NESTING ADAPTATIONS AND CONSERVATION OF A THREATENED TIDAL MARSH-NESTING BIRD THE SALTMARSH SPARROW

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NESTING ADAPTATIONS AND CONSERVATION OF A THREATENED TIDAL MARSH-NESTING BIRD THE SALTMARSH SPARROW

BY

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Wildlife, B.A., Unity College, 2012

THESIS

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NESTING ADAPTATIONS AND CONSERVATION OF A THREATENED TIDAL MARSH-NESTING BIRD THE SALTMARSH SPARROW

by

Bri Benvenuti

University of New Hampshire, December, 2016

Tidal-marsh birds that nest on the marsh surface are faced with numerous reproductive challenges. Most recently, the impact of rising sea-levels threatens to reduce or eliminate reproduction in tidal-marsh nesting birds. One species most vulnerable to sea-level rise is the saltmarsh sparrow (Ammodramus caudacutus), an obligate tidal-marsh breeding bird with reproduction that is strongly linked to the tidal cycle. The saltmarsh sparrow is a species of high conservation priority in the northeast United States (USDI 2008) and is globally vulnerable to extinction within the next 50 years (Bayard and Elphick 2011, Wiest et al. 2016). I combined molecular, behavioral, and ecological techniques to better understand adaptations in female saltmarsh sparrow nesting ecology. Using nest data collected at four New England marshes from 2011-2015, I investigated adaptations in nesting behavior of females with respect to nest placement and offspring sex ratio manipulation. I also conducted a management experiment to test the feasibility of artificial habitats to provide flood-free nesting habitat in the face of sea-level rise.

In Chapter 1, I sought to determine if structural nest characteristics differed by nest fate. I also investigated patterns of female nest site selection, using females with multiple nesting attempts throughout the study period, to determine if female saltmarsh sparrows modify their
nesting behaviors based on prior experience. I found that nest characteristics differed by nest fate with fledged and predated nests built higher in the vegetation and in higher elevation areas of the marsh than those that flooded. Successful nests also had greater canopy cover and a lower proportion of high marsh vegetation than those that were flooded or predated. Nest height and elevation also differed between consecutive nesting events, consistent with a response to previous experience. Females whose first nesting attempt failed due to flooding constructed subsequent nests higher in the vegetation and in areas of higher elevation than those that were successful in their previous attempt. Females whose nests were predated in their first nesting attempt moved their second nests farther than females whose first nesting attempts were successful. I also found evidence for strong nest placement fidelity, as 84.5% of females renested between years within a distance smaller than the average core home range area (77m). These results demonstrate female saltmarsh sparrows exhibit plasticity in nesting behavior by changing structural nest characteristics following a cause-specific nest failure, which may be important for balancing selective pressures in the dynamic salt marsh environment. However, the exhibited plasticity may be insufficient to maintain reproductive success in the face of increased flooding predicted with sea-level rise.

Chapter 2 investigated if female saltmarsh sparrows are able to manipulate offspring sex ratios in response to environmental, temporal, or physiological conditions. The harsh environmental conditions of nesting in salt marshes provide a context for offspring sex manipulation to favor the sex with the greatest chance of survival or reproduction. I tested a priori hypotheses about the influence of environmental, temporal, and maternal effects on patterns of sex allocation at both the site and population level using sets of generalized linear mixed models. Across years and sites, I found an even offspring sex ratio of 1.03:1, with an
alternating pattern of interannual variation between male and female bias at both the population and site level. Offspring sex ratios did not vary as a function of timing within the breeding season or in relation to tidal flooding, and was also independent of female condition at time of nest initiation. I also observed considerable within brood variation in offspring sex ratios with a higher degree of variation than expected under a normal distribution. Our finding of a 1:1 offspring sex ratio and interannual variation in a wild bird population is more consistent with the predictions of Fisher (1930) than those of Trivers and Willard (1973).

In Chapter 3, I tested the efficacy of artificial habitat islands for maintaining flood-free high marsh nesting habitat for saltmarsh sparrows. I created and installed four 4 ft. x 8 ft. floating island rafts, vegetated with Spartina patens and Spartina alterniflora in a marsh pool on Rachel Carson National Wildlife Refuge in Wells, Maine. Islands were monitored through the breeding season and winter. The islands have remained free of tidal inundation and supported vegetation growth and expansion, suggesting that floating habitat islands hold promise as a method for mitigating nest flooding in tidal-marsh-nesting birds. Changes in vegetation, loss of nesting habitat, and increased tidal inundation will reduce, if not eliminate, the reproductive ability of marsh-nesting birds, including the saltmarsh sparrow. Conservation actions are needed in the very near-term to identify solutions to mitigate nest flooding and maintain breeding populations until habitat is created in the longer term by natural marsh processes or habitat restoration efforts. Creation of artificial habitat islands offers such a potential short-term management action.
INTRODUCTION

Tidal Marsh Ecology

Tidal marshes are one type of ecosystem comprising the terrestrial-marine ecotone (Mitsch and Gosselink 2000). They are abundant in plant and animal food resources through both the emergent vegetation and marine food chains, yet, despite their high productivity, tidal marshes can be inhospitable to birds and other vertebrates (Mitsch and Gosselink 2000, Greenberg et al. 2006b). In North America, tidal marshes provide essential habitat to only 25 taxa of endemic terrestrial vertebrates and have among the highest levels of vertebrate endemism of the world (Greenberg 2006). Low levels of terrestrial vertebrate biodiversity are likely due to the harsh physiological conditions that are created by tidal flooding, high salinity levels, and low plant diversity (Thome et al. 2012). Tidal-marsh endemics have adapted to live under the harsh conditions of this unique ecosystem, with the tradeoff being limited interspecific competition and abundant resources (Reinert 2006).

One of the major challenges faced by tidal-marsh endemics, is the intermittent flooding of their critical habitat. Water levels in tidal marshes are highly variable within the intertidal zone and create regular fluctuations between flooded and exposed substrate (Greenberg et al. 2006b). In addition, tide height varies throughout the year and is directly related to the lunar cycle. Tide height fluctuates in a predictable manner with the moon phase, producing peaks in tide height—the spring tides, which occur every two weeks and last one to three consecutive days (Redfield 1972). Of these bi-weekly peaks in tide height, alternating peaks (thus occurring about every four weeks, hereafter referred to as the flood tide) are highest. During the flood tides, marshes are almost entirely flooded. These flood tides can also be coupled with low pressure events and heavy rainfall to produce higher, and longer than average tidal flooding.
The regular cycle of tidal inundation leads to vegetation zonation throughout the tidal marsh ecosystem (Niering and Warren 1980). Slight variations in elevation result in significantly different hydroperiod, salinity, and oxygen availability, such that plant species occur along an elevational gradient in order of flood tolerance (Niering and Warren 1980). The selective gradients and simple biotic assemblages make tidal marshes ideal places to study evolutionary processes, particularly those associated with life history or behavioral shifts in a highly variable environment (Greenberg 2006).

Birds comprise the majority of tidal-marsh endemic species. The tidal-marsh breeding birds that build their nests on the surface of the marsh and are faced with high nest failure rates due to tidal flooding (Gjerdrum et al. 2008b). This has led to an array of adaptive responses such as placement of nests that exceeds the height of tides while minimizing predation, nest repair or egg retrieval behaviors, rapid post-flood renesting, and timing of the breeding behavior to avoid peak seasonal tides (Reinert 2006). These adaptations in nesting strategies of tidal-marsh birds allow them to breed successfully within the predictable patterns of tidal flooding.

Sea-level rise and climate-change induced changes in precipitation events pose an imminent threat to the survival and persistence of coastal ecosystems and their associated species (Wong et al. 2014). Coastal marshes are particularly vulnerable due to their sensitivity to changes in frequency and magnitude of tidal inundation (Wong et al. 2014). The combination of sea-level rise and increased frequency and duration of tidal inundation is converting tidal flats to sub-tidal estuary, low marsh to tidal flats, and high marsh to low marsh (Donnelly and Bertness 2001). Loss of marsh habitat will in turn impact the unique community of bird species found in tidal marshes by drastically reducing or eliminating nesting habitat and reducing the number of flood-free days on the marsh needed for successful nesting (Greenberg et al. 2006b, Bayard and
Elphick 2011a, Nur et al. 2012). With future changes in tidal inundation patterns, tidal-marsh bird nesting adaptations may be insufficient in attenuating the effects of tidal flooding.

**Saltmarsh sparrow**

One species most vulnerable to sea-level rise impacts on tidal marshes is the saltmarsh sparrow (*Ammodramus caudacutus*). The saltmarsh sparrow is a tidal-marsh obligate that has a global distribution limited to marshes along the Atlantic seaboard (Greenberg and Rising 1994). It constructs ground nests 10-20 centimeters off the surface in the marsh vegetation of primarily saltmeadow cordgrass (*Spartina patens*), smooth cordgrass (*S. alterniflora*), and blackgrass (*Juncus gerardii*) (Gjerdrum et al. 2005), and its reproduction is strongly linked to the tidal cycle (Greenlaw and Rising 1994, Shriver et al. 2007). Nests that are initiated within three days of the spring high tides are most likely to be successful by avoiding tidal flooding (Shriver et al. 2007). The primary causes of nest mortality of saltmarsh sparrows are flooding and predation, suggesting there is trade-off in the behaviors that have evolved in response to flooding and predation pressure in tidal-marsh birds (Greenberg et al. 2006). Predation risks follow a latitudinal trend, with higher rates of predation occurring at lower latitudes, while flooding rates vary across the species’ range unrelated to latitude (Ruskin et al. in review). The patterns of nest flooding and predation are also spatially independent at both the latitudinal and local scale, with the risk of nest failure differing even in neighboring marshes (Ruskin et al. in review). The local differences in rates of nest failure by flooding and predation indicate that nesting adaptations may also be variable at the local scale based on biotic and abiotic stressors.
Currently saltmarsh sparrow populations are experiencing a 9% annual decline, leaving the species prone to extinction within the next 50 years, and a species of conservation concern in several northeastern states (Hodgman et al. 2015, Correll et al. 2016). Tidal marshes have been subjected to both natural and anthropogenic stressors that have led to changes in tidal regime and marsh integrity (Morris et al. 2002, Gedan et al. 2009). Tidal restriction, an anthropogenic stressor, is suggested to accelerate marsh degradation and cause the loss of resilience to sea-level rise and ultimately the loss of specialist habitat (Correll et al. 2016). Saltmarsh sparrow populations also show a negative relationship with natural stressors of mean sea level and precipitation (Shriver et al. 2015). The direct impacts of sea level rise will continue to reduce the reproductive success of saltmarsh sparrows due to expected increases in nest flooding rates for local populations (Shriver et al. 2015, Correll et al. 2016, Field et al. 2016 in press, Ruskin et al. 2016).

In tidal-marsh nesting birds, nest site selection is directly correlated with reproductive success and can be used to minimize both flooding and predation risk (Storey et al. 1988). These birds possess a suite of adaptive responses that directly impact their nesting success, and therefore may also be expected to have plasticity in their behaviors to mitigate the effects of nest flooding and predation. Changes in nesting behavior in relation to predation pressure have been observed in multiple bird species (Forstmeier and Weiss 2004). Given the strong selection pressure imposed upon tidal-marsh birds, it may be advantageous for them to assess these risks of failure and respond with plasticity in nesting behavior to increase nesting success. Another adaptation that may be used by tidal marsh nesting birds is offspring sex ratio manipulation. Evolutionary theory suggests that natural selection should favor the ability of animals to modify the sex ratio of their offspring when the fitness benefits of producing one gender over the other
vary in relation to environmental conditions (Trivers and Willard 1973). However, if the costs and benefits of producing males and females is equal, there should be no difference in the number of sons and daughters produced in a population, as equal investment in offspring of both sexes is an evolutionarily stable strategy (Fisher 1930). The harsh environmental conditions of nesting in salt marshes and the unique mating system of the saltmarsh sparrow provide a context for offspring sex manipulation to favor the sex with the greatest chance of survival or reproduction.

By better understanding saltmarsh sparrow nesting behaviors, conservation and management strategies can be adapted to be more effective. Viable management solutions for enhancing saltmarsh sparrow reproduction must be achievable within a short time frame due to the rapid species decline. The use of artificial habitats and nesting structures to enhance reproductive opportunities have been successful in several avian species, including cavity nesting passerines and colonial waterbirds (Willner et al. 1983, Quinn et al. 1996, Shealer et al. 2015, Overton et al. 2015). Specifically, floating habitat islands have been used to successfully increase the nesting habitat and provide a flood-free refuge for common loon (Gavia immer), black tern (Chlidonias niger), and California clapper rail (R. obsoletus obsoletus), another tidal-marsh obligate (Desorbo et al. 2008, Shealer et al. 2015, Overton et al. 2015). Artificial habitats provide an appealing management alternative for vulnerable species in declining habitats because they can provide results within a short time frame. For saltmarsh sparrows, providing salt marsh habitat that does not sustain tidal flooding at nest height levels may increase nesting success and enhance reproductive rates. Floating habitat islands may thereby provide short-term population support, allowing species persistence until the effects of longer-term management and restoration actions are realized.
Research Objective

My research combines molecular, behavioral, and ecological techniques to focus on the nesting ecology of female saltmarsh sparrows. Specifically, I investigated adaptations in nesting behavior of females with respect to nest placement and offspring sex ratio manipulation. I also conducted a management experiment to test the feasibility of artificial habitats to provide flood-free nesting habitat in the face of sea-level rise.

The specific research objectives of my thesis were to:

1. Investigate patterns of nest site selection to determine if saltmarsh sparrow females modify their nesting behaviors based on prior experience.

2. Determine if female saltmarsh sparrows manipulate offspring sex ratios in response to environmental, temporal, or physiological conditions.

3. Present a proof of concept for the utilization of artificial floating habitat islands as a viable management option for the conservation of tidal-marsh sparrows.

Literature Cited


CHAPTER 1

PLASTICITY IN NESTING ADAPTATIONS OF A TIDAL-MARSH ENDEMIC

Abstract

Tidal-marsh birds that nest on the marsh surface are faced with adaptive challenges and a trade-off between flooding and predation pressure. We investigated adaptive responses in nesting behavior of the saltmarsh sparrow (*Ammodramus caudacutus*), an obligate tidal-marsh breeding bird, using 536 nests monitored on four New England marshes from 2011-2015. Using linear mixed effects models, we tested whether structural nest characteristics differed among nests that were successful, predated, or flooded. For females with multiple nesting attempts within the same season, we investigated whether females made changes in nest structure and placement according to the outcome of their previous nesting attempt. Nest characteristics differed among females with different nesting fates. Fledged and predated nests were built higher in the vegetation and in higher elevation areas of the marsh than those that flooded. Successful nests had greater canopy cover and a lower proportion of high marsh vegetation than those that were flooded or predated. Additionally, nest height and elevation differed between consecutive nesting events, consistent with a response to previous experience. Females whose first nesting attempt failed due to flooding constructed subsequent nests higher in the vegetation and in areas of higher elevation than those that were successful in their previous attempt. We found evidence for nest placement fidelity, as 84.5% of females renested between years within a distance smaller than the average core home range area (77m). Females whose nests were predated in their first nesting attempt renested at a greater distance than females whose first nesting attempts were

1 Bri Benvenuti, Jennifer Walsh, Kathleen M. O’Brien, and Adrienne I. Kovach. Manuscript in preparation for *The Auk*
successful. Our findings suggest that saltmarsh sparrows exhibit plasticity in nesting behavior by changing structural nest characteristics and nest placement following a cause-specific nest failure, which may be important for balancing selective pressures in a dynamic environment. This plasticity, however, may be insufficient in the face of increased flooding predicted with sea-level rise.

**Key Words:** Nest site selection, plasticity, saltmarsh sparrow, site fidelity, renesting, tidal marsh

**Introduction**

Nest site selection in birds should be such that it enhances the survival and fitness of offspring, as well as the reproductive success of the parent(s) (Shine and Harlow 1996, Lovich et al. 2014). Accordingly, individuals must balance nest placement, weighing requirements for survival and risks (Hanane 2014). If breeding females are able to both perceive and manage risks to their nesting choices, they may be expected to alter their nesting behaviors based on prior experience. For example, in areas of high nest predation, it may be adaptive to move away from risky sites or make alterations in nest structure to reduce the risk of failure (McAuley et al. 1990, Beckmann et al. 2015). Conversely, by exhibiting fidelity to the same breeding location yearly, one may gain advantages that are positively correlated with breeding success, such as knowledge of food availability and predator densities (Chalfoun and Schmidt 2012). Adaptive responses to multiple environmental factors require that a female learn specific nest site attributes and their vulnerability to specific environmental factors (Marzluff 1988). Multiple studies on nest site selection have found individuals of a variety of other species will use information on their previous breeding success to choose a current breeding site (Gavin and Bollinger 1988, McAuley et al. 1990, Beletsky and Orians 1991, Haas 1998). This informed fidelity for nest site selection
combined with plasticity in nest structure could lead to greater reproductive success (Switzer 1997, Chalfoun and Schmidt 2012).

Nest site selection is directly correlated with reproductive success in tidal marsh nesting birds, which experience high levels of nest failure due to tidal flooding (Storey et al. 1988, Gjerdrum et al. 2005). Associating specific nest site attributes with nesting success may be a learned adaptation, and may be one method of mitigating risks of nest failure in tidal-marsh birds (Gavin and Bollinger 1988, Marzluff 1988). In tidal marshes, water levels fluctuate predictably with the lunar cycle, producing peaks in tide height approximately every two weeks for one to two consecutive days when marshes are flooded almost entirely (Redfield 1972). Tidal marsh specialists have adapted to the challenges of living in this harsh environment, with the trade-off being limited interspecific competition and abundant resources (Greenberg et al. 2006, Reinert 2006). Some adaptive responses of tidal marsh nesting birds directly impact their nesting success, such as placement of nests at a height that exceeds the tides but is low enough to the marsh surface to minimize predation, nest repair or egg retrieval behaviors, rapid post-flood renesting, and timing of nesting attempts to avoid peak seasonal tides (Greenberg et al. 2006, Reinert 2006). Given the strong selection pressure imposed upon tidal-marsh birds by periodic tidal flooding, it may also be adaptive for them to assess risks and respond with plasticity in nesting behavior to increase nesting success (Forstmeier and Weiss 2004).

The saltmarsh sparrow (Ammodramus caudacutus) is a tidal-marsh specialist with reproduction strongly linked to the tidal cycle. Nests that are initiated within three days of a high spring tide are most likely to be successful by avoiding peak tidal flooding (Greenlaw and Rising 1994, Gjerdrum et al. 2005, Shriver et al. 2007). Ground nests are constructed in the marsh vegetation of primarily Spartina patens, S. alterniflora, and Juncus gerardii and located in areas
of higher elevation within the marsh at a height above the mean high water level (Gjerdrum et al. 2005, Shriver et al. 2007). Nest site selection is spatially random with respect to other nesting females (Gjerdrum et al. 2005, Bayard and Elphick 2010), suggesting that structural characteristics of the nest itself may be more important to success than where the nest is located within the preferred nesting habitat (Gjerdrum et al. 2005). While prior research has found vegetation cover characteristics to be important in nest site selection, neither these vegetation characteristics, nor nest height and substrate elevation have been found to consistently influence nest success (Gjerdrum et al. 2005, Humphreys et al. 2007, Shriver et al. 2007, Ruskin et al. 2015).

Nest mortality may be a result of either flooding or predation, suggesting there is a trade-off between flooding and predation risks that might influence nesting behaviors (Greenberg et al. 2006a, Ruskin et al. in review). By nesting higher in the vegetation, a female’s nest is more susceptible to predation, while nesting closer to the marsh surface will increase the likelihood of nest flooding. Further, females may construct a canopy above the nest, which can function in retaining eggs during flooding events and may reduce predation through additional vegetation cover and concealment (Humphreys et al. 2007). Whether females can perceive the mortality risks facing their nests, as well as the characteristics that are associated with these risks, and alter their nesting behaviors in response is unknown.

We investigated characteristics of female nest site selection and sought to determine if females modified their nesting behaviors as a function of prior experience. We collected data on nest characteristics, including location, marsh elevation, and structural features, to address the following questions:
1. **Do nest characteristics differ among nests that are successful and those that fail due to flooding or predation?** We sought to investigate differences in nest site elevation, nest height, canopy presence, and vegetation composition among nests and compared them with ultimate fates of fledged, flooded, and predated. We predicted successful nests would be located in areas of higher elevation and have characteristics that simultaneously minimize the effects of predation and flooding.

2. **Do female saltmarsh sparrows exhibit nest placement fidelity across years?** We aimed to determine if female saltmarsh sparrows returned to the same locations to nest in future years based on the fate of their previous year’s nesting attempt. We hypothesized females would renest within their prior home range core area across subsequent years due to the advantages of local resource knowledge.

3. **Do females make changes in their nest site location and structure based on previous experiences and the outcomes of their prior nesting attempts – whether it failed due to predation or flooding or was successful?** We sought to explore changes in nest placement and structure relative to a female’s prior nesting success. We expected females to alter the location, elevation, and structural characteristics of their nests in a way that would increase nesting success relative to the outcome of their prior nesting attempt. We predicted that females whose nests failed due to flooding would make structural changes to subsequent nests that would mitigate flooding failure, such as an increase in nest height, canopy cover, changes in vegetation composition, or renest in a higher elevation area of the marsh. Furthermore, we predicted that females whose nests failed due to predation would renest at a greater distance from their previous nest, rather than modifying structural characteristics.
Methods

Study area

We conducted intensive monitoring of saltmarsh sparrow nests on four New England tidal marshes during the breeding season (June – August) from 2011-2015. Study sites were located in Stratham, New Hampshire (Chapman’s Landing), Newmarket, New Hampshire (Lubberland Creek Preserve), Wells, Maine (Eldridge Marsh, Rachel Carson National Wildlife Refuge [NWR]), and Newburyport, Massachusetts (Parker River NWR) (Fig. 1.1). The area monitored on each site varied from 10-18 ha. On Chapman’s Landing and Lubberland Creek (11 and 10.5 ha) the study site included the entire marsh. On larger marshes at Parker River and Eldridge Marsh we focused on 18 ha and 15 ha plots, respectively. The sites differed by proximity to the coast and tidal regime: Chapman’s Landing and Lubberland Creek were located more inland within the Great Bay estuary, with a tidal amplitude of 2.7 m, while Eldridge marsh and Parker River were coastal marshes with a tidal amplitude of 3.3 m.

Nest placement and monitoring

Sites were systematically searched for nests 2 to 3 times per week during each of the three annual nesting cycles. Once found, nests were revisited every 3 to 4 days until the nesting attempt was completed. Nests were assigned one of three ultimate nest fates: fledged, failure due to flooding, or failure due to predation, following Gjerdrum et al. (2005). Nests were considered fledged if one individual from the nest reached fledging age (i.e., nests could experience partial failure prior to fledging). Nests were considered to have failed due to flooding if one or more eggs or nestlings were found immediately outside of the nest cup or the nest contents were cold and wet with the female no longer attending the nest. Nests were deemed predated when there
were signs of predatory activity, such as disturbed nests or partial remains of nestlings, and none of the chicks fledged. Females attending nests were captured at the nest with mist nets and uniquely marked with a USGS aluminum leg band, to track multiple nesting attempts from the same individual throughout the breeding season and across years. Nest locations were recorded using a GPS unit (Garmin GPSmap 76Cx). Structural nest measurements of nest height (lip to ground and bottom to ground), canopy presence, percentage of nest cup visible from above, cup depth, and nest exposure (exposed or under vegetation) were recorded upon finding the nest, as they can change with natural disturbances over the life of the nest. Species vegetation composition at the nest was collected upon nest completion to minimize disturbance to active nests and surrounding vegetation. Vegetation composition was recorded as percentage of high marsh vegetation. *Spartina patens, Juncus gerardii,* and *Distichlis spicata* were considered high marsh habitat, while bare ground, open water, and *Spartina alterniflora* were considered low marsh habitat.

In 2015, we used a Trimble TSC3 data logger with Real time kinematic (RTK) R10 Glonass-enabled antenna (Trimble Navigation Limited, Sunnyvale, CA), and CORS base station correction (Keystone Precision, Durham, NH) to determine the surface elevation at found nests. Using these methods, we collected elevation data from 120 nests, including 12 females with >1 nesting attempt, to test for elevational influences on nest fate and changes in nest elevation over repeat nesting attempts. Due to a small sample size of females with multiple nesting attempts whose first nest was predated, we included only females with prior nest fates of fledged and flooded to investigate changes in marsh elevation.

To address hypotheses related to female nest placement across years, we used only nesting attempts from consecutive years. For hypotheses about nest movement within a breeding
season, we used all females with multiple nesting attempts within that breeding season, however, we could not always be certain the nesting attempts were sequential. We used GENALEX 6.5 (Peakall and Smouse 2012) to calculate Euclidean distance between nest locations within and across breeding seasons.

**Statistical Analyses**

Statistical analyses were conducted using R statistical software (R Core Team 2015). We tested for differences in nest structural characteristics (bottom nest height, lip nest height, cup depth, canopy presence, vegetation composition and nest cover (exposure and percent visible) across the three fate categories (fledged, flooded, and predated) using generalized linear mixed models (GLMMs) with assumed normal errors in the R package ‘nlme’ (Pinheiro et al. 2016), with female identity as random effect. First, we used GLMMs to test if nest characteristics differed by site. We found significant effects of location on bottom nest height and canopy presence and therefore included location as a fixed effect covariate in mixed models for those factors.

For questions related to nest elevation, we first tested for site-specific differences in elevation using an ANOVA and Tukey’s highly significant difference test for pairwise differences. We found a significant difference in site elevation for all pairwise combinations except Eldridge Marsh and Parker River, therefore we included site as a covariate in subsequent analyses. We then used a GLMM with nest fate as a fixed effect, female identity as a random effect and nest elevation as the response variable to test for differences in nest fate based on elevation.
To test for changes in nest structure between nesting attempts as a function of nest fate, we used GLMMs with a random effect of female identity, fixed effect of previous nest fate, and response variable of change in nest characteristic measurement. Changes for numerical measurements (nest height, cup depth, vegetation composition, percent visible) were calculated as the difference between measurement 1 and measurement 2. Changes in categorical measurements (canopy presence, exposure) were defined as an increase, decrease, or no change. To determine if females moved to areas of higher elevation in nesting attempts following a failure due to flooding compared to a successful nest, we used change in elevation (elevation nest 2 – elevation nest 1) as the response variable and nest fate as a fixed effect. We assessed the significance of our fixed effect of fate using F-tests and type II sums of squares.

To test for influence of prior nest fate on nest placement fidelity, we used GLMMs with assumed normal errors to test for a relationship of nest fate and distance moved by females between nesting attempts. Models included distance between nesting attempts as the response variable, fate of the first nesting attempt as a fixed effect, and female identity as a random effect for both within year and across year comparisons. Significance was assessed using F-tests and type II sums of squares. To test if females show nest placement fidelity within and across years, we used a one-sided t-test to determine if the mean distance moved was greater than the average diameter of the home range core area of female saltmarsh sparrows (77 m; Shriver et al. 2010).

Results

We located and monitored a total of 556 nests across the four study sites from 2011-2015 (Table 1.1). We assigned fates to 536 nests, of those 393 also had information on the attending
female. We obtained between or within year data from 311 nests with 1-5 repeat nesting attempts from 78 individuals within years and 45 individuals between years.

*Do nest characteristics differ among fledged, flooded, and predated nests?*

Several nest characteristics differed among the fates of fledged, failed, and predated nests. Nest height (bottom to ground) differed across nest fates: successful nests were built lower than predated nests, and flooded nests the lowest ($\chi^2=27.95$, *GLMM*, $P < 0.001$; Fig. 1.2). Nest height (lip to ground) was higher in successful nests than flooded nests, and highest in predated nests ($\chi^2=29.11$, *GLMM*, $P < 0.001$; Fig. 1.2). Nest canopy presence differed across fates ($\chi^2=10.29$, *GLMM*, $P = 0.005$), with fledged nests having significantly greater canopy cover than flooded nests ($t =-3.20$, *GLMM*, $P=0.001$); there was no difference in canopy presence between fledged and predated or predated and flooded nests. The proportion of high marsh vegetation also differed by nest fate ($\chi^2=6.81$, *GLMM*, $P = 0.03$). Predated nests had the greatest proportion of high marsh vegetation, followed by flooded nests, and fledged nests had the least amount of high marsh vegetation (Fig. 1.3). We found no differences in nest exposure (exposed or under thatch), percentage of nest visible, or nest cup depth across fates.

Surface elevation, as measured by RTK data, differed between all pairs of sites except Eldridge Marsh and Parker River ($F = 244.8$, *ANOVA*, $P < 0.001$; Fig. 1.4). Elevation also differed between coastal and inland sites ($F = 545.02$, *ANOVA*, $P < 0.001$), such that coastal sites had higher elevations ($1.54 \pm 0.08$ m) than inland sites ($1.21 \pm 0.05$ m). Fledged nests were located in areas of significantly higher marsh elevation than flooded nests ($\chi^2 = 18.41$, *GLMM*, $P < 0.001$; Fig. 1.4).
Do females exhibit fidelity in their nest placement?

Within and across breeding seasons, we found high fidelity in nesting location. Within a breeding season, 87% of females renested within the diameter of the average female core area; 5% of females moved 78 to 100m, 6% moved 100 to 200m, and 1% of females moved more than 200m from a previous nest (Fig. 1.5). The mean renesting distance (distance between subsequent nesting attempts of the same female) was significantly less than the average home range core area diameter of 77 m ($\bar{x} = 40.5$ m, $t = -9.58$, t-test, $P < 0.001$). Across years, 84.5% of females renested within this core area distance; 5% returned to nest within 78 to 100 m, 7% renested between 100 and 200 m, and only 3.5% renested more than 200 m from the previous year’s nest. The mean renesting distance between years was significantly less than the average core area distance of 77 m ($\bar{x} = 47$ m, $t = -4.76$, t-test, $P < 0.001$).

Do females make changes in their nest site selection and structure based on the outcome of their prior nesting attempts?

Between nesting attempts, there was no difference in marsh elevation for the renesting locations of females whose first nest was successful ($\bar{x} = 0 \pm 0.04$ m), while those whose first nest failed due to flooding renested in locations of higher marsh elevation ($0.04 \pm 0.03$ m) ($\chi^2 = 9.34$, GLMM, $P = 0.002$; Fig. 1.6). Nest height (measured to the bottom of the nest cup) differed between nesting attempts based on the outcome of a female’s previous nesting attempt ($\chi^2 = 6.77$, GLMM, $P = 0.03$). Significant changes in nest height were observed between females that experienced predation and those that were successful ($t$-value = -2.20, $P = 0.04$). Females
that experienced predation in their previous nesting attempt significantly decreased the height of their subsequent nest ($\bar{x} = -4.15$ cm), while those that were successful showed no change in nest height between nesting attempts. Individuals that failed due to flooding did not show a significant change in nest height compared to those that were fledged or predated, however, females increased their nest height an average of 2.6 cm in their next nesting attempt (Fig. 1.7). Similar trends were observed for lip nest height, but were only marginally significant ($\chi^2=5.22$, GLMM, $P=0.07$). We did not find any difference in the changes in canopy presence, vegetation composition, nest cover, or cup depth between nesting attempts for any of the fate categories.

Within years, distances between subsequent nest locations of individual females ranged from 2 to 215 m between nesting attempts (Fig. 1.5). Females renested an average of 42.5 m from their prior nesting attempts when successful, 44 m when flooded, and 66 m when predated. The renesting distance differed significantly between females with fledged and predated prior nesting attempts ($F = 3.02$, $P = 0.05$), but not between flooded and predated prior nesting attempts (Fig. 1.8). Over the 5 years of the study, we monitored 45 females with nesting attempts across years, including one individual that was detected yearly from 2011-2014 (total nests = 195, range = 2 to 6 nests/individual). Across years, the distance between nest locations ranged 4 to 224 m. We found a trend for a larger between year renesting distance for females with prior nest failure (59 m) compared to successful (39.5 m) nests ($\chi^2 = 3.11$, GLMM, $P=0.08$; Fig. 1.9); this pattern was not significant when evaluated across the three specific nest fates of fledged, flooded, or predated ($\chi^2 = 4.32$, GLMM, $P=0.12$).
Discussion

Nest site selection has been well studied in birds, and it has been shown that birds make adjustments to their nest site characteristics to adapt to environmental variation (Burger 1979, Forstmeier and Weiss 2004, Chen et al. 2011, Beckmann and Mcdonald 2016). Nest flooding and predation risks are important selective factors that likely play a role in the evolution of the reproductive strategies in marsh nesting birds (Picman et al. 1993). Saltmarsh sparrows have been associated with tidal marshes for several million years; during this time they have evolved strategies to mitigate flooding risks temporally, by synchronizing nesting to avoid peak inundation periods, rather than choosing nest sites that spatially minimize flooding risk (Rising and Avise 1993, Gjerdrum et al. 2005, Shriver et al. 2007). Our findings suggest that nesting characteristics, including height, canopy cover, and elevation, may also influence nesting success, and that females exhibit plasticity in nesting behavior, which may be important for balancing selective pressures in a dynamic environment.

We found that failed, predated, and successful saltmarsh sparrow nests differed in height, canopy cover and elevation. This contrasts with previous studies that found no relationship between nest structures and nest success, despite strong effects of tidal height on nest flooding probability (Gjerdrum et al. 2005, Shriver et al. 2007, Humphreys et al. 2007, Bayard and Elphick, 2011). We found that successful nests were built higher in the vegetation, had a greater amount of canopy cover, and were located in higher elevation areas of the marsh than those that flooded. Furthermore, successful nests were placed lower in the vegetation than those that were predated but higher than those that flooded, supporting that there is a trade-off between predation and flooding (Greenberg et al. 2006; Ruskin et al. in review). A trade-off between flooding and predation along a gradient of nest height also occurs in the closely related seaside sparrow
(Ammodramus maritimus). Hunter et al. (2016) found that nests located higher in the vegetation had a greater probability of predation and lower probability of flooding, while those located lower in the vegetation had a lower predation probability and higher flooding probability. While optimal nest height may entail a trade-off between predation and flooding, the presence of a nest canopy may confer advantageous against both threats, by providing a structure that prevents egg loss while also conferring concealment (Humphreys et al. 2007).

Elevation has been found previously to influence nest-site selection in saltmarsh sparrows (DiQuinzio et al. 2002) and other tidal marsh nesting species, such as Clapper Rails (Rallus crepitans; Valdes et al. 2016), Nelson’s Sparrows (Ammodramus nelsoni subvirgatus; Shriver et al. 2007), and Willets (Tringa semipamata; Burger and Shisler 1978), which build nests in areas of higher elevation compared to random locations on the marsh. A few centimeters in marsh elevation can make the difference between successful and flooded nests. Our finding that nest elevation differs between successful and flooded saltmarsh sparrow nests indicates that there are subtle elevational differences that influence nesting success within the preferred higher elevation areas of the marsh. This is consistent with the finding that successful nests withstand higher tide heights than those that fail due to flooding (Bayard and Elphick 2011).

Making repairs or changes to nest structure or placement increases the likelihood of success in tidal marsh nesting birds (Burger 1979, Beckmann et al. 2015). We found female saltmarsh sparrows altered their nest placement and structure in subsequent nesting attempts based on the fate of their previous nest. Behavioral plasticity, via adjustments to nest structure and site selection based on immediate environmental conditions, may be important mechanisms for species persistence in the dynamic tidal marsh habitat (Refsnider and Janzen 2012). By exhibiting plasticity in structural nest characteristics following a cause-specific nest failure,
Saltmarsh sparrows may be able to respond to the selective pressure that is stronger at a given time or place, given variation in predation and flooding risks (Ruskin et al. in review). We found changes in nest height, canopy cover, and vegetation composition following a failure due to flooding. Specifically, females that experienced nest flooding increased the height and canopy cover of their nest in successive attempts, thereby adopting behaviors to mitigate flooding, while those that were successful showed no change in height or canopy cover. Females that experienced nest flooding also had a lower proportion of high marsh vegetation in their subsequent nests. High marsh vegetation is relatively simple in structure; nests constructed with a mixture of *Spartina patens* (high marsh) and *Spartina alterniflora* (low marsh) may have greater structural support, better withstand flooding, and be more able to retain overall nest shape during and following flooding events than nests comprised of primarily *S. patens* (Walsh et al. 2016).

Nesting plasticity has been found in two other studies of tidal marsh birds. Diquinzio et al. (2007) found that female saltmarsh sparrows made changes in nest height and vegetation composition following restoration of a tidally restricted marsh, despite no changes in marsh surface elevation. The observed changes in nest height and switch in vegetation composition from *Phragmites australis* to *S. patens*, *S. alterniflora*, and *Distichlis spicata* occurred in the year immediately following tidal restoration, suggesting that saltmarsh sparrows are able to adapt to moderate habitat alteration over a rapid timescale. Hunter et al. (2016) found plasticity in nesting behavior of seaside sparrows in response to variably predictable threat risks. Seaside sparrows nested at lower height in years with high predation risks, but increased nest height following failure due to flooding in years with unpredictable tidal flooding caused by wind events (Hunter et al. 2016).
Plasticity in nesting behavior can also take the form of shifts in habitat selection to areas with a different vegetation composition or different risk of threat, e.g., predation (Chalfoun and Martin 2010). Here we found support for our hypothesis that females who experienced predation in their previous nesting attempt renested at a greater distance than those that were successful or flooded. By renesting farther from a previous nesting attempt, a female may be able find an area with lower predator densities and different vegetation composition, such as taller vegetation or different species, which may increase concealment. In contrast, it may be more beneficial for females that experience nest flooding to renest near their previous nest and make structural changes rather than to renest in a different location, if timing of reproduction in relation to the tidal cycle and nest structure are generally more important than nest placement within the marsh (Shriver et al. 2007).

Females are faced with nest site selection trade-offs across seasons as well. With a limited nesting window, it may be more advantageous for females to spend less time scouting for new nesting locations upon arrival on the breeding grounds and quickly begin nesting using information gained from prior nesting experiences. This informed nest site fidelity would allow them to benefit from awareness of local environmental factors such as food abundance, tidal regime, or predation pressure (Switzer 1997, Chalfoun and Schmidt 2012, Greenlaw and Post 2012). Across years, 84.5% of saltmarsh sparrow females in this study returned to nest within their previous home range core area, with some renesting within a few meters of a previous nest. This high degree of nest-placement fidelity may be informed by prior success in relation to flooding risk, predation pressure, and accessibility to mating opportunities. This high degree of nest-placement fidelity may be informed by prior success in relation to flooding risk and predation pressure. Informed fidelity may also confer reproductive advantages in this highly
promiscuous mating system (Hill et al. 2010), if mate accessibility varies spatially across the marsh.

The rapid rate of global climate change likely limits adaptive genetic changes at a population level (Berteaux et al. 2004, Refsnider and Janzen 2012). Mechanisms occurring at the individual level, however, such as behavioral plasticity, may provide some capacity for adapting to novel environmental effects (Refsnider and Janzen 2012). Plasticity in nesting behavior of saltmarsh sparrows may allow them to quickly adapt to modest changes in tidal regime, habitat loss, and fragmentation. This plasticity, however, is likely insufficient in the face of sea-level rise, which reduces high marsh habitat and modifies tidal regimes that disrupt synchronous breeding of sparrows with the 28-day tidal cycle. The direct impacts of sea-level rise are predicted to reduce the reproductive success of saltmarsh sparrows, which have already declined at a rate of 9% annually from 1998-2012 (Correll et al. 2016), leaving the species vulnerable to extinction within the next 50 years (Bayard and Elphick 2011, Wiest et al. 2016). The apparent adaptive capacity of saltmarsh sparrows, however, may enhance their ability to respond to management interventions targeted to mitigate nest flooding.

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**Literature Cited**


Figures and Tables

Figure 1.1: Locations of the four sites where saltmarsh sparrows nesting data were collected during 2011-2015.
Figure 1.2: Mean height of saltmarsh sparrow nests, as measured from lip of nest cup to ground (A), and bottom of the nest cup to the ground (B) for each nest fate category (fledged, n = 254; flooded, n = 211; predated, n = 54).
Figure 1.3: Percentage of high marsh vegetation within 1m of saltmarsh sparrow nests compared among the three nest fates (fledged, n = 223; flooded, n = 179; predated, n = 45).

Figure 1.4: (A) Mean surface elevation at saltmarsh sparrow nests compared among the four study sites: Chapman’s Landing (CL), Eldridge Marsh (EL), Lubberland Creek (LU), and Parker River (PR) and by nest fate (B) (fledged, n = 74; flooded, n = 32).
Figure 1.5: Distances between subsequent nesting locations of female saltmarsh sparrows within (top) and across (bottom) years; dashed line indicates the 77-m diameter of average female home range core area.

Figure 1.6: Changes in elevation of saltmarsh sparrow nests between subsequent nesting attempts of the same individual female by previous nest fate (fledged, $n = 7$; flooded, $n = 5$). Dashed line indicates no change in surface elevation between nesting attempts.
Figure 1.7: Changes in height of saltmarsh sparrow nests, as measured from bottom of the nest cup to the ground, between successive nesting attempts of the same individual female, compared by fate of the first nest (fledged, $n = 27$; flooded, $n = 52$; predated, $n = 5$). Dashed line indicates no change in bottom nest height between nesting attempts.

Figure 1.8: Distances between locations of saltmarsh sparrow nests for successive nesting attempts of the same individual female by fate of the previous (first) nest (fledged, $n = 29$; flooded, $n = 62$; predated, $n = 7$).
Figure 1.9: Distances between locations of saltmarsh sparrow nests for repeat nesting attempts of the same individual female across years by fate of the previous (first known) nest (fledged, \( n = 35 \); failed, \( n = 22 \)).

Table 1.1: Total number of saltmarsh sparrow nests with assigned fates for four study sites and five years. Percentage of nests for which the female associated with the nest was captured is also shown.

<table>
<thead>
<tr>
<th>Site</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
<th>2015</th>
<th>Total Nests Found</th>
<th>Percentage of Females Captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapman’s Landing</td>
<td>45</td>
<td>52</td>
<td>60</td>
<td>41</td>
<td>39</td>
<td>237</td>
<td>82.7</td>
</tr>
<tr>
<td>Eldridge Marsh</td>
<td>35</td>
<td>33</td>
<td>30</td>
<td>18</td>
<td>32</td>
<td>148</td>
<td>65.5</td>
</tr>
<tr>
<td>Lubberland Creek</td>
<td>--</td>
<td>15</td>
<td>19</td>
<td>13</td>
<td>20</td>
<td>67</td>
<td>65.7</td>
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<tr>
<td>Parker River NWR</td>
<td>--</td>
<td>--</td>
<td>28</td>
<td>34</td>
<td>22</td>
<td>84</td>
<td>66.7</td>
</tr>
<tr>
<td>Total Nests</td>
<td>80</td>
<td>100</td>
<td>137</td>
<td>106</td>
<td>113</td>
<td>536</td>
<td>73.3</td>
</tr>
</tbody>
</table>
CHAPTER 2

ANNUAL VARIATION IN OFFSPRING SEX RATIOS IN SALTMARSH SPARROWS SUPPORTS FISHER’S HYPOTHESIS

Abstract

Evolutionary theory suggests that natural selection should favor the ability of animals to modify the sex ratio of their offspring when the fitness benefits of producing one gender over the other vary in relation to environmental conditions. The saltmarsh sparrow (*Ammodramus caudacutus*) is an extreme habitat specialist that exhibits breeding behavior highly synchronized with the tidal cycle. The harsh environmental conditions of nesting in salt marshes and the unique mating system of the saltmarsh sparrow provide a context for offspring sex manipulation, based on environmental conditions, to favor the sex with the greatest chance of survival or reproduction. We investigated adaptive sex ratio manipulation in this system using a robust sample size across multiple sites and years using a mixed modeling approach. We tested hypotheses about the influence of environmental, temporal, and maternal effects on patterns of sex allocation. We collected data on nest initiation and nestling survival from 370 nests from 210 females 2011-2015 on four marshes in northeastern United States. Using molecular techniques, we determined the sex of 990 offspring and characterized variation in site- and population-level sex ratios. Using binomial linear mixed-effects models, we tested the influence of environmental, temporal, and maternal factors on offspring sex ratios. Across years and sites, we found an even offspring sex ratio of 1.03:1, with an alternating pattern of interannual variation between male

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2 Bri Benvenuti, Jennifer Walsh, Kathleen M. O’Brien, Mark J. Ducey, and Adrienne I. Kovach. Manuscript in preparation for *The Wilson Journal of Ornithology* or *The Auk*
and female bias at both the population and site level. Sex ratios did not vary as a function of timing within the breeding season or in relation to tidal flooding. Offspring sex was also independent of female condition at time of nest initiation. We also found considerable within brood variation in offspring sex ratios with a higher degree of variation than expected under a normal distribution. Our finding of a 1:1 offspring sex ratio and interannual variation in a wild bird population is more consistent with the predictions of Fisher (1930) than those of Trivers and Willard (1973).

**Key Words:** offspring sex ratio, maternal condition, temporal effects, environmental effects, saltmarsh sparrow

**Introduction**

Sex ratio is an important life history trait at both the population and individual levels (Santoro et al. 2015). Offspring sex ratios in particular are known to be affected by both environmental and evolutionary processes (Sheldon 1998, Alonso-Alvarez 2006). Reproductive effort theory states that parents gain a fitness benefit from producing successful sons and daughters, and they should assess the costs and benefits of current and future reproduction (Fisher 1930, Williams 1966, Trivers 1972, Nilsson and Svensson 1996). In avian species, current reproductive investment could include activities directly related to nesting, including finding a territory, copulating, nest building, incubation and care of offspring, as well as physiological processes such as egg production. Future reproductive investment refers to the fitness benefit an individual receives from having successful sons or daughters.
Fisher (1930) postulated that if the costs and benefits of producing males and females were equal, there should be no difference in the number of sons and daughters produced in a population, as equal investment in offspring of both sexes is an evolutionarily stable strategy. However, if the cost or fitness benefit of producing sons and daughters differs, it may be adaptive for parents to manipulate the sex of their offspring (Fisher 1930). Consequently, as this sex-biased fitness benefit leads to the overproduction of one of the sexes, the parents respond by producing more of the rarer sex, as it would result in an increase in lifetime reproductive fitness, with more offspring being recruited into the breeding population. As the adult population sex ratio swings in the other direction, the fitness advantage again shifts to the rarer sex, eventually resulting in an even population sex ratio (Fisher 1930). Trivers and Willard (1973) suggested that natural selection favors females to bias the sex of their offspring in a manner that maximizes parental fitness, by favoring production of the sex with reduced cost and/or higher fitness. Specifically, they predicted that maternal condition directly impacts offspring condition such that as maternal condition changes, the fitness value of the offspring will vary by sex, and adult females will therefore bias offspring production differentially toward the sex with the higher fitness values (Trivers and Willard 1973).

In birds, females are the heterogametic sex and therefore have the potential to control the sex of individual eggs (Pike and Petrie 2003, Alonso-Alvarez 2006, Navara 2013). Advances in molecular sexing techniques have allowed numerous studies to investigate sex allocation in birds (Griffiths et al. 1998, Pike and Petrie 2003, Alonso-Alvarez 2006, Quintana et al. 2008). Multiple studies have found several potential factors to influence sex allocation, such as parental condition (Nager et al. 2000, Whittingham and Dunn 2000, Yamaguchi et al. 2004), laying order (Badyaev et al. 2002, Krebs et al. 2002, Nomi et al. 2015), hatching date (Dijkstra et al. 1990,
Nomi et al. 2015), and food availability (Komdeur et al. 1997, Suorsa et al. 2003). Despite evidence supporting sex-specific allocation in birds, there is a lack of consensus on facultative adjustment of offspring sex ratios. Inconsistent patterns of sex allocation both within and across species make predictions and interpretation of results difficult (Komdeur and Pen 2002, West and Sheldon 2002, Ewen et al. 2004).

The saltmarsh sparrow (Ammodramus caudacutus) has been reported to exhibit a male-biased adult sex ratio with over two males for every female (Greenlaw and Rising 1994, Gjerdrum et al. 2008a), despite no apparent differences in adult survival (Field et al. in press). One explanation for this male-biased adult sex ratio is that it stems, at least in part, from a biased offspring sex ratio, if females are manipulating the sex of their offspring (Hill et al. 2013). Saltmarsh sparrows are a tidal-marsh obligate with reproduction that is strongly linked with the tidal cycle, suggesting a potential role for environmental stressors in driving sex allocation. Environmental stressors may also vary spatially and temporally, due to annual variation and site-specific differences in flooding rates (Ruskin et al. in review) potentially resulting in spatial and temporal variation in sex ratios. Building ground nests on the marsh surface, saltmarsh sparrows experience high levels of nest loss due to flooding (Gjerdrum et al. 2005, 2008b; Shriver et al. 2007, Ruskin et al. in review). Nests that are initiated shortly after high spring tides, which occur approximately every 28 days, are more likely to be successful (Gjerdrum et al. 2005, Shriver et al. 2007). During flooding events, nests are only fully inundated for about 90 minutes during the tidal peak, allowing eggs to survive inundation periods (Gjerdrum et al. 2008b). Older, larger nestlings are able to climb out of the nest and take refuge in the surrounding vegetation to remain above peak water levels during flood tides (Hill et al. 2013). Consequently, if there is a difference in growth rates between the sexes, it may be beneficial for females to produce the
larger/faster growing sex to minimize nestling loss due to flooding. Male nestlings are 31% heavier and grow faster than their female counterparts (Hill et al. 2013). The larger body size of males may better enable them to survive flooding events by reducing the risk of hypothermia and enabling them to climb out of the nest to avoid peak inundation periods (Hill et al. 2013). Because of their greater mass, male nestlings are likely more costly to produce than females, but may be the better investment if they are more likely to survive nest flooding.

Large male nestlings may also have higher lifetime reproductive success than females or smaller male nestlings. Saltmarsh sparrows have a highly polygynous, scramble competition mating system, with nonterritorial males and female-only parental care (Greenlaw and Post 2012). In highly polygynous mating systems, variance in reproductive success is more pronounced, as female reproductive success is limited by the number of eggs she is able to produce, while male success is limited only by the number of eggs he can fertilize (Kempenaers et al. 1997, Whittingham et al. 2002). Female saltmarsh sparrows are multi-brooded but experience a high degree of nest failure. Females typically have one successful reproductive attempt per breeding season, whereas larger males can potentially fertilize many eggs leading to higher than average reproductive success due to the competitive advantage of large body size (Leech et al. 2001, Hill et al. 2010). Nestling body size is influenced by maternal condition (Prince 1998, Nager et al. 1999, Whittingham and Dunn 2000, Whittingham et al. 2002, Brommer et al. 2003). Therefore, a females’ ability to produce a high quality, large son, may be dependent on her condition, and if so, she may face condition-dependent choices in offspring manipulation.

Here we test, with a robust sample size across multiple sites and years using a mixed modeling approach, hypotheses about the influence of environmental, temporal, and maternal
effects on patterns of sex allocation. We build on the prior work of Hill et al. (2013), who found a male-biased offspring sex ratio in Connecticut over two years.

We expected offspring sex ratios would vary as a function of the environment. We predicted deviations from parity in offspring sex ratios based on the extrinsic factors of site, tidal amplitude, precipitation, and year. Site quality has been found to directly relate to female condition with better quality sites producing higher quality females (Stauss et al. 2005). Under this assumption, we hypothesized that sites that are under less environmental stress due to decreased tidal amplitude would have higher quality females. We predicted precipitation would influence site quality and expected drier years to increase site quality. Therefore, we predicted, in accordance with the Trivers and Willard (1973) hypothesis, that sex ratios on good quality sites will be male-biased, under the expectation that good quality females produce a greater proportion of male offspring, due to their competitive advantage in mating and/or their fitness advantage in surviving flooding events in the nest.

We expected the sex ratio of offspring to change throughout the breeding season. We predicted females to produce more male offspring early in the season, when nesting is less synchronized with tidal flooding, as the larger size and faster growth rates of males may increase nestling survival when flooding risk is high. We then expected to observe a switch in offspring sex ratios to produce more female offspring as females become more synchronized with the tidal cycle later in the breeding season as flooding risks become lower for synchronized females.

We also investigated temporal effects of flooding within a nesting cycle, and we predicted that offspring sex ratio would vary based on nest initiation date in relation to the nearest flood tide. We expected that sex differences in nestling growth rates would give larger male nestlings the advantage of being able to leave the nest during peak flooding periods.
Additionally, the probability of nestling survival is negatively correlated with the number of days since a spring tide. We therefore predicted that when a female renests more than three days after the spring tide, more male nestlings would be produced as male nestlings have a faster growth rate than females (Hill et al. 2013).

An individual’s probability of survival and reproduction may be correlated with condition (Trivers and Willard 1973). Body condition may influence the ability to reproduce by affecting territory quality, mate competition, and offspring rearing (Prince 1998, Newton 2004). Here we define condition as a measure of energy reserves, with the assumption that an individual’s energy reserves correlate with performance. Based on the Trivers and Willard (1973) hypothesis, we predicted female saltmarsh sparrows would alter their offspring sex ratio based on body condition, with heavier females producing more male offspring than lighter females.

**Methods**

*Field methods and sample collection*

We monitored saltmarsh sparrow reproduction on four New England tidal marshes: Chapman’s Landing (Stratham, NH), Lubberland Creek Preserve (Newmarket, NH), Eldridge Marsh (Rachel Carson National Wildlife Refuge [NWR], Wells, Maine), and Parker River (Parker River NWR, Newburyport, MA) during the breeding season (June – August) from 2011-2015 (Fig. 2.1). The area monitored on each site varied from 10-18 ha. On Chapman’s Landing and Lubberland Creek (11 and 10.5 ha), the study site included the entire marsh. On larger marshes at Parker River and Eldridge Marsh, we focused on 18 ha and 15 ha plots, respectively. Sites differed in their proximity to the coast and tidal regime: Chapman’s Landing and
Lubberland Creek were located further inland within the Great Bay estuary, with a tidal amplitude of 2.7 m, while Eldridge marsh and Parker River were coastal marshes with a tidal amplitude of 3.3 m.

Systematic nest searching was conducted 2 to 3 times per week at each site during the breeding season, which occurs from June through August with approximately three annual nesting cycles. Once found, nests were revisited every 3 to 4 days until the nesting attempt was completed via fledging or failure. Nests were assigned to one of three nest fates: fledged, failure due to flooding, or failure due to predation. A nest was considered fledged if one individual reached fledging age (Gjerdrum et al. 2005, Ruskin et al. 2016). A nest was considered flooded if nest contents were found outside of the nest cup or nest contents were cold and wet (Gjerdrum et al. 2005). Predation was considered the cause of failure when there were signs of predatory activity, such as disturbed nests or partial remains of nestlings (Gjerdrum et al. 2005). The attending female was captured off the nest using two 12-m, 38-mm mesh, mist nets and uniquely marked with a USGS aluminum leg band and a site-specific color band. Standard morphometric measurements were collected from each female. Clutch initiation dates were calculated using back-counting based on known duration of egg-laying, incubation, and chick development (Greenlaw and Rising, 1994, Gjerdrum et al. 2005, Shriver et al. 2007). All chicks that survived to day 6 were banded with USGS aluminum and site-specific color bands, and a blood sample was taken for molecular sex identification. Failed eggs and chicks both pre- and post-banding were also collected for molecular sex identification in order to maximize the data for full clutches. Eggs were determined to be unviable if there was no evidence of embryo development and thus excluded from analyses. Nest initiation dates were calculated following methods developed by Ruskin et al. (2016) using one of three methods: 1) for nests found during the egg
laying period, we used back-counting based on the number of eggs currently laid (assuming one egg per day); 2) if the nest hatched, we used back-counting based on the estimated age of the chicks post-hatch minus the incubation interval of 12 days and number of eggs in the nest; 3) for nests that failed to hatch, we estimated the average number of days between first egg and when the nests were discovered. We then subtracted the average from the discovery date to determine nest initiation.

Observed daily maximum water levels were retrieved from the National Oceanic and Atmospheric Administration (NOAA) station located in Wells, ME (Station ID: 8419317) for our study site at Eldridge Marsh, in Fort Point, NH (Station ID: 8423898) for Parker River National Wildlife Refuge, and in Squamscott River, NH (Station ID: 8422687) for Chapman’s Landing and Lubberland Creek (Appendix A). Daily maximum water levels were averaged across the breeding season (May – August) for each year. Precipitation data were retrieved from the closest weather stations to our study sites (Wells, ME – NOAA: US1MEYK0022, Durham, NH – NOAA: USW00054795, and Newburyport, MA – Weather Underground KMANEWBU3). Total precipitation was then calculated for the 28 days prior to each nest initiation date.

*Molecular Analyses*

DNA from feathers and embryos was extracted using a Qiagen DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) following the manufacturer protocol. Sex of individual offspring was determined by PCR amplification of the CHD1 gene, using primers 2550F/2718R or P2/P8 following methods developed by Fridolfsson and Ellegren (1999) and Griffiths et al.
(1996). Amplified PCR products were resolved in a 2% agarose gel for visualization by gel electrophoresis. This method is based on a length polymorphism of the variants of the CHD1 gene on the Z and W chromosomes. Due to the size difference of introns on the CHD1-W and the CHD1-Z genes, two fragment sizes are produced in females, and a single fragment in males. Previous research has validated this approach with saltmarsh sparrows (Hill et al. 2013).

**Statistical Analyses**

All statistical analyses were performed in R (R Development Core Team 2015). A binomial test was used to determine if the total number of male offspring produced was different from 50% and to determine if the number of male and female biased broods differed from parity. We used a Shapiro-Wilk normality test to determine if the frequency of brood sex ratios deviated from a normal distribution, which would indicate differential sex allocation among females. All models were constructed as generalized linear mixed effects models (GLMM) in the package lme4. Three sets of binomial GLMMs with a binomial error distribution and a logit link function were created to examine the relationship between predictor variables for environmental effects, temporal effects of flooding, and female condition, with a random effect of female identity, and a response variable of offspring sex (male or female for each individual offspring). We used a fixed effect of nestling weight, random effect of female identity, and nestling sex as the response variable, to test for differences in male and female nestling weights. An information theoretic approach was used for model selection (Burnham and Anderson 2002), where models were considered equivalent if differences in AICc values were < 2.0. We used post hoc analysis of variance (ANOVA) to test for significance of individual variables and interactions.
To evaluate variation in offspring sex ratio as a function of environmental effects, we developed eight models that included singular, additive, and interactive effects of four exploratory variables of year, site, tidal amplitude, and precipitation. Year was included to account for yearly differences in environmental conditions. We also included site based on the inherent differences between our study locations. Tidal amplitude (average maximum observed tide height) was used as a proxy for site quality differences between inland and coastal sites that experience differences in tidal regime. Finally, we included total precipitation values for 28 days prior to nest initiation as precipitation influences overall habitat conditions, saltmarsh sparrow abundance, and likely nesting success (Shriver et al. 2015). All models included a random effect of female identity to control for inherent variation among individual females. The null model consisted of only the random effect of female identity.

We tested for temporal effects of flooding across the breeding season using Julian Day of nest initiation, as well as effects of nest initiation in relation to the nearest flood tide using the number of days the nest was initiated following the highest tide that coincided with the full moon. Predictor variables included singular and additive models of Julian day and site for across breeding season temporal effects; number of days post flood and site for effects of nest initiation for three candidate models for each model set. Models included both female identity and year as random effects. We included year as an additive random effect because year effects were found to be significant in the environmental models described above. Null models included the two random effects.

To evaluate the effects of female condition on offspring sex ratios, we used data from 256 nests and 177 individuals. We first estimated female body condition using a skeletally-corrected mass index (SMI) developed by Pieg and Green (2009) that calculated an SMI score of body
mass relative to a standard size. Under this index, higher mass per size is considered “good condition” (Peig and Green 2009, Borowske 2015). We first assessed the correlation between the female structural measurements of wing cord and tarsus with mass using a standardized major axis regression (SMA) in the package smatr. We determined that wing cord was most strongly correlated with mass ($r^2 = 0.09, P < 0.001$) and produced the SMA regression with the best fit ($b_{SMA} = 3.29$). SMI values ranged from a 15.75 – 25.2 with the mean SMI value of 18.7 ± 1.33.

Models for maternal condition included additive random effects of female identity and year. We included single, additive, and interactive combinations of variables for fixed effects of female SMI score and site, and a null model of only random effects to create four competing models.

We also tested for differences in the number of male and female offspring produced at laying in successful nests and those that failed due to flooding using GLMMs with a binomial response of offspring sex, fixed effect of nest fate, and random effect of female identity.

**Results**

Using the molecular assay, we assigned sex to 990 (88.6%) of 1,117 individuals from 338 nests across all sites and years. Of the 127 that were unassigned, 28 (23%) were due to deteriorated sample quality or ambiguous results and 99 (77%) were eggs determined to be unviable. 104 nests (31%) were missing data from one or more offspring as a result of lost chicks or eggs due to flooding or predation. In total, there were 503 male (50.8%) and 487 female (49.2%) offspring across the five years and four sites, yielding a male to female offspring sex ratio of 1.03:1. This was not significantly different from an even sex ratio (*binomial test*, $P=0.63$).
Offspring sex ratio varied by year with an alternating pattern of male and female bias. We observed a greater proportion of females (43% male) produced in 2014 (binomial test, \( P = 0.03 \)) and a greater proportion of male nestlings (57% male) in 2015 (binomial test, \( P = 0.01 \); Table 2.1). By site, Chapman’s Landing produced more female offspring in 2014 (binomial test, \( P = 0.05 \)), and more male offspring in 2015 (binomial test, \( P = 0.02 \); Table 2.2). These patterns at the Chapman’s Landing site appeared to be driving the overall finding of annual variation in sex ratio. Parker River, Lubberland Creek and Eldridge Marsh all had sex ratios that did not deviate significantly from parity in all years of the study, however they still exemplified a pattern of annual variation although it was non-significant (Table 2.2). When averaged across years, there was no difference in the numbers of male and female offspring produced among sites (Table 2.3). At the brood level, sex ratios varied from 0 (all females) to 1 (all males) across all clutch sizes, with the overall distribution significantly different from the predicted normal distribution (Shapiro-Wilk normality test, \( P < 0.001 \); Fig. 2.2).

A total of 763 nestlings survived to fledging, including those from nests with partial failure. Of the fledged nestlings, 323 (47.5%) were female and 357 (52.5%) were male, for a sex ratio of 1.10:1, which is not significantly different from even (binomial test, \( P = 0.21 \)). Male nestlings were heavier than female nestlings at day of banding (\( \chi^2 = 14.50, \text{GLMM, } P < 0.001 \); Fig. 2.3). Successful nests (those that fledged 1 or more offspring) had a significantly greater proportion of male offspring at laying than nests that failed due to flooding (\( \chi^2 = 4.46, \text{GLMM, } P = 0.03 \); Fig. 2.4).

For the models characterizing environmental effects on offspring sex ratio, the top-ranked model (lowest AICc) included only year and was significantly different from the null model of only the random effect of female identity (\( \Delta AIC_c = 5.9, P = 0.007 \); Table 2.4; Fig. 2.5). Across
all models, year was the only significant variable \((GLMM, P < 0.05)\). Additionally, the model that included both year and tidal amplitude had a \(\Delta AIC_c\) of 1.9, suggesting it was competitive with the model with year only, but the tidal amplitude variable was non-significant. All other competing models had \(\Delta AIC_c\) values that exceeded 2.0.

For models evaluating temporal effects during the breeding season on offspring sex ratio, the null model (random effects of female + year) performed better than all other models, and offspring sex ratio did not vary significantly across the breeding season (\(\Delta AIC_c\) for Julian day = 0.9 vs. Julian day and site = 5.9; Table 2.5). While the model of the single effect of Julian day outperformed the model for Julian day and site, it was not different from the null model based on a \(\Delta AIC_c\) difference of < 2.0. For models evaluating nest initiation date relative to the flood tides, the null model of random effects (female identity + year) was the top performing model (\(\Delta AIC_c\) for days post flood = 1.9; Table 2.6), suggesting no significant effect of nest initiation in relation to flood tides on offspring sex.

For models evaluating the effects of female condition, the null model (random effects of female + year) was the best predictor of offspring sex (Table 2.7). For the model including additive and interactive effect of condition and site, there was a marginally significant interaction between condition and site indicating site may influence female condition (\(\Delta AIC_c = 6.4, \chi^2 = 7.19, GLMM, P = 0.06\)); however, a delta AIC >2 suggested that these variables did not explain sex ratio. All other individual variable effects were non-significant.
Discussion

We found strong support for a 1:1 offspring sex ratio at the population level in four New England saltmarsh sparrow populations averaged across five years of study. Additionally, we detected fluctuations in offspring sex ratio by site and year, with a pattern of alternating annual variation. Previous work by Hill et al. (2013) found a male-biased offspring sex ratio with a male to female ratio of 1.45:1 from a two-year period across 10 coastal Connecticut salt marshes. The observed discrepancy in our finding may be due to differences in sample size, length of study, and data pooled across years and sites. Our larger sample size and longer duration study may have allowed us to better detect longer trend patterns, from which we found support for annual sex ratio manipulation. Additionally, some patterns of variation were masked when data were pooled across sites and years. By analyzing data by site and year, we were able to detect subtle differences within the population including interannual variation.

We found year to be the only environmental variable to explain variation in offspring sex ratios. Sex ratio deviated significantly from even in only two years, but showed an alternating pattern of annual variation in production of male and female offspring from 2011-2015, with male-biased sex ratio trends in three years (2011, 2013, 2015) and female-biased sex ratio trends in two years (2012, 2014). The pattern of interannual variation was observed to varying degrees at all sites (i.e., increases and decreases in annual proportion of male offspring), although the yearly offspring sex ratios were not significantly male or female biased except at Chapman’s Landing in 2014 and 2015. We expected yearly variation in offspring sex ratios due to yearly differences in environmental conditions, such as precipitation and tidal regime. However, the additional variables of precipitation, tidal amplitude, site, and their interactions did not provide any additional support in models predicting offspring sex.
One explanation for the influence of year on offspring sex ratios is Fisher’s (1930) hypothesis that females should produce more of the rarer sex to maintain adult population sex ratio equilibrium. Under this hypothesis, temporal variation in offspring sex ratios would be observed. This is more likely to occur in small, fragmented populations where a substantial proportion of breeding adults return to the local population across years (Harmsen and Cooke 1983, Bensch et al. 1999). The pattern of annual variation was especially pronounced at Chapman’s Landing, a small site that is relatively isolated and has reduced gene flow from other saltmarsh sparrow populations (Walsh et al. 2012) and high numbers of returning breeding adults (AK and BB, unpublished data). In addition, due to its small size, nest detection rates are higher at Chapman’s Landing and sample sizes were the highest among our four sites, likely leading to higher statistical power at the site-level.

We did not detect a relationship between offspring sex ratio and the timing of nest initiation with high spring tides, as male and female offspring were produced at the same rate irrespective of tidal flooding. Saltmarsh sparrow reproduction is strongly linked with the tidal cycle (Gjerdrum et al. 2005, Shriver et al. 2007). We expected nests that were initiated closer to spring tides would have a lower or equal proportion of male offspring, as all nestlings would have an equal probability of survival. Conversely, we predicted nests initiated a greater number of days after peak flooding would produce more male offspring, as these have a decreased probability of success. If nesting was not synchronized with peak inundation due to nest initiation being more than three days following peak flooding, it may be beneficial to produce the larger, faster growing male offspring that could climb above high water levels. The lack of correlation found between nest initiation and spring tides is consistent with the findings of Hill et al. (2013) and suggests females are either unable to adaptively manipulate offspring sex in the
short time period of 2-3 days, or there is no benefit of producing one sex over the other in relation to tidal flooding, despite differences in nestling mass and growth rates.

We expected the sex ratio of offspring to change steadily throughout the season with females producing more male offspring early in the season as the larger size and faster growth rates of males may increase nestling survival. We then expected a switch in offspring sex ratios to the production of more female offspring as females became more synchronized with the tidal cycle later in the breeding season. We found no evidence for seasonal effects on offspring sex ratios. Within season changes in offspring sex ratio have been found in birds as an effect of local food availability (Badyaev et al. 2002, Krebs et al. 2002, Nomi et al. 2015). In tidal marshes, insect communities change seasonally but are abundant and not believed to be a limiting resource; accordingly, saltmarsh sparrows show annual variation in their diets based on prey availability (Post and Greenlaw 2006). Additionally, there has been no evidence of changes in nestling or female body mass across the season, again suggesting local food availability is not a limiting factor in this system (Post and Greenlaw 1982, Hill et al. 2013). If female body condition does not vary throughout the breeding season, females should be able to consistently produce the larger (i.e. male) offspring, consistent with our findings of the absence of seasonal changes in offspring sex ratios.

The Trivers and Willard (1973) maternal condition hypothesis predicts that females should adjust the sex of their offspring according to their own condition when eggs are laid. We found no significant relationship between our measure of female quality and offspring sex. This finding may suggest that there are no condition-dependent fitness differences in saltmarsh sparrow offspring. Alternately, our measure of quality may not have been an accurate indication
of female condition, or the variation in female quality was not sufficient to detect variance among offspring in our population (Leech et al. 2001).

Additionally, we observed differences in offspring sex ratios at the population and the individual brood level with some broods of only female offspring, others of only males, and few broods with equal numbers of male and female offspring. This is again consistent with Fisher’s (1930) prediction, as one would expect a higher degree of variance at the brood level than expected under a normal distribution if females are actively adjusting the sex ratio of their clutch (Fisher 1930, Harmsen and Cooke 1983). We investigated variation in individual broods by examining complete, four egg clutches, as they would allow us to best detect differences in brood sex ratios. We observed a lower proportion of full, four egg clutches with an even sex ratio (31.7%, n=126) than those with a biased offspring sex ratio (female-biased = 41.2%, male-biased = 26.9%). Differences in clutch size and nests with incomplete data due to nest failure make looking at individual variation in brood sex ratios challenging in saltmarsh sparrows. Our finding of a high degree of variation in brood sex ratios combined with an even population sex ratio suggests further investigation into brood level sex ratios in saltmarsh sparrows is needed.

Multiple attempts to quantify adult sex ratios in saltmarsh sparrows have found it to be highly skewed between 1.97 and 2.7 adult males per adult female (Greenlaw and Rising 1994, Gjerdrum et al. 2008a). A male-biased offspring sex ratio would help to explain a male-biased adult sex ratio, however, we found neither a male-biased offspring sex ratio nor evidence for sex-specific nestling mortality that would lead to the observed differences in adult sex ratios. Further, studies have also found no apparent sex differences in adult survival with a mean survival rate of 0.44 for females and 0.49 from males (Field et al. 2016 in press). We used capture data from systematic and targeted trapping of females from our five-year study period to estimate adult sex
ratio. We found the adult sex ratios to be less male-biased than previously reported, with annual mean adult sex ratios ranging from 1.05 to 2.01 males per female. The reduced bias in adult sex ratios in this population is consistent with our findings of an even offspring sex ratio, no evidence of sex-specific nestling mortality, and equal adult survival probabilities. Further, adult sex ratios also display an alternating pattern of annual variation between male and female bias (Table 2.8). The observed annual pattern in adult sex ratios is the opposite of the pattern in offspring sex ratios, such that in years where the adult sex ratio is female biased, more male nestlings are produced and vice versa (Figure 2.6). This supports Fisher’s (1930) prediction that parents should respond to sex-biased differences in adult sex ratios by producing more of the rarer sex.

In conclusion, we found little support for the adaptive modification of offspring sex based on environmental factors or maternal condition as suggested by Trivers and Willard (1973). Our findings of an even population offspring sex ratio, interannual variation in the number of male and female offspring produced, and high degree of variation within individual broods are consistent with the predictions of Fisher (1930).

Acknowledgements

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**Literature Cited**


Figure 2.1: Locations of the four sites where saltmarsh sparrows nesting data were collected for this study during 2011-2015.
Figure 2.2: Distribution of brood sex ratios (proportion male) of saltmarsh sparrows from 338 nests across all clutch sizes from 2011-2015 across four study marshes in New England deviates significantly from the expected normal distribution.

Figure 2.3: Mean weights at day of banding for 432 male and female saltmarsh sparrow nestlings from four New England marshes.
Figure 2.4: Average proportion and 95% confidence interval of the number of male and female saltmarsh sparrow offspring produced at laying by nests that were successful (fledged) and those that failed due to flooding. Values of 0.5 indicate an equal proportion of male and female offspring; values less than 0.5 (dashed red line) indicate a greater proportion of female offspring; and those greater than 0.5 indicate a greater proportion of male offspring.
Figure 2.5: Interannual fluctuations in mean offspring sex ratio of saltmarsh sparrows averaged across four New England study marshes with 95% confidence intervals. A value of 0.50 (dashed red line) indicates an equal proportion of male and female offspring. More male offspring were produced in 2011, 2013, and 2015, and a greater proportion of female offspring were produced in 2012 and 2015. In 2014, sex ratio was significantly female-biased and in 2015 it was significantly male-biased.
Figure 2.6. Patterns of interannual fluctuation of mean adult (red) and offspring (blue) sex ratios of saltmarsh sparrows from 2011 to 2015 across four New England marshes. Values of 0.50 (dashed red line) indicate an equal proportion of male and female offspring. A greater proportion of male nestlings were produced in 2011, 2013, and 2015. There were more adult males on the study plots from 2012-2015, however patterns of interannual variation are present with some years (2013, 2015) being less male biased than others (2012, 2014).

Table 2.1: Offspring sex ratios of saltmarsh sparrows averaged across four study sites for each of five years of the study and results of the binomial test for an even sex ratio. * indicates a significant p-value (<0.05) for the binomial test.

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<td>89</td>
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<td>0.61</td>
<td>0.03*</td>
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Table 2.2: Offspring sex ratios of saltmarsh sparrows by site and year and results of the binomial test for an even sex ratio. * indicates a significant p-value (<0.05) for the binomial test.

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</tr>
</tbody>
</table>
Table 2.3: Offspring sex ratios of saltmarsh sparrows from four study sites averaged across five years with binomial test results for an equal sex ratio.

<table>
<thead>
<tr>
<th></th>
<th>Chapman’s Landing</th>
<th>Eldridge Marsh</th>
<th>Lubberland Creek</th>
<th>Parker River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Broods</td>
<td>168</td>
<td>64</td>
<td>49</td>
<td>57</td>
</tr>
<tr>
<td>Number of nestlings &amp; embryos</td>
<td>477</td>
<td>212</td>
<td>141</td>
<td>160</td>
</tr>
<tr>
<td>Number Males</td>
<td>240</td>
<td>107</td>
<td>72</td>
<td>84</td>
</tr>
<tr>
<td>Number Females</td>
<td>237</td>
<td>105</td>
<td>69</td>
<td>76</td>
</tr>
<tr>
<td>Proportion males</td>
<td>0.503</td>
<td>0.505</td>
<td>0.511</td>
<td>0.525</td>
</tr>
<tr>
<td>p-value (binomial test)</td>
<td>0.93</td>
<td>0.95</td>
<td>0.866</td>
<td>0.580</td>
</tr>
</tbody>
</table>

Table 2.4: Model evaluating variation of offspring sex ratio as a function of environmental effects. Competing models including singular, additive, and interactive effects of four exploratory variables of year, site, tidal amplitude (average maximum observed tide height (m)), and precipitation (total precipitation values for 28 days prior to nest initiation). All models also included a random effect of female identity.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Model P-value vs Null</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>Variable</th>
<th>Parameter Estimate ± SE</th>
<th>Chi Sq</th>
<th>DF</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>0.007</td>
<td>1368.8</td>
<td>--</td>
<td>Year</td>
<td>-0.284 ± 0.25</td>
<td>13.97</td>
<td>4</td>
<td>0.01</td>
</tr>
<tr>
<td>Year¹ + Tidal Amp.</td>
<td>0.015</td>
<td>1370.7</td>
<td>1.9</td>
<td>Year</td>
<td>-0.399 ± 0.25</td>
<td>13.99</td>
<td>4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tidal Amp</td>
<td>0.044 ± 0.21</td>
<td>0.04</td>
<td>1</td>
<td>0.83</td>
</tr>
<tr>
<td>Year¹ + Site</td>
<td>0.045</td>
<td>1374.3</td>
<td>5.5</td>
<td>Year</td>
<td>-0.320 ± 0.26</td>
<td>14.07</td>
<td>4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Site</td>
<td>0.075 ± 0.20</td>
<td>0.44</td>
<td>3</td>
<td>0.93</td>
</tr>
<tr>
<td>Null Model (female random effect)</td>
<td>--</td>
<td>1374.7</td>
<td>5.9</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Tidal Amp.</td>
<td>0.846</td>
<td>1376.6</td>
<td>7.8</td>
<td>Tidal Amp</td>
<td>-0.041 ± 0.21</td>
<td>0.04</td>
<td>1</td>
<td>0.85</td>
</tr>
<tr>
<td>Precip.</td>
<td>0.474</td>
<td>1376.7</td>
<td>7.9</td>
<td>Precip</td>
<td>-0.010 ± 0.014</td>
<td>0.51</td>
<td>1</td>
<td>0.47</td>
</tr>
<tr>
<td>Year¹ + Precip. + Year * Precip.</td>
<td>0.102</td>
<td>1378.1</td>
<td>9.3</td>
<td>Year</td>
<td>-0.048 ± 0.88</td>
<td>13.78</td>
<td>4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Precip</td>
<td>0.041 ± 0.14</td>
<td>0.40</td>
<td>1</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Year*Precip</td>
<td>-0.051 ± 0.15</td>
<td>0.28</td>
<td>4</td>
<td>0.99</td>
</tr>
<tr>
<td>Year + Precip. + Tidal Amp. + Year * Precip.</td>
<td>0.145</td>
<td>1380.0</td>
<td>11.2</td>
<td>Year</td>
<td>0.027 ± 0.88</td>
<td>13.81</td>
<td>4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Precip</td>
<td>0.043 ± 0.14</td>
<td>0.39</td>
<td>1</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tidal Amp</td>
<td>0.060 ± 0.22</td>
<td>0.07</td>
<td>1</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Year * Precip</td>
<td>-0.053 ± 0.15</td>
<td>0.31</td>
<td>4</td>
<td>0.99</td>
</tr>
<tr>
<td>Site</td>
<td>0.954</td>
<td>1380.3</td>
<td>11.5</td>
<td>Site</td>
<td>0.047 ± 0.19</td>
<td>0.33</td>
<td>3</td>
<td>0.95</td>
</tr>
</tbody>
</table>
Table 2.5: Models for within season variation in offspring sex ratio. Competing models included singular and additive effects of Julian day and site. All models included additive random effects of female identity and year.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Model P-value vs Null</th>
<th>AIC_c</th>
<th>ΔAIC</th>
<th>Variable</th>
<th>Parameter Estimate ± SE</th>
<th>Chi Sq</th>
<th>DF</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null model (Year + female random effect)</td>
<td>--</td>
<td>1372.4</td>
<td>0</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Julian Day</td>
<td>0.29</td>
<td>1373.3</td>
<td>0.9</td>
<td>Julian Day</td>
<td>-0.004 ± 0.00</td>
<td>1.12</td>
<td>1</td>
<td>0.29</td>
</tr>
<tr>
<td>Julian Day + Site</td>
<td>0.823</td>
<td>1378.3</td>
<td>5.9</td>
<td>Julian Day</td>
<td>-0.004 ± 0.00</td>
<td>1.16</td>
<td>1</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Site</td>
<td>0.065 ± 0.19</td>
<td>0.40</td>
<td>3</td>
<td>0.94</td>
</tr>
</tbody>
</table>

Table 2.6: Competing models for variation in offspring sex ratio as a function of nest initiation date in relation to the nearest spring tide. Models included singular and additive effects of the total number of days a nest was initiated following a flood tide. All models included additive random effects of female identity and year.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Model P-value vs Null</th>
<th>AIC_c</th>
<th>ΔAIC</th>
<th>Variable</th>
<th>Parameter Estimate ± SE</th>
<th>Chi Sq</th>
<th>DF</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null model (Year + female random effect)</td>
<td>--</td>
<td>1372.4</td>
<td>0</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Days Post Flood</td>
<td>0.722</td>
<td>1374.3</td>
<td>1.9</td>
<td>DaysPostFlood</td>
<td>0.007 ± 0.02</td>
<td>0.13</td>
<td>1</td>
<td>0.72</td>
</tr>
<tr>
<td>Days Post Flood + Site</td>
<td>0.973</td>
<td>1379.9</td>
<td>7.5</td>
<td>DaysPostFlood</td>
<td>0.007 ± 0.02</td>
<td>0.13</td>
<td>1</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Site</td>
<td>0.064 ± 0.20</td>
<td>0.37</td>
<td>3</td>
<td>0.95</td>
</tr>
</tbody>
</table>
Table 2.7: Models evaluating the effects of maternal condition on offspring sex ratio included singular, additive, and interactive effects of female condition and site. All models included additive random effects of female identity and year.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Model P-value vs Null</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>Variable</th>
<th>Parameter Estimate ± SE</th>
<th>Chi Sq</th>
<th>DF</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null Model (Year + female random effect)</td>
<td>--</td>
<td>1026.6</td>
<td>0</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Condition</td>
<td>0.787</td>
<td>1028.5</td>
<td>1.9</td>
<td>Condition</td>
<td>0.063 ± 0.25</td>
<td>0.07</td>
<td>1</td>
<td>0.79</td>
</tr>
<tr>
<td>Condition + Site + Condition * Site</td>
<td>0.369</td>
<td>1033.0</td>
<td>6.4</td>
<td>Condition</td>
<td>0.121 ± 0.07</td>
<td>0.06</td>
<td>1</td>
<td>0.80</td>
</tr>
<tr>
<td>Are Site</td>
<td>5.298 ± 3.44</td>
<td>0.15</td>
<td>3</td>
<td>0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condition*Site</td>
<td>0.369</td>
<td>1033.0</td>
<td>6.4</td>
<td>Condition</td>
<td>0.121 ± 0.07</td>
<td>0.06</td>
<td>1</td>
<td>0.80</td>
</tr>
<tr>
<td>Site</td>
<td>0.065 ± 0.23</td>
<td>0.19</td>
<td>3</td>
<td>0.98</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.8. Sex ratios of adult saltmarsh sparrows (ASR) for four New England study marshes in each of five years of this study. A value of 0.50 indicates a 1:1 male to female ratio. Values less than 0.50 indicate a female bias and those greater than 0.50 indicate a male bias. * indicates a significant p-value (<0.05) for the binomial test

<table>
<thead>
<tr>
<th>Years</th>
<th>ASR</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
<th>2015</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapman’s Landing</td>
<td>2011-2015</td>
<td>0.51</td>
<td>0.50</td>
<td>0.51</td>
<td>0.48</td>
<td>0.57</td>
</tr>
<tr>
<td>Eldridge Marsh</td>
<td>2011-2015</td>
<td>0.60</td>
<td>0.46</td>
<td>0.64</td>
<td>0.71</td>
<td>0.62</td>
</tr>
<tr>
<td>Lubberland Creek</td>
<td>2012-2015</td>
<td>0.56</td>
<td>NA</td>
<td>0.57</td>
<td>0.53</td>
<td>0.64</td>
</tr>
<tr>
<td>Parker River</td>
<td>2013-2015</td>
<td>0.66</td>
<td>NA</td>
<td>NA</td>
<td>0.62</td>
<td>0.67</td>
</tr>
<tr>
<td>Mean ASR</td>
<td>2011-2015</td>
<td>--</td>
<td>0.48</td>
<td>0.57</td>
<td>0.58</td>
<td>0.63</td>
</tr>
<tr>
<td>All Sites</td>
<td>2011-2015</td>
<td>0.60</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Total Adults</td>
<td>--</td>
<td>--</td>
<td>94</td>
<td>298</td>
<td>187</td>
<td>151</td>
</tr>
<tr>
<td>Number Males</td>
<td>--</td>
<td>--</td>
<td>45</td>
<td>193</td>
<td>108</td>
<td>106</td>
</tr>
<tr>
<td>Number Females</td>
<td>--</td>
<td>--</td>
<td>49</td>
<td>105</td>
<td>79</td>
<td>45</td>
</tr>
<tr>
<td>p-value (binomial test)</td>
<td>--</td>
<td>--</td>
<td>0.75</td>
<td>&lt;0.001*</td>
<td>0.04*</td>
<td>&lt;0.001*</td>
</tr>
</tbody>
</table>
CHAPTER 3

FLOATING TO RECOVERY: CAN ARTIFICIAL FLOATING HABITAT ISLANDS MITIGATE NEST FLOODING IN TIDAL-MARSH NESTING BIRDS?³

Abstract

Obligate nesting birds of tidal marshes are severely threatened by the impacts of rising sea levels on salt marsh ecosystems. Changes in vegetation, loss of nesting habitat, and increased tidal inundation will reduce, if not eliminate, the reproductive ability of marsh-nesting birds, such as the saltmarsh sparrow. Conservation actions are needed in the very near-term to identify solutions to mitigate nest flooding and maintain breeding populations until habitat is created in the longer term by accelerated marsh migration or other habitat restoration efforts. Creation of artificial habitat islands offers such a potential short-term management action. We tested the efficacy of artificial habitat islands for maintaining flood-free high marsh nesting habitat for saltmarsh sparrows. We installed four 4 ft. x 8 ft. floating island rafts, vegetated with *Spartina patens* and *Spartina alterniflora* in a marsh pool on Rachel Carson National Wildlife Refuge in Wells, Maine. Islands were monitored through the breeding season and winter. The islands remained free of tidal inundation and supported vegetation growth and expansion, suggesting that floating habitat islands hold promise as a method for mitigating nest flooding in tidal-marsh-nesting birds.

**Keywords:** tidal-marsh birds, floating habitat island, saltmarsh sparrow, resource supplementation

³ Bri Benvenuti, David M. Burdick, Kathleen M. O’Brien, and Adrienne I. Kovach. Manuscript in preparation for Ecological Engineering or Journal of Environmental Management
Introduction

Resource supplementation through artificial habitats and breeding sites has become a common conservation practice in the management of wildlife species that face limiting resources and variable environments (Overton et al. 2015). Artificial habitats and nesting structures to enhance reproductive opportunities have been particularly successful in several avian species including cavity nesting passerines and colonial waterbirds (Willner et al. 1983, Quinn et al. 1996, Shealer et al. 2015). Artificial habitats provide an appealing management alternative for vulnerable species and declining habitats, because they can provide results faster than the time required to restore natural habitats.

Tidal marsh ecosystems are in need of conservation solutions that may be provided by artificial habitats. Tidal marshes have been subjected to natural and anthropogenic stressors since the early 1800s that have led to changes in tidal regime as well as habitat loss and fragmentation, and they will continue to face future threats from sea-level rise (Morris et al. 2002, Gedan et al. 2009). Tidal-marsh endemics face the challenge of intermittent flooding of their critical habitat. In tidal marshes, water levels fluctuate in a predictable manner with peak inundation periods, flooding marshes almost entirely (Armstrong et al. 1985, Bertness and Ellison 1987, Odum et al. 1995). Birds that nest in this environment have developed a suite of adaptations to minimize nest flooding, including synchronizing nesting with the lunar cycle and elevating nests above the marsh surface (Reinert 2006). However, less predictable flooding events are becoming more common as storm systems are coupled with daily tidal fluctuations to produce higher and longer than average flooding events (Wong et al. 2014), thereby limiting the effectiveness of reproductive adaptations and affording the need for management intervention to increase breeding success of vulnerable species.
One of the most vulnerable species reliant on this ephemeral tidal-marsh habitat is the saltmarsh sparrow, with reproduction that is strongly linked to the tidal cycle (Greenlaw and Rising 1994, Shriver et al. 2007). Saltmarsh sparrows are limited to coastal marshes along the Atlantic seaboard and are a species of conservation concern by the International Union for Conservation of Nature (IUCN) Red List. They construct ground nests an average of 11.6 cm from the marsh surface in the high marsh vegetation of *Spartina patens, S. alterniflora,* and *Juncus gerardii,* and these nests are highly susceptible to failure due to flooding from tidal inundation (Gjerdrum et al. 2005). Saltmarsh sparrow populations are in imminent danger, with populations declining at a rate of 9% annually (1997-2012), and continued declines are expected with further loss of high marsh habitat (Correll et al. 2016). Additionally, sea-level rise will directly impact reproductive success by reducing the number of flood-free days on the marsh, increasing nest flooding rates, and leaving the species vulnerable to extinction within the next 50 years (Bayard and Elphick 2011, Correll et al. 2016, Wiest et al. 2016). Consequently, immediate management solutions are needed to mitigate nest flooding and enhance nesting success of saltmarsh sparrows to ensure the species persistence.

Viable management solutions for enhancing saltmarsh sparrow reproduction must be achievable within a short time frame due to the rapid species decline. While the natural response of salt marshes to sea-level rise is landward migration, urbanized coastlines have dramatically reduced or eliminated the opportunity for inland migration (Morris et al. 2002, Gedan et al. 2009, Wong et al. 2014). The current rates of marsh migration are slow. A study of marsh migration along the Delaware Estuary from 1930 to 2006 found marshes expanded inland at a rate of 0.54 m/year (Smith 2013). However, the loss of salt marsh due to erosion is approximately 3 meters per year, approximately 5.5 times greater than the amount gained by inland migration (Phillips
1986, Smith 2013). Recent work along coastal Connecticut also found few indicators of inland marsh migration with low mortality and high growth rates of trees in the surrounding forests, indicating inland marsh migration is likely to proceed too slowly in the near future to provide significant habitat replacement for that lost to sea-level rise (Field et al. 2016a). Hence, the loss of coastal forests in the migration process is decoupled from the loss of lower marsh habitat (Smith 2013, Field et al. 2016a) and ultimately a timescale that is relevant to conservation of tidal-marsh birds. This suggests that artificial habitats may prove to be a better option than waiting for marsh migration to occur or other restoration options due to the immediacy of the habitat improvement (Overton et al. 2015). As such, artificial habitat islands that float as rafts on the water’s surface present a promising management tool. Floating habitat islands have been used to successfully increase the nesting habitat and provide a flood-free refuge for common loon (Gavia immer; Desorbo et al., 2008), black tern (Chlidonias niger; Shealer et al., 2015), and California clapper rail (R. obsoletus obsoletus; Overton et al., 2015), another tidal-marsh obligate. For saltmarsh sparrows, providing salt marsh habitat that does not sustain tidal flooding at nest height levels may increase nesting success and enhance reproductive rates. Floating habitat islands may thereby provide short-term population support, allowing species persistence until the effects of longer-term management actions, such as assisted marsh migration or thin-layer sediment deposition, are realized.

Here we present a proof of concept for the utility of artificial floating habitat islands as a management option for the conservation of saltmarsh sparrows and other tidal-marsh birds. Our aims were to determine if 1) saltmarsh vegetation growth could be supported in a high salinity, hydroponic environment; and 2) floating islands would remain flood-free at saltmarsh sparrow nest-height level for a complete nesting season.
Methods

Pilot Study 2014

In 2014, we created a pilot floating habitat island constructed from simple materials and established marsh vegetation. This island was constructed with a 10 foot by 5-foot frame of 2-inch PVC pipe with an overlay of plastic garden fencing; closed-cell polyethylene tubes were added along the main supports for additional floatation. A layer of wrack was added on top of the fencing as additional substrate for the vegetation. Vegetation for the island was collected from the marsh site from pieces of vegetated peat that had broken off during winter storms. Two primary species of marsh vegetation, *Spartina patens* and *Spartina alterniflora*, were collected and peat was trimmed to a thickness of 4 cm to reduce the overall weight of the island. Overall approximately 50 square feet of vegetation was collected and placed directly on the fencing and wrack substrate (Fig. 3.1). The island was placed in a shallow, marsh pool and anchored with cinderblocks attached at each corner with 10 feet of rope, such that the island would avoid hitting the pool edges when moved by the wind. Water depth within the pools fluctuated between 20 and 100 cm (2014) depending on weather and tide conditions.

The pilot island was deployed on July 22, 2014 on the north side of Furbish Road on Rachel Carson National Wildlife Refuge (NWR) (Wells, ME). The island was monitored weekly from July through September, and then monthly from October to May for vegetation survival and island buoyancy. Additional monitoring was conducted during peak spring tides (August 8-14, 2014) to monitor the islands for flooding at nest height. During these events, wooden dowels with Thermochron iButton temperature data loggers (Maxim Integrated, San Jose, CA) attached at 0, 5, 10, 15, and 20 cm were placed on the island and a reference location with similar vegetation characteristics adjacent to the pool to determine if the island sustained tidal flooding.
at critical nest height. A pair of temperature data logging iButtons were deployed in the water and above maximum tide height as controls to record pool water and ambient temperatures. A dowel covered in chalk was also placed on the island and adjacent to the pool to corroborate maximum water levels.

**Proof of Concept 2015**

In 2015, we constructed four islands following a design created by Biohabitats Incorporated (Streb 2012), with slight modification. These 4 foot by 8 foot islands were created using 2x2 cedar, 2-inch poly-flow filter media (Americo Manufacturing Company Inc., Acworth, GA), and 0.75-inch aperture geo-grid stabilization fabric. For floatation, we used 3-inch foam-core PVC instead of 1L plastic bottles used by Streb (2012). Each island was vegetated with approximately 150 2-inch plugs of either *Spartina patens* or a combination of *S. patens* and *Spartina alterniflora* (75:25) planted directly into the filter fabric. Vegetation was purchased from American Native Plants (Perry Hall, MD) and New England Wetland Plants (Amherst, MA). Once the islands were deployed, two anchors were placed on opposite corners using rope and cinderblocks. Water depth within the pools ranged 60 to 120 cm and salinity levels within the pools ranged 28-31 ppt, depending on weather and tide conditions (Fig. 3.2).

The floating habitat islands were deployed in two adjacent pools on the south side of Furbish Road on Rachel Carson NWR (Wells, ME) on May 21, 2015. Weekly monitoring occurred from May 2015 – September 2015, and monthly monitoring occurred from October 2015– June 2016, as described above. Due to plant loss from early season drought conditions and lack of saltwater acclimation, vegetation was replanted twice between June and August 2015. Vegetation growth was successful for plants that were first acclimated to gradual increases in salinity prior to planting, by raising the salinity during watering by ~5 ppt weekly until 25 ppt.
Additional monitoring was conducted during peak fall tides (September 24 – October 15, 2016) to monitor the islands for flooding at nest height. We used Thermochron iButton temperature data loggers (Maxim Integrated, San Jose, CA) attached to wooden dowels at 0 and 10 cm on each of the four islands and a reference location with similar vegetation characteristics adjacent to the pool to determine if the island sustained tidal flooding at critical nest height. An additional temperature data logging iButton was deployed above maximum tide height as a control to record ambient temperature.

**Results**

**Pilot Study 2014**

Maximum recorded water level was 12 cm on the island and 27 cm at the marsh control. iButton dataloggers indicated the island did not experience flooding at nest height: iButtons at nest height recorded temperatures consistent with ambient (1-22°C), while those at ground level recorded temperatures consistent with the water temperature (9-22°C) (Fig. 3.3). At the end of the 2014 growing season the vegetation produced seeds and appeared to be thriving. The island remained floating and free of tidal inundation through December 2014. It experienced freezing within the pool from January through March 2015.

Spring observations found the island to have reduced buoyancy and experience daily inundation. This likely resulted from the extensive snow cover and freezing temperatures experienced over winter. The freezing and thawing also resulted in the loss of the majority of the wrack, which provided substrate, and its removal allowed water to move through the garden fencing. Despite the reduced buoyancy, in the spring of 2015 the vegetation appeared healthy
and was greening up. There were no direct observations of wildlife use, however several feathers and feces were found on the island during the fall of 2014 indicating use by waterfowl.

**Proof of Concept 2015**

To date, the islands deployed in 2015 have been free of any tidal inundation, are fully buoyant, and are supporting vegetation growth and expansion, including colonization by tidal marshes species that were not planted (*Atriplex patula* and *Salicornia spp.*). The greatest challenge faced was the growth and survival of vegetation in a hydroponic environment. Drought conditions in June 2015 caused the loss of approximately 75% of the vegetation. Replanting was successful and by the end of the growing season, plants were producing seeds and new shoots. Winter observations showed the islands were not damaged by winter storms or freezing. Through the spring and summer of 2016, the vegetation greened up, sent out new shoots, and appeared similar to that of the surrounding marsh, indicating the species are able to survive in a hydroponic environment. However, the height of the new vegetation growth appeared to be stunted. This was likely due to drought conditions that resulted in higher than normal salinity levels within the pools.

iButtons temperature data at nest height (10 cm) on the islands corroborated with the ambient air temperature (-2 - 40°C). iButtons located on the surface of the islands remained consistent with the air temperature (-2 - 40 °C). Deviations from ambient temperature were observed with the control at ground level and nest height (-3 - 35°C) (Fig. 3.4)
Discussion

Saltmarsh restoration and management has become common practice (Gedan et al. 2009, Kirwan and Megonigal 2013). It is expected in the coming years that tidal-marsh obligate species will become reliant on continual conservation actions of restoration and population level support as sea levels rise (Erwin et al. 2006, Overton et al. 2015). The effects of restoration are often time-lagged, and conditions may never return to ideal (Zedler and Callaway 1999, Elphick et al. 2015). One common method of marsh restoration includes restoring tidal flow to remove invasive Phragmites australis and increase sedimentation (Roman and Burdick 2012). This method of restoring tidal marsh habitat has not been found to create suitable nesting habitat for tidal-marsh birds, but rather to increase nest failure rates immediately following restoration activities (Diquinzio et al. 2002, Elphick et al. 2015). While current restoration practices are helpful in restoring habitat at large spatial scales over an extended time period, they currently do not provide habitat improvement across a timescale that is relevant to species conservation.

The results of our proof of concept study suggest that floating habitat islands could provide the critical flood-free habitat needed to sustain populations of declining tidal-marsh birds, while allowing the maintenance of ecosystem services of salt marshes. While further research is needed to evaluate the use of the islands by nesting saltmarsh sparrows, we have demonstrated here that they can support saltmarsh vegetation that remains free of tidal flooding at nest height. Our island design was on a small scale (4 ft. x 8 ft.); however, we believe the small spatial scale of the islands will not be a limiting factor for application of this approach, as saltmarsh sparrows have been observed using small, natural islands within the marsh (B. Benvenuti, pers. obs.). Saltmarsh sparrows are non-territorial and often nest within close proximity to one another (Shriver et al. 2010), suggesting that even small habitat islands might
be used by multiple nesting females. Bayard and Elphick (2012) found no evidence of saltmarsh sparrow response to conspecific density cues to promote colonization of marsh patches, suggesting habitat selection strategies are likely responsible for settlement. The creation of a vegetation composition on habitat islands that replicates ideal nesting habitat, as we demonstrated, would likely promote use of artificial habitat islands by saltmarsh sparrows and other tidal-marsh nesting birds. If it is desirable to have a larger artificial island, we would recommend rafting several islands of the original size together to reduce the challenges related to changes in the overall design, availability of materials, and increase in buoyancy. Island size may be limited by the maximum dimensions of the polyflo filter fabric (1m by 3m maximum) in an effort to avoid seaming two pieces of fabric together. One could also seek alternative planting substrates that are available in larger dimensions such as those developed by Biohaven Technology (Shepherd, MT, USA). We also recommend planting a high density of well-established *S. patens* and *S. alterniflora* and acclimating the plants to local salinity conditions to reduce plant die-off and shorten the time to optimal habitat conditions.

As sea levels increase, tidal flooding will continue to reduce the reproductive success of tidal-marsh birds, particularly the saltmarsh sparrow, leaving the species with very low reproductive success and vulnerable to extinction within this century (Hodgman et al. 2015, Shriver et al. 2015, Correll et al. 2016, Wiest et al. 2016). The creation of supplemental habitat, free of flooding, as we’ve demonstrated here, could help alleviate reproductive failure, which is critical for the long-term persistence of tidal-marsh obligate species.

**Acknowledgements**

We would like to thank W. Feurt of Rachel Carson National Wildlife Refuge for his continued support of this project. We thank C. Streb at BioHabitats Incorporated for allowing open use of
his island design and insights in construction and troubleshooting, and D. Anderson at New England Wetland Plants for assistance with vegetation. We also thank B. Flemer, L. Natola, S. Clements, L. Maxwell, and D. Surrell for help with island construction and deployment. Funding for this project was provided by the United States Fish and Wildlife Service, Region 5 Division of Refuges and the New Hampshire Agricultural Experiment Station.

**Literature Cited**


Figure 3.1: Construction and deployment of 2014 pilot island. (1) Sample of vegetation with peat harvested from local marsh. (2) Island PVC frame with plastic fence netting. (3) Addition of closed-cell polyethylene tubes and wrack substrate. (4) Netting folded over edged of wrack to limit removal of wrack substrate from the island by wind. (5) Fully vegetated island and anchoring cinderblocks at time of deployment.
Figure 3.2: Construction and deployment of four floating habitat islands in 2015. (1) Construction of island frames and insertion of capped PVC tubes for flotation; (2) Attaching top and bottom frames of islands; (3) Planting vegetation into the filter fabric mat; (4) Deploying island into marsh pool at Furbish Marsh, Rachel Carson NWR; (5-8) Images of vegetation density and plug size at deployment.
Figure 3.3: Ibutton temperature logger data collected from the pilot floating habitat island during peak tidal period in October 2014. Ibbuttons were placed at ground level (0 cm) and at nest height (20 cm) on both the island and corresponding high marsh land location. Additional ibbuttons were placed in the pool water and at ambient temperature (80 cm), as controls. Both island (solid orange line) and land nest height (dashed orange line) temperatures were consistent with the ambient temperature, indicating they did not experience tidal flooding. At the ground level, island temperatures (solid green line) were more consistent with ambient temperatures while the land ground temperatures (dashed green line) tracked more closely to the water temperature, indicating that the island did not sustain flooding at the ground level but the surrounding high marsh did experience flooding.
Figure 3.4: Ibutton temperature logger data collected from the four 2015 floating habitat island during peak tidal period from September 24 through October 15, 2016. Ibuttons were placed at ground level (0 cm) and at bottom nest height (10 cm) on all of the islands and comparable high marsh land location. Additional ibuttons were placed in the pool water and at ambient temperature (80 cm), as controls. All island nest height and ground temperatures were consistent with the ambient temperature, indicating they did not experience tidal flooding. At the ground level, marsh control iButton temperatures were generally less consistent with ambient temperatures, suggesting they experienced periodic flooding. Similarly, the nest height control iButton (on the marsh) differed from the ambient temperature during periods of peak inundation. This suggests flooding was absent on the islands while the surrounding high marsh did experience periods of inundation.
CONCLUSION

Tidal marshes are a unique ecosystem that experiences high degrees of environmental stress. As a result, tidal marshes have some of the highest levels of vertebrate endemism in the world, making them an ideal system to study questions of evolutionary ecology (Greenberg et al. 2006c). Tidal-marsh birds are particularly vulnerable to marsh loss because they are specialist species in an anthropogenically modified habitat that is experiencing rapid changes in environmental stressors. In this thesis, I focused on the saltmarsh sparrow, a species that is currently recognized by the International Union for the Conservation of Nature (IUCN 2012), the North American Bird Conservation Initiative (Roseberg et al. 2014), and multiple state agencies as a species of conservation concern (USGS 2014). The direct impacts of sea-level rise and low reproductive success from increased nest flooding rates leave the species vulnerable to extinction within the next 50 years (Correll et al. 2016) and a prime candidate for listing under the Endangered Species Act (USFWS 1973). By characterizing adaptations in the nesting abilities of this tidal-marsh obligate bird, I discovered vital information about their vulnerability and plasticity to future climatic events. I used a combination of molecular, behavioral, and ecological techniques with the overarching goal of investigating whether saltmarsh sparrows have adaptations in their nesting abilities that enable them to respond plastically to environmental conditions and prior experience. Additionally, I experimented with the use of artificial floating habitat islands as a management option to mitigate the effects of sea-level rise on nesting success.

Understanding female nest site selection and response to prior experience allows an assessment of their vulnerability and adaptive potential to rapid environmental change. I found support for plasticity in nesting behavior in saltmarsh sparrows, which may be important for
balancing selective pressures in a dynamic environment. Additionally, I identified key structural
nest characteristics – nest height, canopy cover, and elevation – that influence nest success.
Specifically, successful nests were built higher in the vegetation, had a greater amount of canopy
cover, and were located in higher elevation areas of the marsh than nests that failed due to
flooding. My findings support a trade-off between the selective pressures of predation and
flooding, as successful nests were built lower in the vegetation than those that were predated, but
higher that those that flooded. Elevational differences between successful and flooded nests,
identified by high resolution RTK data, indicated that subtle differences in surface elevation
within the high marsh zone differed between successful nests and those that failed due to
flooding.

Structural nest characteristics also differed according to the fate of a female’s prior
nesting attempt, suggesting that females can assess their prior nesting behaviors and make
adaptive changes based on experience. I observed changes in the structural characteristics of nest
height, canopy cover, as well as surface elevation and vegetation composition at the nest
following a failure due to flooding. Females showed an increase in flood resistant nest
characteristics by increasing canopy cover, including a greater proportion of low marsh
vegetation species, increasing nest height, and moving to areas of higher surface elevation
following a nest failure due to flooding.

I found support for cause-specific changes in nesting location within years. Females that
experienced predation in their previous nesting attempt moved farther in subsequent attempts
than those that were successful or flooded. I also found that females exhibited a high degree of
fidelity in the placement of their nests both within a breeding season and across years. Within a
breeding season 87% of females, and across years, 84.5% of females returned to nest within the
average female home range core area diameter (77 m; Shriver et al. 2010). The observed site fidelity is likely beneficial over time as females become aware of local resources and environmental factors related to reproductive success. The benefits of local knowledge combined with a limited nesting window may make it advantageous for females to minimize the time spent scouting for new nesting locations and rather to quickly begin nesting in an area that is already familiar to them.

The harsh environmental conditions of nesting in salt marshes provide a context for offspring sex manipulation. My findings of an even population offspring sex ratio, interannual variation in the number of male and female offspring produced, and high degree of variation within individual broods are consistent with the predictions of Fisher (1930). I tested a number of hypotheses about environmental, temporal, and physiological effects on offspring sex ratio and found year to be the only variable with a significant explanatory effect. Offspring sex ratios displayed a strong pattern of interannual variation, with more male offspring produced in some years and more female offspring produced in alternating years. The yearly variation in offspring sex ratios tracked yearly changes in adult sex ratios at both the population and site level. This is consistent with Fisher’s (1930) hypothesis that females should produce more of the rarer sex to maintain adult sex ratio equilibrium over time.

We did not detect a relationship between offspring sex ratio and our measures of tidal synchrony or maternal effects. This lack of correlation between tidal synchrony and nest initiation is consistent with the findings of Hill et al. (2013) and suggests that females are either unable to adaptively manipulate offspring sex, or there is no benefit of producing one sex over the other in relation to tidal flooding, despite differences in nestling mass and growth rates. From our test of the Trivers and Willard (1973) maternal condition hypothesis, we did not detect a
relationship between female condition and offspring sex. This suggests that there are no condition-dependent fitness differences in saltmarsh sparrow offspring.

Saltmarsh sparrows exhibit adaptations in their nesting behavior through offspring sex ratio manipulation and plastic responses in nest construction. This apparent plasticity may afford the species the potential to adapt to small environmental changes; however, the large-scale impacts of sea-level rise will likely create conditions beyond the adaptive potential of the species in the near future. Therefore, conservation actions are needed in the very near-term to mitigate nest flooding and maintain breeding populations until nesting habitat conditions can be restored in the longer term.

I demonstrated a proof of concept for the feasibility of artificial habitat islands in maintaining flood-free high marsh nesting habitat for saltmarsh sparrows. I created four 4 ft. x 8 ft. floating island rafts vegetated with *Spartina alterniflora* and *Spartina patens*. Islands were monitored through two breeding seasons and winter, during which they remained free of tidal inundation and supported vegetation growth and expansion. The success of the islands demonstrates that artificial habitat islands are a viable management tool that may help mitigate reproductive failure due to nest flooding. The biggest challenge of using islands as a management tool will be attracting the target species. Saltmarsh sparrows are unlikely to respond to traditional methods of colonization such as the use of calls and decoys as the species does not respond to conspecific density cues (Bayard and Elphick 2012). I recommend placing 5-10 islands in areas with high densities of nesting sparrows in areas that are most likely to experience marsh degradation in the coming years. Fully developed islands should also be placed prior to large-scale restoration activities to mitigate any immediate changes in hydrology that may increase nest failure. I also recommend that placement of artificial habitat islands not be limited
to pools. I suggest additional trials of using habitat islands on areas of the marsh that undergoing conversion from high marsh to low marsh or have experienced complete loss of vegetation. Artificial habitat islands as a management tool will likely be critical for the long-term persistence of tidal-marsh obligate species while helping to maintain the ecosystem services of salt marshes through nutrient cycling.

To conclude, I have provided insight into the nesting adaptations of saltmarsh sparrows and a potential management option to enhance reproduction through nesting habitat supplementation. Our finding of an even population offspring sex ratio contributes to knowledge about the life history of saltmarsh sparrows and suggests further investigation into the causes of mortality following fledging to better understand survival at different life stages. Knowing that saltmarsh sparrows exhibit plasticity in their nest site location and structural characteristics over a short timescale will allow land managers to better target tidal marsh restoration strategies by having a better understanding of the response time saltmarsh sparrows have to environmental changes. During times of large scale restoration activities, such as thin layer deposition, the strategic placement and use of floating habitat islands may provide a beneficial strategy for maintaining local populations until the impacts of the larger scale habitat restoration effort can be realized. While the outlook for saltmarsh sparrows in the next 50 years is bleak, continued monitoring of nesting success and adaptations, along with creative management options, may help slow population declines until marsh migration expands habitat and large scale restoration efforts are achieved.
Literature Cited


IUCN. 2012. International Union for Conservation of Nature (IUCN)


USGS. 2012. Species of Greatest Conservation Need lists by state. Swap-analysis.appspot.com
APPENDIX A

SUPPLEMENTARY TABLES AND FIGURES FOR VALUES OF PRECIPITATION AND NESTLING GROWTH RATES

Table A.1. Total monthly precipitation (cm) and average tide height as mean high water (MHW) per year from May – August for each of four study marshes. Tide height data for Great Bay marshes (Chapman’s Landing and Lubberland Creek) were calculated using a NOAA correction factor of 0.75 from the Portland, Maine tidal gauge.

<table>
<thead>
<tr>
<th>Squamscott River, NH (8422687)</th>
<th>Chapman’s Landing, Lubberland Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portland, ME * 0.75</td>
<td></td>
</tr>
<tr>
<td></td>
<td>May</td>
</tr>
<tr>
<td>2011</td>
<td>2.26</td>
</tr>
<tr>
<td>2012</td>
<td>2.22</td>
</tr>
<tr>
<td>2013</td>
<td>2.26</td>
</tr>
<tr>
<td>2014</td>
<td>2.29</td>
</tr>
<tr>
<td>2015</td>
<td>2.17</td>
</tr>
<tr>
<td>AVERAGE</td>
<td>2.24</td>
</tr>
</tbody>
</table>

| Wells, ME (8419317)            | Eldridge Marsh                       |
|                                |                                     |
|                                | May     | June   | July   | August | Average MHW (m)   |
| 2011                           | 2.92    | 2.93   | 2.91   | 2.94   | 2.93              |
| 2012                           | 2.86    | 2.98   | 2.92   | 2.90   | 2.92              |
| 2013                           | 2.91    | 2.96   | 2.95   | 2.90   | 2.93              |
| 2014                           | 2.95    | 2.92   | 2.90   | 2.92   | 2.92              |
| 2015                           | 2.80    | 2.85   | 2.95   | 2.95   | 2.89              |
| AVERAGE                        | 2.89    | 2.93   | 2.93   | 2.93   | 2.92              |

Fort Point, NH (8423898)        Parker River
Figure A.1: Mean weights by age at banding of saltmarsh sparrow nestlings, showing difference in male and female nestling growth rates. Male nestlings achieve greater weights by age compared to female nestlings.
APPENDIX B

INSTUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC) APPROVAL

University of New Hampshire
Research Integrity Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

22-Jul-2010

Kovach, Adrienne I
Natural Resources & The Environment, Rudman Hall
Durham, NH 03824

IACUC #: 100605
Project: Saltmarsh Sparrow Metapopulation Dynamics and Response to Stressors, including Mercury Contamination
Category: D
Approval Date: 14-Jul-2010

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladis Porschke, UNH Health Services.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,
Jessica A. Bolker, Ph.D.
Chair

cc: File
    Bebbitt, Kimberly
University of New Hampshire

Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

26-Jun-2013

Kovach, Adrienne I
Natural Resources & The Environment, Rudman Hall Rm G87
Durham, NH 03824

IACUC #: 130604
Project: Ecology, Genetics and Conservation of Saltmarsh and Nelsons Sparrows
Category: D
Approval Date: 19-Jun-2013

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

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If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

[Signature]

Jill A. McLaughy, Ph.D.
Chair