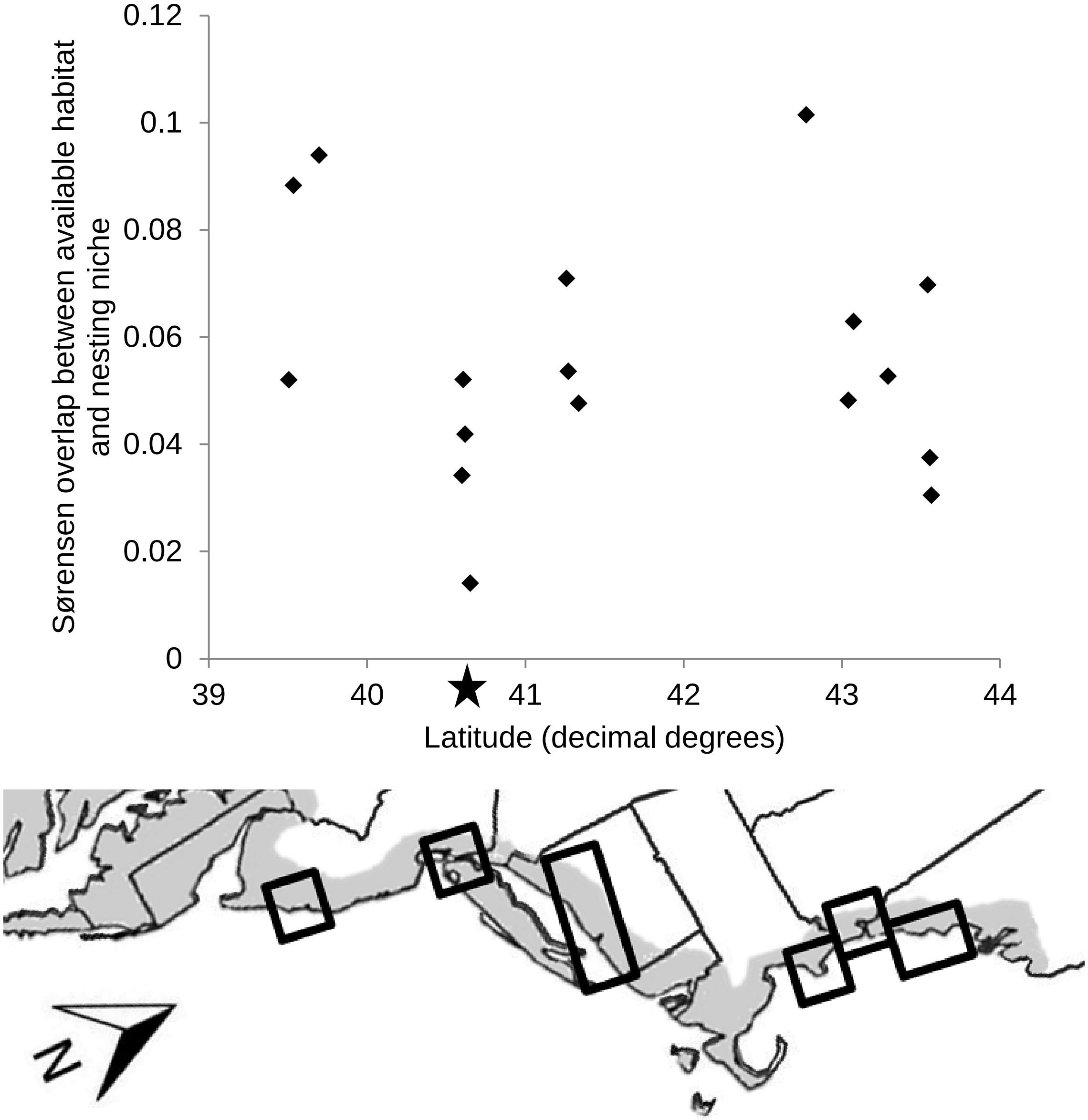


Figure 4.4. Habitat marginality by latitude. The similarity between available habitat and nesting niche for saltmarsh sparrows at each study plot was not predicted by latitude or distance from range center ($F=0.2_{1,15}$, $p=0.65$, adjusted $R^2<0.0001$). The star indicates the latitudinal center of the global saltmarsh sparrow breeding range.

4.4.5. What are the fitness consequences of differences in niche across the range of a species?

The similarity between available and selected habitat was not related to seasonal fecundity ($F=0.2_{1,15}$, $p=0.67$, adjusted $R^2<0.0001$; Fig. 4.5). Moreover, the similarity of nesting niches did not predict observed differences in seasonal fecundity in the pairwise study plot comparisons ($F=0.5_{1,134}$, $p=0.48$, adjusted $R^2<0.0001$; Fig. 4.6).

4.5. Discussion

We observed that in contrast to the predictions consistent with niche conservatism, saltmarsh sparrow nesting niche varies intraspecifically across its geographic range. Some axes of the nesting niche varied by study plot, while others appeared to be conserved. The similarity between both nesting niches and available environmental space for pairwise comparisons of study plots was not related to latitudinal distance or range position. Thus, saltmarsh sparrow habitat and habitat selection is variable on a local scale and its variation is not consistent with niche conservatism. The similarity of available environmental space predicted the similarity of nesting niches between study plots, however, suggesting that some, but not all, of the intraspecific variation in nesting niche is explained by local habitat availability. No aspects of the intraspecific niche variation we observed were related to seasonal fecundity. Thus, we observed no signs of habitat marginality near the high-latitude margin of the saltmarsh sparrow range. Instead, nest-site selection seems to vary locally and is not likely the driver of the high-latitude margin of the saltmarsh sparrow range.

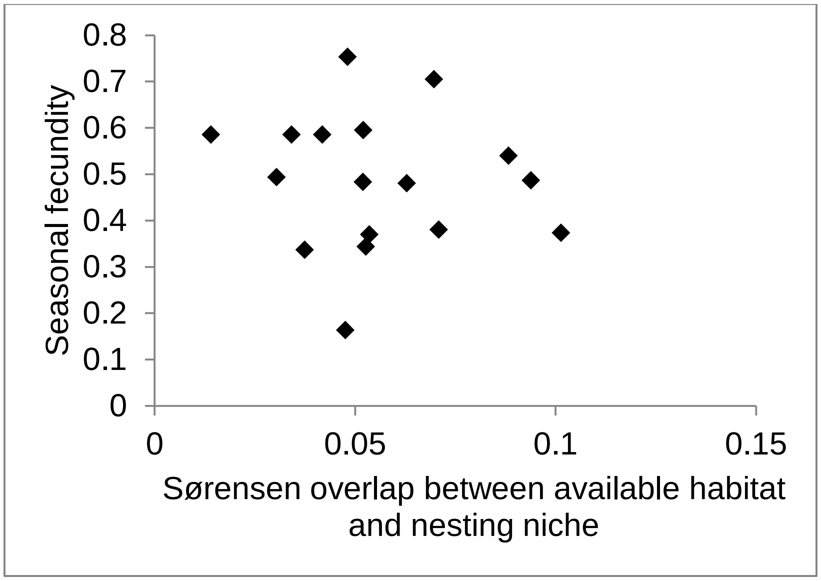


Figure 4.5. Seasonal fecundity was not related to habitat marginality. Our results suggest no patterns of habitat marginality near the periphery of the saltmarsh sparrow range.

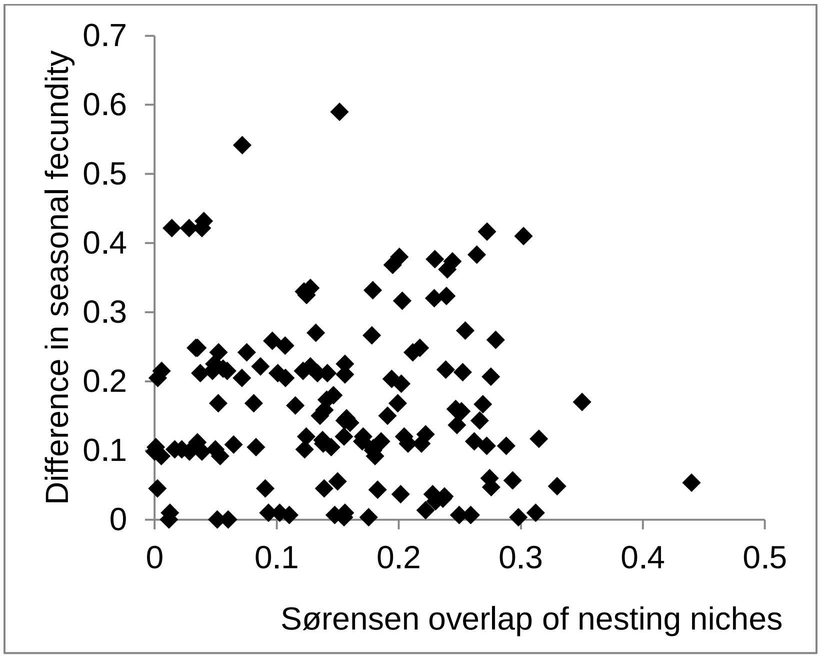


Figure 4.6. Similarity between nesting niches not related to the difference in fecundity. Our results suggest that intraspecific variation in saltmarsh sparrow nesting niches do not result in negative fitness consequences.

Saltmarsh sparrows exhibit clear habitat selection throughout their geographic range, and nesting niche was relatively constant in position for some habitat axes. At all study plots, the breadth of available habitat was greater than that of habitat selected by saltmarsh sparrows for nest sites on a small spatial scale (Table 4.2). Moreover, we observed a strong signal of selection for most of the vegetation characteristics, which were both structural and compositional, for at least several study plots (Table 4.3, Appendix D). Our results are consistent with three previous studies of the small-scale habitat selection of saltmarsh sparrows. All previous investigations have found that saltmarsh sparrows generally build their nests in areas with thicker thatch layers and greater cover of *Spartina patens* than randomly selected points (Gjerdrum et al 2005; Shriver et al 2007, Ruskin in press). We also found that saltmarsh sparrow nests were associated with thicker thatch layers ($p<0.10$ for 11 of 17 study plots). We found that nests were associated with a higher percent cover of *S. patens* at most study plots ($p<0.05$ for 11 of 17 study plots), but at two study plots, nests were associated with significantly less *S. patens* than randomly selected points ($p=0.005$ and $p=0.0003$ for Eldridge Road and Lubberland Creek, respectively).

The position of the saltmarsh sparrow nesting niche differed for some axes across the range, however. First, the magnitude of the coefficient of effect for habitat selection varied among study plots. For example, across most study plots, saltmarsh sparrows selected nest sites with significantly deeper thatch than the available habitat, but the depth of the thatch they chose varied by study plot. Similarity between available environmental space significantly predicted similarity of nesting niches between pairs of study plots, which suggests that for some habitat axes, saltmarsh sparrow nesting niche is influenced by local habitat availability (Fig. 2). However, we observed habitat selection that varied not only in the magnitude of selection by study plot, but also the direction of selection. For example, saltmarsh sparrows selected nest sites with significantly higher than average vegetation at some study plots and sites with significantly lower than average vegetation at other study plots; these differences were not due to convergence upon a single preferred vegetation height. These differences likely contribute to the high amount of variability in the pairwise comparisons of available environmental space and nesting niches between study plots, which was statistically significant but noisy (Fig. 4.1). Taken together, our results suggest that the saltmarsh sparrow nesting niche consists of both constant and variable elements, the latter of which are dependent on habitat availability and other drivers on a local scale.

Though our results do not suggest that niche conservatism is upheld in this system for nesting niche position, the breadth of nesting niche was remarkably consistent across the species range (Fig. 4.3). Our study may have been limited by statistical power, however, because our sampling unit was at the level of study plot and therefore led to a relatively small sample size (n=17). Thus, we cannot differentiate between conservatism of niche breadth and a lack of statistical power. We did, however, observe that the breadth of available environmental space increased with latitude using an identical sample size. Given this result, we argue that a relationship between nesting niche breadth and latitude, if present, is sufficiently small that variation from other sources is likely more biologically meaningful.

Habitat selection differed across the saltmarsh sparrow range but was not consistent with niche conservatism. The similarity between available and selected habitat did not vary with latitudinal distance or range position (Fig. 4.4). The Sørensen index between nesting niches and the available environmental space varied by an order of magnitude among study plots, but was low across the range. The similarity between study plots for both selected and available habitat was not related to their latitudinal distance; that is, the available habitat or nesting niche at any study plot can be, and often is, more similar to those of distant marshes than of nearby marshes. These results point to high levels of local habitat heterogeneity (Fig. 4.1). Some of this local heterogeneity is natural, because there are multiple types of marshes (e.g., marshes behind barrier beaches, marshes fringing rivers) and large differences in tidal amplitude on the Atlantic coast of North America (Tiner 2013). Humans have also increased the heterogeneity of tidal marshes in this region, notably via ditching, channelizing, and tidally restricting marshes for human development (Silliman, Grosholz, and Bertness 2009).

Further, the similarity between nest and random-point hypervolumes was not related to mean seasonal fecundity by study plot (Fig. 4.5), nor did the similarity of nesting niches between study plots predict their differences in fecundity (Fig. 4.6). Therefore, differences in nesting niche position and breadth did not appear to have fitness consequences for saltmarsh sparrows. We observed no signal of range-wide trends in habitat marginality, either characterized by changes in niche breadth or a relationship between nesting niche and fecundity, as predicted under a paradigm of niche conservatism.

These results suggest that rather than large-scale trends in habitat suitability, intraspecific variation in the saltmarsh sparrow nesting niche is shaped by local processes across the range. Saltmarsh sparrow populations may adapt locally or vary plastically, driven by spatially-variable risks to fecundity. Previous research has demonstrated that populations at different points of the breeding range face different risks to fecundity. Specifically, risk of nest depredation increases toward low latitudes, while nest flooding poses greater risk near the high-latitude range margin (Ruskin et al. in review). These large-scale patterns may influence saltmarsh sparrow habitat selection, as high predation risk has been shown to correlate with certain nest traits across several avian species (e.g. increased nest concealment, Martin 1992).

Alternatively, intraspecific variation in saltmarsh sparrow nesting niche may be driven by local habitat availability. Our results support this hypothesis in part. Using comparisons of the Sørensen overlap index for nesting niches and available environmental space, we found that available environmental space predicted nesting niche characteristics across all study plots (Fig. 4.1). However, the predictive power was low (adjusted R^2=0.14) due to high amounts of scatter, likely because saltmarsh sparrows exhibited signs of variable nest preferences (e.g. used nest sites with higher than average vegetation at some study plots and lower than average vegetation at other study plots). Future studies should relate fecundity to habitat selection at an individual level to test whether local differences in habitat selection are adaptive or simply constrained by local habitat availability.

Our results also suggest that the high-latitude margin of the saltmarsh sparrow breeding range is not caused by lack of habitat for the small-scale niche axes we examined. We observed mosaics for both available and selected habitat across the range, with no changes in niche breadth to signal habitat marginality near the high-latitude range margin. The niche space of available habitat increased with latitude toward the range edge, while nesting niche breadth remained constant. Based on the means of available habitat for the vegetation characteristics that appear to be relatively constant aspects of the saltmarsh sparrow nesting niche (*S. patens*, thick thatch layer), we observed no signs of saltmarsh sparrows being “squeezed out” of available habitat near the range margin. Further, those characteristics exist north of the saltmarsh sparrow range (Lonard et al. 2010, M. Correll unpublished data). Rather than running out of suitable habitat at the small spatial scale we examined, the saltmarsh sparrow range may be limited by axes of the species niche outside of the small-scale nesting niche we examined. For example, the distribution of the saltmarsh sparrow breeding range may be caused by larger-scale factors such as habitat patch size. Marsh patches become markedly smaller and patchier near the high-latitude range margin of saltmarsh sparrows (W. Wiest et al. in review). Future studies should include other modules of the saltmarsh sparrow niche, such as large-scale factors and biotic interactions. Further, future studies should include data from the low-latitude range margin of saltmarsh sparrows, which we did not examine in this study.

CHAPTER 5: DIVERGENT OVIPOSITION PREFERENCES OF SISTER SPECIES ARE NOT DRIVEN BY NEST SURVIVAL: THE EVIDENCE FOR NEUTRALITY

5.1. Summary

Both adaptive and neutral trait evolution can contribute to divergence, but the relative contributions of the two remain unclear. Oviposition preference, a trait that has been demonstrated to contribute to divergence among populations, is often presumed to be an adaptive trait. Few studies explicitly test this assumption, however, and several researchers have demonstrated non-adaptive oviposition preferences in wildlife populations. In this study, we test whether adaptive divergence can explain current differences in the oviposition preferences of two sister species. In 2012 and 2013, we conducted a demographic study of sympatrically breeding populations of two sparrow species (*Ammodramus caudacutus* and *A. nelsoni*) and measured vegetation characteristics at nest and non-nest points. We found evidence for oviposition preference in both species and significant differences between the species' preferences. The vegetation characteristics that vary between species did not predict nest survival or offspring production, however. Our results provide an example of oviposition preference at a population level that appears non-adaptive as measured by productivity. We discuss other mechanisms by which oviposition preference can be adaptive, and make a case for the role of neutral evolution in shaping the oviposition preferences of these species. If divergence in oviposition preference is at least periodically neutral, as we hypothesize,

such differences could provide fodder for future adaptation or reproductive isolation among populations.

5.2. Introduction

Both adaptive and neutral trait evolution can contribute to divergence among populations, but the relative contributions of the two mechanisms remain unclear. Though genetic drift is acknowledged to contribute to divergence between populations in allopatry (Lenski and Travisano 1994; Gavrilets 2003; Papke et al. 2003; Coyne and Orr 2004; Petren et al. 2005; Comes et al. 2008), much work on sympatric speciation centers on selective forces promoting divergence, such as in the model stickleback system (Rundle et al. 2000; Coyne and Orr 2004). However, some authors argue that most evolution is neutral or nearly so. They suggest that populations evolve along relatively flat planes within a highly dimensional niche space and have demonstrated these results with modeling experiments (Kimura 1983; Gavrilets 2003, 2004).

Oviposition preference, specifically where an organism chooses to lay and keep its eggs, has been observed to contribute to divergence and is often presumed to be adaptive. Oviposition preference has contributed to divergence among populations in a wide range of taxa (Brykov et al. 1996; Etges 1998; Hawthorne and Via 2001; Friesen et al. 2007). In fact, the most convincing cases of sympatric speciation in animals are related to divergence in oviposition preferences (Sorenson et al. 2003; Coyne and Orr 2004; Machado 2005; Rønsted et al. 2005; Althoff et al. 2006). Oviposition preference is often presumed adaptive for good reason; it can dramatically affect individual fitness via both fecundity (Resetarits 1996) and adult survival (Scheirs et al. 2000; Spencer 2002;

Miller et al. 2007). Many ecological studies, however, presume oviposition preference is adaptive without explicitly testing for a relationship between oviposition behaviors and fitness (Arlt and Pärt 2007).

In a review of bird nest site preferences, Clark and Shutler (1999) found that only 54% of oviposition studies related preferences to nest success and only 10% of studies examined found evidence for adaptive oviposition preference. Finally, several researchers who have explicitly examined the relationship between oviposition preference and fecundity across a wide range of taxa have reported oviposition preferences that are not adaptive (Review: Robertson and Hutto, 2006; Birds: Dwernychuk and Boag 1972; Filliater, Breitwisch, and Nealen 1994; Arlt and Pärt, 2007; Chalfoun and Schmidt 2012; Insects: Rausher 1979; Thompson 1988; Kriska, Horváth, and Andrikovics 1998; Ries and Fagan 2003; Reptiles: Kamel and Mrosovsky 2005).

There are many reasons why oviposition preference, or any trait that impacts fitness, can be non-adaptive. In this study, we define non-adaptive as a trait that does not increase an organism’s fitness. This definition includes both neutrality and maladaptation. A characteristic is neutral if it confers no benefit or disadvantage to its carrier, whereas a trait is maladaptive if it decreases an organism’s fitness. Gould and Lewontin’s (1979) classic “non-exhaustive list” of causes for lack of adaptation includes evolutionary constraints, methodological shortcomings, and neutral evolution. It is important to understand the non-adaptive forces behind the evolution and divergence of oviposition preferences because differences in these traits appear to be important for multiple modes of speciation (e.g. allopatric, sympatric, and ecological).

In this study, we explicitly test for adaptive differences in the oviposition preferences of two Emberizid sparrows, saltmarsh (*Ammodramus caudacutus*) and Nelson's (*A. nelsoni*) sparrows. These sister species are known collectively as sharp-tailed sparrows. Together, they provide an exemplary study system for exploring the adaptive versus non-adaptive evolution of oviposition preferences because their distinctive life history sets the stage for non-adaptive divergence in a number of ways.

First, the characteristics of the tidal marsh where sharp-tailed sparrows breed may weaken selective pressure. Bayard and Elphick (2010) observed that saltmarsh sparrow nest placement was spatially random in Connecticut, and they suggested this random nest placement developed as a result of a lack of opportunity for adaptation. Female sharp-tailed sparrows nest a few centimeters above the ground in the high marsh zone, which is characterized by flooding events each month (Tiner 2013). As a result, the majority of sharp-tailed sparrow nest failure is isolated in time, but spatially widespread. The spatial homogeneity of nest failure in tidal marshes thus leaves little meaningful variation in oviposition preference upon which selection can act. Previous research supports this hypothesis; saltmarsh sparrow oviposition preferences have not been predictive of nest success in multiple studies of the species across New England (Gjerdrum et al. 2005; Shriver et al. 2007).

Second, the evolutionary history and breeding biology of sharp-tailed sparrows eliminate many mechanisms that would cause adaptive trait evolution. There is no evidence for competitive exclusion between these species. Males and females of both species are non-territorial, and the home ranges of both species overlap widely with both conspecifics and heterospecifics (Greenlaw and Rising 1994; Shriver et al. 2011).

Because males of both species do not contribute parental care, oviposition preferences and female fecundity are not constrained by territory availability, dominance hierarchies, or male behavior. Given their overlapping home ranges, similar mating systems, and the spatial homogeneity of nest failure, saltmarsh and Nelson's sparrows breeding in sympatry are subject to similar, if not equivalent, local selection for oviposition preference.

Finally, evolutionary and developmental constraints are unlikely to be the cause of divergence between the taxa. As sister species that became reproductively isolated as recently as 600,000 years ago (Rising and Avise 1993), saltmarsh and Nelson's sparrows share most of their evolutionary history and the accompanying phylogenetic constraints. The two species also interbreed readily where their ranges overlap (Greenlaw and Rising 1994; Walsh et al. 2011), illustrating that they share most developmental constraints. Through the process of elimination, we are left with genetic drift as one of the most likely drivers for the development, or at least maintenance, of divergence in oviposition preferences.

In this study, we use sympatrically breeding populations of sharp-tailed sparrows as a case study to investigate selection versus drift as major drivers of divergence in oviposition preferences. We first confirm whether, consistent with previous studies, sharp-tailed sparrows exhibit oviposition preferences. We then test whether oviposition preference differs between saltmarsh and Nelson's sparrows with broadly overlapping home ranges. Finally, we test whether any observed differences in oviposition preference between the species are positively related to fecundity, and therefore are potentially adaptive.

5.3. Methods

5.3.1. Study site and field methods

We compared oviposition preferences of saltmarsh and Nelson's sparrows in Scarborough Marsh, Cumberland County, Maine, USA, located in the sympatric sharp-tailed sparrow range (Hodgman et al. 2002). We surveyed two, 10-ha study sites that are separated by 2.5 km, including a wide river and active train tracks. In two years of study, we have captured over 450 unique individuals, only one of which was captured at both of these study sites. Thus, we consider the populations to be largely independent.

We searched for nests once or twice per week from May through August, 2012-2013. Following discovery, we revisited nests every one to three days until the nesting attempt was completed via fledging or failure. We captured attending females at the nest site with mist nets to determine species. Each female was uniquely marked a numbered aluminum leg band from the United States Geological Survey to track multiple nesting attempts throughout the breeding season and across multiple years.

In Scarborough Marsh, saltmarsh and Nelson's sparrows interbreed readily. Based on morphology, they exhibit a gradient of introgression. Genetic analysis of sharp-tailed sparrows captured in northern New England indicate high levels of introgression, suggesting that the species have interbred extensively (Rising and Avise 1993; Shriver et al. 2005; Walsh et al. 2011). Samples collected in southern Maine in the late nineteenth century show characteristics of hybridization, suggestive that the species have interbred at our study site for at least 150 years (KJR unpub. data).

Because of the extensive introgression between these species, we treated species as a continuous variable as measured by plumage (sensu Shriver et al. 2005) rather than using a binary species assignment. For each of 13 plumage characteristics (e.g. color and definition of breast streaking, width of crown stripes) we assigned each adult sparrow a score ranging from one to five. Low scores represent traits typical of Nelson's sparrows, while high scores represent traits typical of saltmarsh sparrows. The scores in the 13 categories are then summed to produce an integrated species index ranging from 13 to 65. Previous studies have found general concordance between plumage and genetic hybrid status (Shriver et al. 2005; Walsh et al. 2015). To minimize observer subjectivity, we averaged the summed plumage score of each female across all captures within a single breeding season.

At each nest site, we measured sixteen characteristics. These included four characteristics of the built nest structure and twelve vegetation characteristics within a square 1-m^2 plot centered on each nest. Nest structure measurements included total nest height (lip of nest bowl to ground), nest depth, distance from bottom of the nest to the ground, and amount of nest canopy as measured by estimating the percentage of the nest bowl that was visible through the canopy while viewing the nest from directly above. For vegetation characteristics, we measured thatch depth and maximum vegetation height, and we visually estimated average vegetation height at the center (at the nest) and midpoints of the 1-m^2 plot sides. We also visually estimated percent cover of all species present within the 1-m^2 plot (Table 5.1), with all cover classes summing to 100%. We chose characteristics based on previous research on sharp-tailed sparrows (Gjerdrum et al. 2005; Shriver et al. 2007) and the predominant vegetation at our site.

Table 5.1. Vegetation characteristics and nest and non-nest points. Shown are vegetation characteristics (mean ± SD) at nest and non-nest points in current and previous studies of sharp-tailed sparrows in New England saltmarshes, USA.

Vegetation Characteristic	Nest site	Non-nest point	*P*	Gjerdrum (2005)[a]	Shriver (2007)[b]
Thatch depth at 1 m^2 quadrat midpoints (cm)	9.2 ± 3.7	6.4 ± 4.4	<0.001	-	sig.
Thatch depth at center (cm)	16.3 ± 5.7	6.9 ± 6.0	<0.001	sig.	-
Maximum vegetation height at 1 m^2 quadrat midpoints (cm)	54.3 ± 10.7	45.8 ± 13.8	<0.001	sig.	-
Maximum vegetation height at center (cm)	61.7 ± 12.4	46.3 ± 15.4	<0.001	-	-
Average vegetation height at 1 m^2 quadrat midpoints (cm)	37.5 ± 8.9	33.7 ± 11.6	<0.01	-	-
Average vegetation height at center (cm)	41.4 ± 9.9	33.6 ± 12.6	<0.001	-	-
Water (% cover)	2.2 ± 5.7	3.7 ± 12.5	0.29	-	-
Spartina patens (% cover)	56.2 ± 26.2	33.9 ± 37.9	<0.001	sig.	sig.
Spartina alterniflora (% cover)	27.4 ± 24.4	22.1 ± 30.4	0.15	non-sig.	non-sig.
Distichlis spicata (% cover)	9.9 ± 20.3	9.8 ± 19.9	0.97	sig.	non-sig.
Juncus gerardii (% cover)	1.8 ± 9.3	10.6 ± 24.7	0.01	sig.	non-sig.
Other species (% cover)	1.8 ± 5.2	17.4 ± 28.1	<0.001	-	-

The means shown are averages among the midpoints of four sides on a 1-m^2 quadrat. For the present study, we show mean ± standard deviation of vegetation characteristics for nest site and non-nest points. Reported *P*-values are derived from post hoc one-way comparisons of variance between nest and non-nest points. We also include indications of vegetation characteristics found to be significantly related to nest sites in these species in previous studies. Dashes indicate that a characteristic was not measured in the previous study.

We recorded the four nest structure characteristics upon discovery of the nest and the remaining vegetation characteristics upon nest completion (fledging or failure) to minimize disturbance to the nesting female. We measured the same suite of vegetation structure and cover characteristics within a 1-m^2 plot centered at non-nest points that we randomly selected within the study sites using the "Create Random Points" tool in the "Data Management" toolbox of ArcGIS version 10.0 (Environmental Systems Research Institute, Redlands, USA). We surveyed non-nest points throughout the breeding season, within a week of the completion of a paired nest site to control for plant phenology over the study period. We excluded randomly selected points that were located in standing water during field surveys.

5.3.2. Statistical analyses

Statistical analyses were performed using R 3.0.2 (R Core Team 2014). We first used a multiple analysis of variance to test whether sharp-tailed sparrows as a whole exhibit an oviposition preference as measured by twelve vegetation characteristics (Table 1). We used one-way analyses of variance to identify whether mean vegetation characteristics differed significantly between nest and non-nest points. To ensure that both species exhibit a preference, we performed a multiple analysis of variance on saltmarsh and Nelson's sparrows separately as well. We separated the dataset into two subsets based on plumage score limits. We defined saltmarsh sparrows as females with summed plumage scores of 45 or greater, which is the 95th percentile of birds captured in Connecticut. This is the closest breeding population outside of the hybrid zone where we collected plumage score data (Hodgman et al. 2002; Walsh et al. 2011). We defined

Nelson's sparrows as females with a summed plumage score of 31 or less based on the limit established by Shriver et al. (2005). Hybrids were thus excluded from both subsets of data. We tested for oviposition preferences in both species with the full analysis of variance model on each of these subsets.

We then created a general linear model to test whether the species identity of nesting females (as measured continuously by summed plumage score, using all females) covaried with the same twelve vegetation characteristics and four additional nest characteristics. We also included covariates to control for year and study site. We used stepwise AIC model selection (R package MASS, Ripley et al. 2014) to choose the most parsimonious suite of nest and vegetation characteristics that predicted the species of nesting females as measured by summed plumage score.

Finally, we modeled the relationship between the vegetation characteristics that best predicted species of a nesting female and two estimates of fecundity, daily nest survival probability and brood size (number of nestlings produced by a successful nest). First, we used the program MCestimate to generate daily nest survival probabilities. MCestimate estimates daily nest survival probabilities similarly to the logistic exposure method (Mayfield 1975; Dinsmore et al. 2002; Rotella et al. 2004; Shaffer 2004), but within a Markov-Chain framework (Environmental Protection Agency Mid-continent Ecology Division, Duluth, USA; see Etterson et al. 2007, 2014; Jackson et al. 2011). For all nests, we estimated daily nest survival probability as a function of year and the vegetation characteristics from the top model for distinguishing among species as measured by summed plumage score from the previous step. We created a null model in which daily nest survival rate was held constant among all nests. We compared the top model to the null model using Akaike's Information Criterion (Akaike 1974; Burnham and Anderson 2002) to test whether differences in oviposition preferences can lead to differences in nest survival between saltmarsh and Nelson's sparrows. To estimate local variation in nest survival, we also used MCestimate to estimate daily nest survival rate as a function of study site. Second, we used a Poisson regression to estimate brood size, an alternate estimate of fecundity, as a function of year and the nine vegetation characteristics from the top model for distinguishing among species as measured by summed plumage score (R base package, R Core Team 2014).

Finally, we created two Poisson regression models to test for differences in additional fecundity parameters along the species gradient as measured by summed plumage score. In separate models, we estimated number of nesting attempts and clutch size as functions of the summed plumage score of associated females (R base package, R Core Team 2014). Goodness of fit tests indicated that for brood size, clutch size, and number of nesting attempts, the data fit the assumptions of Poisson regressions.

5.4. Results

We compared vegetation characteristics at 190 randomly-selected points to 92 sharp-tailed sparrow nest sites. Of these, 27 nest sites were chosen by Nelson's sparrow females, 47 by saltmarsh sparrows, and 18 by females within the hybrid range according to the plumage limits described. With a total of 1159 exposure days, we observed daily nest survival probabilities of 0.9402 ± 0.01 (mean ± SE; n=33 nests) and 0.9486 ± 0.01 (mean ± SE; n=59 nests) by study site.

Vegetation structure and cover characteristics reliably distinguished between nest and non-nest points (Table 1; n=282, approximate F= $18.7_{12,269}$, *P*<0.001). This pattern persisted in the subsets of data that included only saltmarsh (n=47 nests and 47 randomly-selected points; F= $8.6_{12,81}$, *P*<0.001) and Nelson's sparrows (n=27 nests and 27 randomly-selected points; F= $4.6_{12,41}$, *P*<0.001), demonstrating that both species exhibit an oviposition site preference. We found that nine of the vegetation characteristics examined had population means that significantly differ between nest and non-nest points (Table 5.1).

Our results also indicated that nest and vegetation characteristics varied across the sharp-tailed sparrow species gradient (n=92, R^2= 0.28, F=$3.1_{17,74}$, *P*<0.001; Table 5.2). The best model included nine of the sixteen measured nest and vegetation characteristics and the year covariate (n=92, R^2= 0.33, F= $5.5_{10,81}$, *P*<0.001). The best model did not include study site, indicating that nest site preferences did not vary based on local habitat availability.

Using year and the nine characteristics included in the best model for predicting species as measured by summed plumage score, oviposition site did not predict daily nest survival probability. The nest characteristics that best predicted species performed worse than the null model for predicting daily nest survival probability (ΔAIC_c=+3.14, model weight=0.17; Table 5.3). Using year and the nine characteristics included in the best model for predicting species, oviposition site also did not predict brood size (X^2(10, n=30), *P*=0.82).

Table 5.2. Parameter estimates for predictors of female species. Predictors of female species as measured by summed plumage score in Scarborough, ME, USA (positive beta values correspond to vegetation characteristics with higher values for females toward the saltmarsh sparrow end of the plumage gradient) for vegetation characteristics chosen in the top model.

Predictor variable	*b*	SE	*t*	*P*
Year	-3.20	1.82	-1.75	0.08
Distance from bottom of the nest to the ground (cm)	0.90	0.23	3.84	<0.001
Nest depth (cm)	-1.35	0.55	-2.44	0.02
Thatch depth at center (cm)	0.44	0.17	2.61	0.01
Thatch depth at 1 m^2 quadrat midpoints (cm)	-0.35	0.26	-1.36	0.18
Maximum vegetation height at 1 m^2 quadrat midpoints (cm)	-0.18	0.10	-1.69	0.09
Average vegetation height at center (cm)	-0.36	0.12	-2.95	<0.01
Spartina patens (% cover)	-0.18	0.04	-4.79	<0.001
Distichlis spicata (% cover)	-0.18	0.04	-4.02	<0.001
Juncus gerardii (% cover)	-0.13	0.09	-1.50	0.14

Table 5.3. Parameter estimates for predictors of daily nest survival probability. Predictors of daily nest survival probability in Scarborough, ME, USA for vegetation characteristics chosen in the top model.

Predictor variable	*b*	SE
Year	0.67	0.33
Distance from bottom of the nest to the ground (cm)	-0.07	0.04
Nest depth (cm)	-0.12	0.11
Thatch depth at center (cm)	-0.03	0.03
Thatch depth at 1 m^2 quadrat midpoints (cm)	0.05	0.05
Maximum vegetation height at 1 m^2 quadrat midpoints (cm)	-0.01	0.02
Average vegetation height at center (cm)	0.03	0.02
Spartina patens (% cover)	0.01	0.01
Distichlis spicata (% cover)	-0.004	0.01
Juncus gerardii (% cover)	0.002	0.01

Individual females nested an average of 1.26 ± 0.06 times per year (mean ± SE; n=73). Mean clutch size across all nests was 3.65 ± 0.09 eggs or nestlings per nest (mean ± SE; n=92). Among successful nests, mean brood size was 2.53 ± 0.19 nestlings per nest (mean ± SE; n=30). We found no evidence that number of nesting attempts (X^2(71, n=73), *P*=0.50) or clutch size (X^2(92, n=90), *P*=0.61) varied by species as measured by summed plumage score.

5.5. Discussion

Differences in oviposition preference have been often cited as mechanisms of reproductive isolation and a driver of ecological speciation between sister taxa (Coyne and Orr 2004; Nosil 2012). However, we demonstrate evidence of sympatric sister taxa with oviposition preferences that are divergent but appear not to be under current selection pressure for maximizing nest survival. Alternative mechanisms for maximizing fitness via oviposition site exist. We present multiple lines of evidence that suggest that variation in oviposition site between Nelson’s and saltmarsh sparrows is maintained despite a lack of selective pressure, however.

Similar to the two previous studies that examined small-scale nest-site preference in sharp-tailed sparrows, we found that both saltmarsh and Nelson’s sparrows breeding in Scarborough Marsh exhibit oviposition preferences (Table 5.1). Previous studies and our own found that both structural and vegetation cover characteristics were important in distinguishing between nest and non-nest points (Gjerdrum et al. 2005; Shriver et al. 2007). Moreover, the characteristics in our best model were similar to those reported by previous studies. For example, our results agree with those of both Gjerdrum et al.

(2005) and Shriver et al. (2007), who also found that nest sites were positively associated with percent cover of *Spartina patens* and exhibited a deeper thatch layer compared to randomly selected non-nest points. The Gjerdrum et al. (2005) study was conducted in southern New England, and the Shriver et al. (2007) study was conducted in the same marshes as our investigation. Together, this suggests that the oviposition preferences of sharp-tailed sparrows are similar across both space (~300 km) and time (~a decade). Additionally, we found that compared to randomly selected points, the 1-m^2 plot surrounding nest sites included less water, a trait that was not examined by the two previous studies.

Saltmarsh and Nelson's sparrow females exhibit consistently different oviposition preferences as measured by vegetation characteristics. For example, females with plumage more typical of saltmarsh sparrows built nests that were higher above the ground, had shallower nest bowls, and placed them in areas with less *Spartina patens* compared to females that exhibited plumage more typical Nelson's sparrows. Because these species interbreed in sympatry, the observed differences in oviposition preferences between them in this population are conservative underestimates for the species in general, because some degree of convergence is expected from genetic introgression.

The nest characteristics that differed by species did not predict either of two estimates of fecundity, however. Though the oviposition preferences of saltmarsh and Nelson's sparrows vary consistently across study sites, they do not appear to confer any adaptive advantage in terms of fecundity as measured by nest survival or brood size during the years of our study. In fact, the nest traits that together explain 33% of the observed variance in female species perform worse at predicting nest survival than an intercept-only null model.

We should note, however, that our sample size may have been too small to detect differences in fecundity, particularly because small differences in daily nest survival probability compound into larger differences in overall nest survival probability. Additionally, if even small differences in nest success have been consistent during the entire period of secondary contact (documented empirically for 150 years at our study site), this can lead to marked differences in selection and population growth rate between the species. Thus, our findings of no selection should be interpreted cautiously.

However, our findings are consistent with previous research, which has found no placement differences between successful and unsuccessful nests (Gjerdrum et al. 2005; Shriver et al. 2007). Furthermore, we found no evidence that saltmarsh and Nelson’s sparrows exhibit differences in two life history traits that could result in patterns of fecundity that differ from those observed in nest survival probabilities (renesting rate and clutch size). Thus, nest survival is likely a reasonable index of the fitness consequences of oviposition divergence in this system and a better index than has been reported in other songbirds (Streby and Andersen 2013; Streby et al. 2014).

Here we show direct evidence that two estimates of fecundity are not related to divergent oviposition preferences of saltmarsh and Nelson’s sparrows. However, oviposition preference can maximize fitness in a number of other ways. Refsnider and Janzen (2010) review nest survival (more generally, embryo survival) in addition to five alternative hypotheses for how oviposition site can maximize fecundity. Sharp-tailed sparrows provide an ideal system that offers good reason to eliminate the alternative hypotheses, however, suggesting that the divergent oviposition preferences between saltmarsh and Nelson's sparrows are currently non-adaptive.

We can rule out four of Refsnider and Janzen's (2010) hypotheses because of the unique mating systems and life histories of saltmarsh and Nelson's sparrows. First, Refsnider and Janzen describe a hypothesis that oviposition site can indirectly maximize fitness through mate choice, but both saltmarsh and Nelson's sparrows are promiscuous, non-territorial, and males do not contribute to parental care (Greenlaw and Rising 1994; Shriver et al. 2010). Second, the authors propose that oviposition site can impact fitness through offspring phenotype, usually via microclimatic conditions. This hypothesis is commonly invoked for species that do not exhibit parental care, such as fish, amphibians, and reptiles. In most bird species, including sharp-tailed sparrows, adults mediate the environmental conditions at the oviposition site through incubation and nest attendance. Nonetheless, this idea has been applied to several avian systems, providing mixed results as to whether differences in nest microclimates are typically ameliorated by parental behavior (Rauter et al. 2002; Amat and Masero 2004; Dawson et al. 2005; Robertson 2009; Tieleman et al. 2014). Sharp-tailed sparrow females nest under natural or woven grass canopies, which create shade and moderate the nest microclimate. Thus, we think microclimate is unlikely to affect offspring phenotype in this system, but future studies should measure microclimatic conditions at the nest site to address this possibility. Third, oviposition site can also maximize fitness via juvenile survival, for example by proximity to suitable habitat for juveniles after leaving the nest. Sharp-tailed sparrow juveniles roam the marsh after leaving the nest, however, in home ranges that overlap with non-parental adults and parental adults, conspecifics and heterospecifics (Shriver et al. 2010; KJR unpub. data). Therefore, juvenile habitat use and any consequent differences in juvenile survival are not likely to result from any differences in oviposition preference between the species. Instead, juveniles of both of these non-territorial species are exposed to similar post-fledging risks to survival that are independent of oviposition site. Fourth, oviposition preference is hypothesized to maximize fitness by maintaining natal philopatry in some systems. Both saltmarsh and Nelson’s sparrows exhibit natal philopatry, but on the larger spatial scale of marsh habitat patches, which is on the order of hectares rather than within 1-m^2 plots that were examined in this study (Greenlaw and Rising 1994; DiQuinzio et al. 2001; KJR unpub. data).

The fifth and final alternative hypothesis described by Refsnider and Janzen (2010) is that oviposition site can maximize fitness via female survival. We cannot conduct a survival analysis with only two years of data, and we observed too few females that nested in both years of this study to make any inferences about female survival based on species (2 within the saltmarsh sparrow plumage limit, 1 Nelson’s sparrow, and 2 apparent hybrids). However, we also conducted systematic mist-netting at these study sites for another project, and we detected similar proportions of saltmarsh and Nelson’s sparrow females captured in 2012 that returned in 2013 (8.7% of Nelson’s sparrow females, 5.5% of saltmarsh sparrow females; KJR unpub. data). Additionally, adult survival estimates calculated from systematic mist-netting at these and additional sites demonstrated that saltmarsh and Nelson’s sparrow females exhibit equivalent adult survival rates across northern New England (CR Field unpub. data). Moreover, Sillett and Holmes (2002) observed that monthly rates of mortality were fifteen times greater during migration months than in the breeding season for another songbird species. While oviposition site may influence female survival in sharp-tailed sparrows, in these and many songbirds, adult mortality related to oviposition site is likely small relative to migration-related mortality. Nonetheless, future studies should include explicit tests for female survival and more robust estimates of fecundity that include juvenile survival.

Despite the limitations of our study, our findings are consistent with the hypothesis that neutral processes have shaped or currently maintain species-level differences in oviposition preference. The two sharp-tailed sparrow species in Scarborough Marsh share evolutionary history, sympatric habitat, a unique mating system, and developmental constraints, and thus we can reject many mechanisms for adaptive divergence. We are left with drift as a likely driver of the maintenance of the observed divergence between saltmarsh and Nelson's sparrow oviposition preferences. The possibility that either species currently exhibits an oviposition preference that arose through adaptive selection elsewhere in space or time is impossible to eliminate. At the very least, we can conclude that the current divergence in saltmarsh and Nelson's sparrow oviposition preferences is maintained without strong selection in sympatry. Should these traits become important for reproductive isolation between the species in the future, that outcome will have been shaped at least partly by periods of neutral evolution.

These results challenge the often-assumed paradigm that traits, particularly those related to survival, fecundity, and reproductive isolation, are optimized. In light of these and other similar findings, researchers should explicitly measure the fecundity consequences of variation in oviposition preferences. In particular, wildlife managers should consider that observed preferences and behaviors in wildlife are not necessarily adaptive when planning for conservation action such as habitat restoration. Otherwise, they may take conservation action that while based on observed habitat use, will not result in increased population growth.

Our results suggest that, as with all traits, oviposition preference can vary neutrally and is perhaps a work in progress. Oviposition preference is not perfectly optimized to the environment, nor is it without superfluity. This standing variation in oviposition preference, which exists not just at the individual but at the population level, provides fodder for divergence and ultimately could increase the probability of ecological speciation. More research should address how common neutral variation in oviposition preferences is in nature, and its relative importance in the speciation process.

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Appendix A – Chapter 1: Study plots and associated covariate information

Table A.1. Study plots and associated covariate information.

Study Plot	State	Latitude (decimal degrees)	Longitude (decimal degrees)	Nearest Observed Water Level Station	Maximum High Tide May-August, 2011-2013 (meters)	Nearest Observed Exceedance Level Station	1% Exceedance Probability Value	Nearest sea level rise location (Boon et al. 2012)	Sea level rise probability 1969-2011 (millimeters)
Oyster Creek	NJ	39.5	-74.4	Atlantic City, NJ	1.60	Atlantic City, NJ	1.47	Atlantic City, NJ	4.63
Mullica Wilderness	NJ	39.5	-74.4	Atlantic City, NJ	1.60	Atlantic City, NJ	1.47	Atlantic City, NJ	4.63
AT&T	NJ	39.7	-74.2	Atlantic City, NJ	1.60	Atlantic City, NJ	1.47	Atlantic City, NJ	4.63
Four Sparrow Marsh[1]	NY	40.6	-73.9	Sandy Hook, NJ	1.64	Sandy Hook, NJ	2.06	Sandy Hook, NJ	4.19
Sawmill Creek[1]	NY	40.6	-74.2	Bergen Point West Reach, NY	1.65	The Battery, NY	1.68	The Battery, NY	3.47
Marine Nature Park[1]	NY	40.6	-73.6	Sandy Hook, NJ	1.64	Sandy Hook, NJ	2.06	Sandy Hook, NJ	4.19
Idlewild[1]	NY	40.7	-73.8	Sandy Hook, NJ	1.64	Sandy Hook, NJ	2.06	Sandy Hook, NJ	4.19
East River	CT	41.3	-72.7	New Haven, CT	2.50	Bridgeport, CT	1.65	New London, CT	3.53
Hammonasset	CT	41.3	-72.5	New Haven, CT	2.50	New London, CT	1.89	New London, CT	3.53
Pattagansett	CT	41.3	-72.2	New London, CT	1.50	New London, CT	1.89	New London, CT	3.53
Waterford	CT	41.3	-72.1	New London, CT	1.50	New London, CT	1.89	New London, CT	3.53
Barn Island	CT	41.3	-71.9	New London, CT	1.50	New London, CT	1.89	New London, CT	3.53
John H. Chaffee	RI	41.4	-71.5	Newport, RI	1.44	Newport, RI	1.84	New London, CT	3.53
Sachuest Point	RI	41.5	-71.2	Newport, RI	1.44	Newport, RI	1.84	New London, CT	3.53
Parker River	MA	42.8	-70.8	Fort Point, NH	2.27	Seavey Island, ME	1.14	Boston, MA	2.88
Chapman's Landing	NH	43.0	-70.9	Fort Point, NH	2.27	Seavey Island, ME	1.14	Portland, ME	0.94
Lubberland Creek	NH	43.1	-70.9	Fort Point, NH	2.27	Seavey Island, ME	1.14	Portland, ME	0.94
Eldridge Road	ME	43.3	-70.6	Wells, ME	2.41	Seavey Island, ME	1.14	Portland, ME	0.94
Little River	ME	43.3	-70.5	Wells, ME	2.41	Seavey Island, ME	1.14	Portland, ME	0.94
Jones Creek	ME	43.5	-70.4	Portland, ME	2.46	Portland, ME	1.23	Portland, ME	0.94
Nonesuch River	ME	43.6	-70.3	Portland, ME	2.46	Portland, ME	1.23	Portland, ME	0.94
Libby River	ME	43.6	-70.3	Portland, ME	2.46	Portland, ME	1.23	Portland, ME	0.94
Scarborough River	ME	43.6	-70.4	Portland, ME	2.46	Portland, ME	1.23	Portland, ME	0.94

Appendix B – Chapter 1: Model Comparisons

Table B.1. Model selection for daily nest depredation probability. Latitude most parsimoniously predicted nest depredation probability.

Predictors of nest depredation	Predictors of nest flooding	AIC_c	ΔAIC_c	weight
latitude	intercept-only	2996.59	0	0.57
latitude + serial date	intercept-only	2997.18	0.59	0.43
intercept-only	intercept-only	3017.74	21.15	<0.01
serial date	intercept-only	3019.74	23.15	<0.01

Table B.2. Model selection for daily nest flooding probability. An additive combination of maximum high tide, exceedance value, and serial date were selected as the most parsimonious model of nest flooding probability.

Predictors of nest depredation	Predictors of nest flooding	AIC$_c$	ΔAICc	weight
intercept-only	maximum high tide + 1% exceedance value + serial date	2988.25	0	0.35
intercept-only	latitude + maximum high tide + 1% exceedance value + serial date	2989.20	0.95	0.22
intercept-only	maximum high tide + sea level rise rate + 1% exceedance value + serial date	2989.53	1.29	0.18
intercept-only	latitude + 1% exceedance value + serial date	2991.09	2.84	0.08
intercept-only	latitude + maximum high tide + sea level rise rate + serial date+ 1% exceedance value	2991.19	2.94	0.08
intercept-only	sea level rise rate + 1% exceedance value + serial date	2992.64	4.39	0.04
intercept-only	latitude + sea level rise rate + 1% exceedance value + serial date	2993.03	4.79	0.03
intercept-only	1% exceedance value + serial date	2996.30	8.05	0.01
intercept-only	maximum high tide + 1% exceedance value	3002.21	13.97	<0.01
intercept-only	maximum high tide + sea level rise rate + serial date	3002.40	14.15	<0.01
intercept-only	latitude + maximum high tide + sea level rise rate + serial date	3003.43	15.18	<0.01
intercept-only	latitude + maximum high tide + 1% exceedance value	3004.14	15.89	<0.01
intercept-only	maximum high tide + sea level rise rate + 1% exceedance value	3004.21	15.97	<0.01
intercept-only	latitude + maximum high tide + serial date	3005.09	16.84	<0.01
intercept-only	latitude + 1% exceedance value	3005.15	16.91	<0.01
intercept-only	latitude + sea level rise rate + serial date	3005.35	17.10	<0.01
intercept-only	serial date	3005.86	17.61	<0.01
intercept-only	1% exceedance value	3005.90	17.66	<0.01
intercept-only	latitude + maximum high tide + sea level rise rate + 1% exceedance value	3005.91	17.66	<0.01
intercept-only	maximum high tide + serial date	3006.17	17.93	<0.01
intercept-only	sea level rise rate + 1% exceedance value	3006.20	17.95	<0.01
intercept-only	latitude + sea level rise rate + 1% exceedance value	3006.81	18.56	<0.01
intercept-only	sea level rise rate + serial date	3007.15	18.90	<0.01
intercept-only	latitude + serial date	3007.83	19.58	<0.01
intercept-only	maximum high tide + sea level rise rate	3013.02	24.77	<0.01
intercept-only	latitude + maximum high tide + sea level rise rate	3014.20	25.95	<0.01
intercept-only	latitude + sea level rise rate	3015.25	27.01	<0.01
intercept-only	sea level rise rate	3016.36	28.12	<0.01
intercept-only	latitude + maximum high tide	3016.38	28.13	<0.01
intercept-only	intercept-only	3017.74	29.50	<0.01
intercept-only	latitude	3018.26	30.01	<0.01
intercept-only	maximum high tide	3019.63	31.39	<0.01

Table B.3. Best combined model. The combined model performed better than the top models for either nest depredation probability or nest flooding probability.

Predictors of nest depredation	Predictors of nest flooding	AIC_c	ΔAICc	weight
latitude	maximum high tide + 1% exceedance value + serial date	2967.73	0	1
intercept-only	maximum high tide + 1% exceedance value + serial date	2988.25	20.52	<0.01
latitude	intercept-only	2996.59	28.86	<0.01
intercept-only	intercept-only	3017.74	50.02	<0.01

Appendix C – Chapter 1: Saltmarsh Habitat and Avian Research Program (SHARP) Nest Protocols

Saltmarsh Habitat and Avian Research Program Nest Protocols

Available online at www.tidalmarshbirds.org

6.3.1. Nest searching

Formal nest searches should be conducted as frequently as possible, but not so frequently as to cause detrimental disturbance to the birds. At a minimum, plots should be comprehensively searched at least once per week throughout the breeding season. When nest searching, the procedure is simply to walk back and forth in a zigzag fashion, with each path ~5-10 m from the previous one. Look carefully for behavioral cues, particularly birds that flush within 15 meters of you as you walk. Also watch for repeated flushes from the same spot, noticing when birds are carrying food (your impression will be of a decidedly "front-heavy" bird, because of the bits of prey sticking out of the bill) or fecal sacs (gleaming white). There is also an indescribable element involved with finding nests that just comes with experience. Your best bet is to go out with someone who has found some nests and look at where the nests are. Most people get quite good at finding nests quite quickly, though no one ever believes that they will. Finally, always pay attention for behavioral cues and opportunistically nest search at all times on the plot (e.g. while conducting nest checks, vegetation surveys).

6.3.2. Marking nests

Once nests have been found, they should be marked with flags and the geographic coordinates taken directly over the nest recorded with a geographic positioning system device. A nest card should be filled out right away, and it is usually helpful to draw a small map of the immediate area on the back of the card, in order to help re-find the nest on subsequent visits (especially if it is not you who will be coming back). The types of thing worth marking on the map include the relative position within the plot, location of nearby ditches or pools, any boundaries between vegetation types (e.g., the border of a patch of *Juncus* sp.), etc.

We avoid putting flags right next to nests so as not to alert predators to the nest's location. Instead, use one of these methods; (a) place a flag ~5 m (5 strides) away, such that the nest lies on a line between the flag and some easily identified marker (e.g., an osprey platform or plot boundary marker), (b) if there is no suitable marker, put out two flags each ~5 m away from the nest, such that the nest lies directly between them, or (c) use a standard compass bearing to set the line between the flag and the nest. For any particular research group it is a good idea to make the convention consistent.

6.3.2.1. Nest numbering

To make it easier to combine data sets from different research groups, we will all use a common nest numbering system. Each nest should be given a number that consists of (1) the two letter study plot code, (2) the last two digits of the year, (3) the 4-letter banding code denoting the species, and (4) three numbers denoting the Nth nest found that year, so that numbers take the form: ZZYYXXXX###, where ZZ is the two-letter code for the study plot where the nest occurred, YY denotes the year, XXXX is the species code, and ### is the nest number.

Within each research group, all nests are numbered sequentially, without regard to species. For example, if the first three nests found in Connecticut in 2011 were a saltmarsh sparrow at Barn Island, a willet at Hammonasset, and another saltmarsh sparrow at East River, they would be numbered BI11SALS001, HM11WILL002, ER11SALS003.

If multiple field teams are working in the same area in the same year, or if people are working separately during nest searching, then each should be designated a separate set of numbers to use, so as to ensure that no number is used twice. For example, one person could take numbers starting from ZZYYXXXX001, while another takes numbers starting from ZZYYXXXX201.

6.3.2.2. Under-construction nests

For nests found without eggs, usually via a female flush during the construction phase, mark them as you would an active nest with a stake flag. Record the date found and the location using geographic coordinates for each nest found under construction on a new nest card.

To prevent disturbance that could lead a female to abandon her nesting attempt during the construction stage, do not revisit under-construction nest until at least 5 days after discovery when it might have eggs. In the meantime, stay away from the nest as much as possible; ideally leave an approximately 50m buffer, although the presence of other nests that need monitoring may influence the buffer radius). To this end, you might find it useful to mark the flag differently, such as with colored flagging that denotes "under construction" so the area can be avoided at a distance.

If an under-construction nest has eggs on a subsequent visit, assign it a unique number and open a new nest card for it if you haven't already. If the nest never has eggs on subsequent visits, be sure you recorded the date of discovery and geographic coordinates, and then remove the flag after a few weeks.

6.3.3. Nest monitoring

Nests should be visited every 3-4 days after finding to track nest contents. Three days is preferred for use in the fecundity model required by a SHARP deliverable. Nest visits should be brief and every attempt should be made to minimize disturbance. If you can see into the nest and count contents without getting right up close, then do so (carrying a narrow bamboo stick can be helpful as it allows you to part the vegetation without getting right up next to the nest). If nestlings are present, make note of physical features indicating their approximate age (feather development, body size, open eyes). If any eggs or nestlings are seen outside of the nest (especially after a flooding event), make note of that.

If any eggs or chicks are missing since your last visit, make a thorough search of the area around the nest to see if there are drowned chicks, or eggs that have floated out. If a nest appears to have flooded and has lost an egg or two, continue monitoring with nest checks at the normal intervals, because females will persist in incubation and the remaining eggs often hatch. If a nest with chicks appears to be empty, but it is too soon for them to fledge, also keep monitoring, because young chicks can climb out of nests and hide in the surrounding vegetation. Make sure to check where you put your feet.

Details of each visit should be recorded on the appropriate nest record card (see below). When nest contents have gone missing, it is important to provide as much detail as possible, both about what you do see and what you do not (e.g., broken egg shell, chewed body parts, any nest damage, nest empty but dry, etc.) Information about other nests lost in the same area and timeframe can be especially helpful to record, although the fate of one nest should not be simply inferred from the fate of others. All of this information will be used to assign nest fates at a later date.

6.3.4. Nest cards

Whenever you go out in the field, carry a batch of blank nest cards so that you can fill in basic information when you first find a nest. When doing a series of nest checks, take the relevant nest cards with you so that you (a) have a map and directions to the nest, (b) know the conditions on the last visit, which can sometimes help explain what you find, and (c) can fill the information in directly to avoid transcription errors later on. Nest cards should be printed on fairly stiff card stock or Rite in the Rain paper so that they can withstand some abuse, but remember that these are primary data so take care not to get them wet, muddy, etc.

6.3.4.1. General nest info

Fill in the top section with the appropriate information about the nest and study plot when you first find the nest. Use the nest numbering system described above.

Record the geographic coordinates of each nest using a geographic positioning system device. Record the band number of the associated female if she is trapped off of the nest. As noted previously, sketch a map of the nest location on the back of the nest card to assist finding the nest on subsequent nest checks.

6.3.4.1. Individual visit info

For each nest visit, the nest card has places where you should note:

- date and time of nest visit, observer initials
- the number of eggs and chicks in the nest,
- whether the nest bowl is wet (i.e. from flooding),
- whether eggs were warm or not (lightly touch them in the nest to check),
- the age of any chicks (estimated from the Nestling Aging SOP, available on SHARP website: www.tidalmarshbirds.org),
- whether any dead eggs or chicks were collected,
- whether a female was seen to flush as you approached the nest,
- how far you were from the nest when the female flushed,
- whether the female called (also known as ‘chipping’) at you as you approached the nest,
- how far you were from the nest (NOT the female) when mobbing began.

There is also a column for nest status on each visit (e.g., partially failed due to flooding, completely failed due to depredation). Codes for use in this column are in the margin on the right of the card. Assigning codes is not always straightforward and a full assessment may not be possible until after the nest has completed. During the nest visits, however, simply assign the code that you think most accurately reflects the nests' status for the period since the previous visit. Criteria for each status are described below.

In the "Notes" space below each visit's row of boxes you can describe any changes in the nest's integrity (e.g., pulled apart by a predator), whether the nest appears damp (e.g., due to flooding), whether and how many dead eggs/chicks were found, and any other information that may help assign a fate to the nest.

6.3.5. Nest fate assignment

To minimize variation in how fates are assigned, nest fates should be completed by the graduate student responsible for each study plot (in consultation with others, as necessary). Described below are nest fate assignment rules, which should be followed closely to ensure consistency across individuals.

Ultimate nest fates relate to the factor that determined the "completion" of the nest, and is measured according to mutually exclusive categories. In other words it is the fate that relates to the last individual(s) in a nest.

- If any individual fledges, then the nest would be assigned an ultimate fate of "Fledged" (="successful").
- If no individual fledges, then the nest would be assigned an ultimate fate of "flooded", "depredated", or "failed, unknown cause" (all of which = "unsuccessful").
- In cases of conflicting evidence, specifically both nest flooding and nest depredation evidence, nest fate is considered "completely failed, unknown cause".

- If it is not certain whether any individuals fledge, then the nest would be assigned an ultimate fate of “unknown fate”.

Nest fate assignment requires tracking the nestling period of each nest that hatches to determine if missing chicks were old enough to fledge. Although eggs are laid a day apart, most species (including sparrows, shorebirds, ducks) will not start incubating until the clutch is complete. This means that the eggs will usually hatch on the same day. Our conventions are that the first day of the complete clutch is considered the first day (day 1) of incubation, and that the day on which eggs hatch is considered day 0 of the nestling phase (i.e., nestlings are considered 1 day old on the day after hatching occurs). Incubation lasts approximately 12 days for saltmarsh sparrows, and the last day of incubation is also hatch day when the chicks are aged 0 days. Nestlings usually fledge after 10 days, when they are aged 9 days with our hatch day = 0 days old convention (Greenlaw and Rising 1994). In summary, the entire brooding cycle proceeds as follows. Egg-laying: 1-5 days; incubation: approximately 12 days (last day is hatch day when chicks are 0 days old); nestling phase: typically 10 days, between 9 and 13 days.

6.3.6. Nest fate assignment key

Below is a dichotomous key for nest fate classification. Apply these rules to the ultimate fate of the nest, as defined as the fate of the last egg or chick surviving within the nest. For example, though a nest may lose an egg to flooding during incubation but the remaining eggs hatch and the chicks fledge, the ultimate nest fate is

1 - At previous visit, chicks were 9+ days old (5)

1 - At previous visit, chicks were <9 days old (2)

2 - At current visit, chicks would be 9+ days old (8)*

2' - At current visit, chicks would be < 8 days old (13)*

2" - At current visit, chicks would be 8 days old (17)*

5 - Spring tide or heavy rainfall occurred since previous visit (6)

5' - No spring tide or heavy rainfall occurred since previous visit (7)

6 - Evidence of flooding (**flooded**)

− the nest is observed underwater during a high tide and a subsequent nest check confirms that the nest is missing contents

− the nest is found with intact eggs outside the nest

− the nest is found with intact cold or dirty eggs in the nest, and eggs do not subsequently hatch

− the nest is found with intact dead chicks in, or close to, the nest

− the nest is found with barely-alive nestlings

− the nest is found to be empty and soaking wet immediately (next day) after a high tide, was known to have been active immediately prior to the high tide, and there are no signs of depredation (see 7 for criteria required to assign depredation)

6' - No evidence of flooding (7)

6’’ **–** Evidence of flooding and depredation (**failed, unknown cause**)

7 - Evidence of depredation (**depredated**)

− the nest is found with its structure pulled apart

− the nest is found with obvious depredation remains

− dead chicks or eggs are found with injuries that likely resulted in death

− the nest is found empty, or with partial loss, on a day when the tides could not have accounted for the losses

7' - No evidence of depredation (**fledged**)

8 - No eggs/chicks missing, cold, or past hatch date (**active**)

8' - At least one egg/chick missing, cold, or past hatch date (9)

9 - Spring tide or heavy rainfall occurred since previous visit (10)

9' - No spring tide or heavy rainfall occurred since previous visit (11)

10 - Evidence of flooding (**flooded**)

− the nest is observed underwater during a high tide and a subsequent nest check confirms that the nest is missing contents

− the nest is found with intact eggs outside the nest

− the nest is found with intact cold or dirty eggs in the nest, and eggs do not subsequently hatch

− the nest is found with intact dead chicks in, or close to, the nest

− the nest is found with barely-alive nestlings

− the nest is found to be empty and soaking wet immediately (next day) after a high tide, was known to have been active immediately prior to the high tide, and there are no signs of depredation (see 7 for criteria required to assign depredation)

10' - No evidence of flooding (11)

10’’ **–** Evidence of flooding and depredation (**failed, unknown cause**)

11 - Evidence of depredation (**depredated**)

− the nest is found with its structure pulled apart

− the nest is found with obvious depredation remains

− dead chicks or eggs are found with injuries that likely resulted in death

− the nest is found empty, or with partial loss, on a day when the tides could not have accounted for the losses

11' - No evidence of depredation (12)

12 - Nest intact, well worn, may have droppings in the nest or immediately adjacent (**fledged**)

12' - Conflicting evidence (**unknown if successful or failed**)

13 - No eggs/chicks missing, cold, or past hatch date (**active**)

13' - At least one egg/chick missing, cold, or past hatch date (14)

14 - Spring tide or heavy rainfall occurred since previous visit (15)

14' - No spring tide or heavy rainfall occurred since previous visit (16)

15 - Evidence of flooding (**flooded**)

− the nest is observed underwater during a high tide and a subsequent nest check confirms that the nest is missing contents

− the nest is found with intact eggs outside the nest

− the nest is found with intact cold or dirty eggs in the nest, and eggs do not subsequently hatch

− the nest is found with intact dead chicks in, or close to, the nest

− the nest is found with barely-alive nestlings

− the nest is found to be empty and soaking wet immediately (next day) after a high tide, was known to have been active immediately prior to the high tide, and there are no signs of depredation (see 7 for criteria required to assign depredation)

15' - No evidence of flooding (16)

15’’ – Evidence of flooding and depredation (**failed, unknown cause**)

16 - Evidence of depredation (**depredated**)

− the nest is found with its structure pulled apart

− the nest is found with obvious depredation remains

− dead chicks or eggs are found with injuries that likely resulted in death

− the nest is found empty, or with partial loss, on a day when the tides could not have accounted for the losses

16' - No evidence of depredation (**failure, unknown cause**)

17 - No eggs/chicks missing, cold, or past hatch date (**active**)

17' - At least one egg/chick missing, cold, or past hatch date (18)

18 - Spring tide or heavy rainfall occurred since previous visit (19)

18' - No spring tide or heavy rainfall occurred since previous visit (20)

19 - Evidence of flooding (**flooded**)

− the nest is observed underwater during a high tide and a subsequent nest check confirms that the nest is missing contents

− the nest is found with intact eggs outside the nest

− the nest is found with intact cold or dirty eggs in the nest, and eggs do not subsequently hatch

− the nest is found with intact dead chicks in, or close to, the nest

− the nest is found with barely-alive nestlings

− the nest is found to be empty and soaking wet immediately (next day) after a high tide, was known to have been active immediately prior to the high tide, and there are no signs of depredation (see 7 for criteria required to assign depredation)

20' - No evidence of flooding (19)

20’’ – Evidence of flooding and depredation (**failed, unknown cause**)

20 - Evidence of depredation (**depredated**)

− the nest is found with its structure pulled apart

− the nest is found with obvious depredation remains

− dead chicks or eggs are found with injuries that likely resulted in death

− the nest is found empty, or with partial loss, on a day when the tides could not have accounted for the losses

20' - No evidence of depredation (**unknown if successful or failed**)

6.3.7. Nest and visit censoring

For nest survival analysis (e.g. logistic exposure), nest monitoring data must be censored to eliminate known biases. For example, if nestlings *could* have fledged on a given visit date (chicks were 9+ days old, in the case of saltmarsh sparrows) and their nest is found empty, the visit must be removed. In this case, the nest is assumed to be fledged while it may have failed after the previous visit with no evidence of failure left. By removing the final visit when the nestlings *could* have fledged, the potential positive bias is eliminated and all previous visits contribute to survival estimates. See Shaffer (2004) for discussion of this issue and an illustrative example.

Data that must be censored from nest monitoring before deriving survival estimates and the known problems they introduce:

- Nests that were found after failure – Even when evidence of cause of failure is available at the nest site, the timing of failure is not known and therefore the nest cannot be included.
- Nest visits when nestlings *could* have fledged, specifically nests with chicks that would be 9+ days old – See above. We also exclude nest visits when nestlings were 8 days old because previous research suggests that at 8 days (with hatch day = day 0), nestlings may fledge though it is rare (Greenlaw and Rising 1994). To

correct nest visits when chicks were 8 days old, remove the final nest visit and change the ultimate nest fate from “unknown if fledged or failed” to “fledged”, which allows the nest to contribute to daily survival probabilities without introducing bias.

- Nest visits when the nest was already inactive on the previous visit – Note that, in the field it is best to be conservative (continue to visit a nest until you are sure it has failed); however, this practice results in nests that were visited more than once after failure. Left unchanged, these additional visits can result in erroneous assigned times of failure and exposure intervals.
- Nest visits that are 6 or more days after the previous visit - We restrict our analyses to nests visited more frequently to limit uncertainty in nest fate assignment and the timing of nest completion.

Appendix D – Chapter 4: Comparison of vegetation characteristics of randomly selected points and saltmarsh sparrow nests

Table D.1. Vegetation characteristics at nest and randomly-selected points Vegetation characteristics mean values ± standard deviation of randomly selected points and saltmarsh sparrow nests at study plots from Maine to New Jersey, U.S.A., 2012-2013. Study plots are arranged in order from low to high latitude.

	Thatch height (cm)		Average height (cm)		Water (% cover)		*Spartina patens* (% cover)	
Study plot	Random	Nest	Random	Nest	Random	Nest	Random	Nest
Oyster Creek	2.7±3.6	3.7±3.3	31.6±11.1	41.0±11.0	0.6±3.9	3.6±10.8	24.0±35.4	52.2±33.0
Mullica Wilderness	6.0±4.0	7.5±3.1	34.0±16.9	32.9±9.2	0.5±3.2	0.2±1.4	59.0±34.8	73.1±27.7
AT&T	4.6±3.0	5.5±2.5	30.5±9.9	32.3±10.7	1.1±5.4	1.1±4.8	63.9±34.4	77.4±26.5
Four Sparrow Marsh	9.9±7.2	23.8±12.4	42.4±20.5	63.4±12.3	1.8±6.3	4.6±8.8	42.3±30.2	11.2±15.5
Sawmill Creek	10.0±5.9	15.2±4.2	38.5±20.3	40.4±10.2	0.0±0.1	1.2±4.6	49.4±28.9	51.5±24.7
Marine Nature Park	5.3±4.7	12.6±4.2	34.5±14.5	40.9±6.6	1.0±4.5	0.8±3.4	9.5±23.5	38.4±25.4
Idlewild	12.3±12.7	12.8±5.0	51.7±17.8	47.4±15.0	2.3±10.6	0.3±0.9	13±23.9	37.4±33.3
Hammonasset	3.3±3.7	5.6±3.3	28.3±9.8	34.0±7.9	0.0±0.0	0.9±4.7	28.4±35.2	47.9±26.7
East River	2.0±3.5	6.3±3.0	28.7±11.0	35.2±6	0.7±4.5	0.1±0.7	20.5±34.9	56.0±26.0
Barn Island	1.6±2.4	4.6±3.8	28.8±12.4	40.9±10.7	3.0±10.7	0.0±0.0	19.0±26.1	55.3±29.7
Parker River	7.0±4.0	9.1±3.2	46.8±14.3	47.5±9.6	0.0±0.0	2.3±6.2	70.1±47.2	59.8±37.2
Chapman's Landing	4.7±4.7	10.3±3.3	48.9±32.0	40.3±7.1	10.6±24.1	3.0±6.2	34.4±38.6	49.9±22.6
Lubberland Creek	5.3±4.2	8.8±3.4	42.6±15.4	40.8±8.1	5.3±19.0	4.6±10.8	76.7±38.4	72.3±24.7
Eldridge Road	5.4±4.0	10.1±3.6	42.6±26.5	43.2±9.4	5.2±19.7	0.7±4.2	49.5±37.8	46.9±27.5
Jones Creek	8.7±6.7	12.6±4.5	49.2±20.5	51.1±12.6	7.8±15.8	2.7±5.7	12.9±26.0	35.3±26.9
Nonesuch River	7.2±5.6	10.1±3.3	35.8±16.0	38.3±8.9	2.0±8.3	3.3±7.1	36.5±35.8	53.5±20.3
Scarborough River	6.1±3.7	10.0±3.3	32.1±9.8	35.8±8.2	4.6±14.1	2.5±5.4	33.1±38.9	55.6±24.5

Table D.1. continued.

	Spartina alterniflora (% cover)		*Distichlis spicata* (% cover)		*Juncus gerardii* (% cover)		Other species (%cover)	
Study plot	Random	Nest	Random	Nest	Random	Nest	Random	Nest
Oyster Creek	64.7±39.0	40.8±31	3.9±12.2	2.8±6.9	0.0±0.0	0.0±0.0	0.5±2.7	0.0±0.0
Mullica Wilderness	26.8±35.6	15.5±23	11.5±19.3	9.2±17.6	0.0±0.0	0.0±0.0	0.2±1.1	0.6±3.5
AT&T	17.8±30.0	13.1±22.2	12.7±23.0	4.1±12.5	0.0±0.0	0.0±0.0	0.8±2.9	1.7±4.9
Four Sparrow Marsh	27.6±33.5	79.0±18.4	19.1±21.2	1.9±6.4	0.0±0.0	0.0±0.0	2.9±6.6	0.0±0.2
Sawmill Creek	16.5±21.6	15.7±21.8	21.9±22.2	25.1±24.1	0.0±0.2	0.0±0.0	4.0±8.9	6.4±10.1
Marine Nature Park	61.8±28.4	45.3±26.4	4.3±14.4	9.9±19.8	0.0±0.0	0.0±0.0	1.6±2.8	1.1±2.8
Idlewild	54.7±35.8	40.9±37.7	15.7±23.0	18.6±27.2	0.0±0.0	0.0±0.0	3.7±11.4	0.5±1.2
Hammonassett	38.1±32.5	26.4±21.1	11.5±20.4	12.3±24.0	5.5±18.7	3.5±9.9	4.0±11.5	2.1±4.6
East River	53.3±38.5	28.1±25.9	8.4±18.8	10.5±16.5	1.4±6.7	1.5±8.7	2.8±4.9	0.9±2.4
Barn Island	50.9±36.6	22.7±23.7	8.4±18.2	10.3±18.3	3.6±14.2	7.0±21.8	3.7±13.3	3.2±7.0
Parker River	20.1±41.6	32.3±35.8	2.9±7.8	5.5±17.0	6.9±21.8	0.0±0.0	0.0±0.0	0.2±0.5
Chapman's Landing	30.3±33.3	43.7±21.0	10.9±25.8	2.3±9.4	1.9±10.8	0.0±0.3	10.4±25.5	0.6±3.1
Lubberland Creek	6.6±20.4	20.6±22.8	9.2±27.7	0.0±0.0	0.0±0.0	2.0±9.8	2.2±4.3	0.8±2.8
Eldridge Road	26.9±28.8	43.7±27.7	3.0±15.6	0.3±1.7	2.0±9.3	0.0±0.2	8.3±22.3	7.4±17.2
Jones Creek	72.3±31.9	60.9±27.2	0.9±8.5	0.1±1.1	0.0±0.0	0.0±0.0	5.2±16.2	0.9±4.9
Nonesuch River	34.3±34.1	40.7±19.2	4.5±12.0	1.2±4.4	6.7±20.9	0.0±0.0	11.7±20.4	0.8±1.8
Scarborough River	17.5±27.5	25.7±23.1	11.5±21.6	7.6±12.9	11.8±25.6	5.5±19.1	19.0±30.0	2.0±5.2

BIOGRAPHY OF THE AUTHOR

Kate was born and raised in New Jersey, where she graduated from North Plainfield High School in 2004. From there, Kate attended Columbia University in the city of New York. There she earned a Bachelor of Arts in Ecology, Evolution, and Environmental Biology, as well as a concentration in English. As part of her undergraduate experience, Kate got her feet wet with her first field job and avian research experience, studying the effects of contaminants on double-crested cormorant behavior with the help of Dr. Susan Elbin of New York City Audubon. After graduation, Kate continued her work with Dr. Elbin, and joined Dr. Nellie Tsipoura at the New Jersey Audubon Society to coordinate a citizen science survey of wading birds in New York/New Jersey Harbor. Kate's work has also taken her to cloud forests in rural Mexico and salt ponds in the Bay Area of California. Throughout, Kate's research has focused on the ecology and evolutionary biology of birds, climate change, and conservation. Kate was inducted into the University of Maine chapter of the Phi Kappa Phi honor society in 2012. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Science from the University of Maine in August 2015.