

Testing the Role of Social Cues in Saltmarsh Sparrow Habitat Selection Decisions

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ABSTRACT

The saltmarsh sparrow *Ammodramus caudacutus* is a species of national and global conservation concern that is threatened by its limited breeding range and vulnerability to sea-level rise. Despite detailed studies of its nesting habitat, our ability to predict this species' distribution remains deficient. Several lines of evidence suggest that these sparrows may combine social information with their assessment of the physical environment in order to select nesting habitat, yet the way in which birds integrate these disparate types of information is not understood. To resolve this uncertainty, I investigated how conspecific social cues may influence breeding habitat selection. My research indicates that nesting activity is more strongly related to cues describing total sparrow activity than to those specifically related to breeding activity, such as male song or female provisioning behavior. Although this result suggests that sparrow abundance could be a reliable cue of habitat quality, experimental manipulations of apparent sparrow densities indicate that saltmarsh sparrows do not use conspecific attraction either to select breeding sites within marshes, or to select which marshes to settle in. In addition, although previous accounts have described saltmarsh sparrows as semi-colonial, spatial tests of aggregation failed to detect any evidence for non-random patterns in nest placement, consistent with the hypothesis that nest placement is random with respect to other nests and that females are not attracted to settle near other nesting females. Finally,

because nest flooding is a major cause of nest failure for this species and is not generally well understood, I studied the mechanics of nest flooding. During 2007-2009, all but 28 of 191 nests sampled were flooded at least once. Some nests, including those that produced young, were flooded up to 10 times within the nesting cycle. On average, the maximum tide height at which nests did not flood differed between successful nests and those that failed due to flooding by just 5 cm. When I modeled nest fate using variables related to tide height and nest timing, the top performing models all included variables related to tidal metrics. This suggests that avoidance of flooding is likely a major component of habitat selection decisions.

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Dedicated to my parents,
Pete and Mary Schneider

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INTRODUCTION

How animals select habitat and distribute themselves in space has fundamental consequences for their demography, ecology and evolution. Habitat selection, thus, has been well studied, yet our ability to predict species distributions remains mixed, suggesting there is much to be learned (Scott et al. 2002). Behavioral studies indicate that social cues can critically influence avian settlement patterns (Hildén 1965; Stamps 1994; Danchin et al. 2004; Ward and Schlossberg 2004), yet the way in which birds incorporate this information into their habitat selection decisions is not well understood. Integrating this knowledge with other aspects of habitat selection provides a clear opportunity to develop a comprehensive model for understanding fine-scale distribution patterns.

Habitat Selection

In migratory birds, the behavioral process of habitat selection can be divided into the search phase and the settlement phase (Fletcher 2006). During the search phase, individuals may either return to their natal site (inexperienced breeders), past breeding site (experienced breeders), or disperse to a new site. For those dispersing to new locations, habitat quality – features that contribute to the growth, survivorship, and production of offspring (Greene and Stamps 2001) – must be assessed. Important habitat quality cues might include ecological features such as the size of potential habitat areas, relative isolation from other suitable habitats, the characteristics of the matrix habitat, structural vegetation features, access to food and cover, and protection from predators. In addition to physical features, decisions regarding nest-site location may incorporate

information on past breeding experience, conspecific reproductive success in the area, and access to mates. Habitat quality cues operate over a wide range of scales, making the study of the behavioral process of habitat selection necessarily complex.

Conspecific Attraction

Birds selecting breeding sites should choose in ways that enhance their ability to find suitable mates and raise young. Both the time constraints involved in the initiation of breeding attempts and the high cost of nesting in poor quality habitat should favor the use of strategies that reduce the costs of sampling the environment (Doligez et al. 2004).

Although relying on personal information such as past breeding success or natal experience (Switzer 1993; Davis and Stamps 2004) to make settlement decisions may be the least costly approach, individuals inhabiting unpredictable environments, first-time breeders, failed breeders, and dispersing individuals must acquire substantial information to assess potential breeding areas (Doligez et al. 1999; Reed et al. 1999). One potential strategy for inexperienced breeders or dispersing individuals is to prospect in potential breeding habitats during the post-breeding season, gathering information about conspecific breeding density and local reproductive success (Reed et al. 1999), thereby reducing costs of pre-breeding season sampling.

Individuals that base their settlement decisions upon the presence or density of conspecifics employ the strategy of conspecific attraction (Kiestner 1979; Shields et al. 1988; Stamps 1988; Stamps 1991; Boulinier and Danchin 1997; Reed 1999; Ward and Schlossberg 2004; and see review in Danchin and Wagner 1997). A key benefit of this approach is that the presence of conspecifics in potential settlement areas represents the

integration of many social and environmental factors, whereas ecological cues of habitat quality may change over the course of the breeding season or be difficult to sample (Brewer and Harrison 1975). The use of conspecific density as a cue may therefore minimize search costs by reducing the need to sample the environment, and can be an effective strategy if conspecifics are an honest indicator of habitat quality (Stamps 1994). Theoretical modeling of habitat selection strategies supports this idea, suggesting that conspecific attraction during the searching and settlement phases may result in increased survival and fecundity, respectively, with increased fecundity driven by the aggregation of individuals in quality habitat (Fletcher 2006). This result challenges the customary expectation that individual fitness declines with increased density (Brown 1964; Fretwell and Lucas 1970). If conspecific attraction is widespread in animal populations, it would have significant implications for both habitat selection theory and conservation practice.

Public Information

For individuals engaged in the process of habitat assessment, cues of fine-scale resource availability and reproductive activities are highly valuable types of information.

Although cues of conspecific density can be insightful in this regard, the behavior of conspecifics as they engage in daily activities and interact with the environment is potentially a much richer resource. In fact, use of this inadvertently produced public information (*sensu* Valone and Templeton 2002) has been demonstrated empirically in the process of habitat selection by breeding birds, where individuals use information about local reproductive success to inform their subsequent settlement decisions (Danchin et al. 1998, 2004; Doligez et al. 1999, 2003; Pärt and Doligez 2003; Parejo et

al. 2007). The use of public information has also been tested widely in studies of avian foraging ecology (see review in Galef and Giraldeau 2001). These and other studies (Boulinier and Danchin 1997; Doligez et al. 2004b; Betts et al. 2008) demonstrate that some birds are not only able to distinguish between more and less successful areas based on public information concerning brood size and quality, but that they retain this information and employ it during habitat selection decisions in subsequent years. The use of this type of public information can enhance fitness when individuals copy the habitat choices of successful breeders (Danchin et al. 2004).

Model System: Saltmarsh Sparrow

Many animals use a combination of environmental and social cues when deciding where to settle, but separating the importance of these influences can be difficult. The saltmarsh sparrow *Ammodramus caudacutus* provides an ideal system for testing the role of social cues because it is a non-territorial and socially promiscuous species and thus does not face limits imposed by pair bonds or territorial behavior. It is also an obligate saltmarsh specialist and nests in grassland-like stands of tidal marsh vegetation that make detection of nests relatively straightforward. Observation of behaviors such as flights, male displays, singing, perching, chasing, and provisioning are uncomplicated by visual barriers, although ground level movement and interactions are frequently obscured. Moreover, nesting cycles and nest failures are often synchronized with tidal phase (Gjerdrum et al. 2005; Shriver et al. 2007), making detection of cues related to specific reproductive activities relatively straightforward.

The saltmarsh sparrow is currently considered a species of conservation concern in the states of New Hampshire, Connecticut, New York, and Delaware. It is also recognized nationally (*Redlist*; American Bird Conservancy 2007) and globally (IUCN: *Vulnerable*; BirdLife International 2009) as a species of concern and has been identified by Partners in Flight (an international cooperative partnership for bird conservation efforts) as a species in need of immediate conservation action (Rich et al. 2004). The entire global breeding range of this species is contained within the narrow band of tidal marsh present from coastal Maine to Virginia; up to half of the global breeding population is estimated to breed in southern New England (Dettmers and Rosenberg 2000). A lack of comprehensive surveys throughout the species' range makes estimation of global population size difficult; however, recent preliminary estimates put the population size in the range of ~ 30,000 – 50,000 individuals, with an estimated 5,000 breeding in Connecticut (Elphick et al. 2009).

Members of my lab have studied the saltmarsh sparrow since 2002 (Elphick et al. 2005; Gjerdrum et al. 2005, 2008a, 2008b; Humphreys et al. 2007; Hill et al. 2010). Although sparrow occurrence is closely tied to vegetation type (Greenlaw and Rising 1994; Gjerdrum et al. 2005, 2008a), breeding season abundance varies considerably, both within and between marshes, and only a small portion of this variation can be attributed to habitat characteristics (Gjerdrum et al. 2005, 2008a). Compelling evidence also suggests that the species engages in habitat prospecting and post-breeding exploration: (i) in the spring, small numbers of singing birds occur in marshes where no breeding appears to subsequently occur, (ii) a post-breeding influx of hatch year birds has been observed in

marshes with no apparent breeding, and (iii) a small number of between-marsh movements have been noted from banding studies (Elphick et al. 2005).

Research Summary

A systematic treatment of potential social cues and their influence on behavior is needed to distinguish between the potentially confounding effects of environmental and social factors. My research integrates developing ideas about the role of social information cues with conventionally recognized ecological cues to build on our understanding of habitat selection in saltmarsh sparrows. The primary goals were to:

1. Identify and characterize potential social cues reflecting reproductive success in a non-territorial avian system and determine the strength of the relationships between these cues and local nesting activity.

Context: If social cues relating to conspecific behaviors are proximate measures used by birds to determine habitat quality, these cues and local reproductive success should show a significant, positive relationship for the use of these cues to persist over evolutionary time.

2. Characterize female nest placement patterns within marshes and determine whether females place their nests near other nesting females.

Context: Interactions among conspecifics can affect how animals settle and distribute themselves once they have selected a habitat. I specifically address the use of social cues in the nest-site selection process by studying how nests are distributed within marshes, the relationship between nest placement patterns and

the underlying habitat structure, and the role of public information in determining re-nesting attempt locations.

3. Test whether conspecific attraction is used during breeding habitat selection by performing experimental audio broadcasts of sparrow vocalizations in marshes with both high and low sparrow densities.

Context: If selection of breeding habitat is influenced by the presence or density of conspecifics, artificial enhancement of apparent conspecific density should attract saltmarsh sparrows into experimental plots. By conducting this experiment in both known, occupied, saltmarsh sparrow breeding habitat and in seemingly suitable but unoccupied or low-density marshes, I address the possible use of conspecific attraction in two distinct contexts of the breeding habitat selection process.

4. Finally, in light of its importance for nest success, I studied the mechanics of nest flooding in this system. I quantified (i) the frequency and duration of nest flooding events, (ii) the relative tide heights associated with nest flooding versus non-flooding, and with lethal flooding events versus non-lethal flooding events, and (iii) modeled the effects of various tide and timing variables on nest fate.

Context: Because nest flooding is the primary factor influencing nesting success, its avoidance is likely to influence settlement decisions. However, detailed understanding of exactly how flooding affects success is lacking, making it difficult to interpret settlement decisions in the context of nest flooding. In addition, documenting the extent of nest flooding experienced under current sea

levels is critical to understanding the magnitude of the threat posed to saltmarsh sparrow persistence by sea-level rise.

Implications

The importance of social cues in habitat selection decisions has powerful implications for conservation, restoration and species management. Recent experimental work has demonstrated that artificially produced social cues can be effective in restoring endangered territorial songbirds to suitable habitat (Ward and Schlossberg 2004). This finding warrants further consideration; if unoccupied areas are not inherently unsuitable, but are instead deficient in social cues, what role, if any, should unoccupied areas play in our approach to land conservation? To understand the potential value of unoccupied habitat areas to wildlife species persistence we must first identify the mechanisms that promote colonization of habitat patches.

Although the specific applied questions concerning habitat use were an important motivation for this research, there are also important theoretical implications. Traditional theoretical approaches to habitat selection, including use of the ideal free distribution (Fretwell and Lucas 1970), habitat suitability indexes (Kahl et al. 1985), and hierarchical models (Kristan and Scott 2006), have generally overlooked the positive role of conspecific attraction (Stamps 1994; see review in Ahlering and Faaborg 2006).

Stamps (1994) and others (Reed 1999; Blumstein and Fernandez-Juricic 2004) have suggested that a greater understanding of the behavioral process of habitat selection and settlement is needed to improve our theoretical and practical understanding. My research addresses this need using a systematic approach, allowing me to distinguish

between the potentially confounding effects of the physical environment and social factors. The results of this work serve to broaden our conceptual understanding of habitat selection behavior and animal distribution patterns, as well as help to advance conservation and restoration science.

Statement Concerning Use of Animal Subjects

All bird banding activities for this project were conducted under my advisor, Dr. Chris Elphick's, Federal master banding permit (# 22664), and State of Connecticut banding permit (# 0207012). My work with this and other saltmarsh avian species has been approved and authorized by the Institutional Animal Care and Use Committee (IACUC protocols # A05-024 and A08-024).

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CHAPTER 1: EXPLORING THE RELATIONSHIP BETWEEN NESTING ACTIVITY AND POTENTIAL
BEHAVIORAL CUES IN THE SALTMARSH SPARROW *AMMODRAMUS CAUDACUTUS*

ABSTRACT

Although studies of avian social cue use in the habitat selection process are becoming increasingly common, the range of possible behaviors that could potentially act as cues for a given species, is not generally explored in a systematic manner. In this study I characterized a number of saltmarsh sparrow behaviors that could act as cues of reproductive activity, and test whether different measures of sparrow nesting activity are associated with these behavioral cues. Environmental and temporal variables were incorporated into all models to simultaneously address how sparrow behavior varies according to conditions such as time of the breeding season, temperature, and wind speed. The results of this work indicate that behavioral cues indicating the total number of sparrows are more strongly predicted by nesting activity than are cues that specifically reflect local breeding activity, such as male song or female provisioning behavior. This result suggests that density related indicators may serve as a useful cue of local reproductive activity and thus habitat quality. If sparrows use these cues during habitat selection, one would expect them to be attracted to habitats where a high number number of conspecifics occur and avoid those with low density populations. By allowing the relationships between reproductive parameters and behavioral activity to point us towards cues that are actually associated with nesting activity, we can now move forward with experimental tests of social cue use, focusing specifically on density-related cues.

INTRODUCTION

Individuals selecting breeding habitat should choose among patches in ways that enhance their ability to find suitable mates and raise young (Hildén 1965). Both time constraints and the high cost of breeding in poor quality habitat should favor the use of strategies that reduce the costs of sampling the environment (Stamps and Krishnan 2005) and habitat selection strategies should thus be under strong selective pressure (Martin 1993).

Relying on private information such as past breeding success or natal experience to make settlement decisions may be the least costly approach in terms of time and energy expended (Switzer 1993; Davis and Stamps 2004). However, animals inhabiting unpredictable environments, first-time breeders, failed breeders, and dispersing individuals must acquire substantial information to assess potential breeding areas (Doligez et al. 1999; Reed et al. 1999). A greater understanding of the behavioral processes involved in habitat assessment and settlement decisions is thus needed to improve our theoretical and practical understanding of habitat selection.

Recent work in behavioral ecology has explored the idea that birds may use social information cues such as the presence, density, or performance of conspecifics as an indicator of habitat quality (e.g., Fisher and Fisher 1969; Reed and Oring 1992; Danchin et al. 2004; Ward and Schlossberg 2004; Fletcher 2006). A key benefit of using social cues is that the presence and behavior of conspecifics at a particular locale represents the net effect of many social and environmental factors, whereas other cues of habitat quality may change over the course of the breeding season, be difficult or time-consuming to sample (Brewer and Harrison 1975), or interact in a complex multivariate way. Use of social cues that have already integrated relevant information can thus be an important

time-saving practice, particularly for animals such as migratory birds that must commence breeding in a timely manner.

The use of conspecific cues in avian habitat selection decisions has been demonstrated in two distinct but related ways. Settlement in response to conspecific presence or density has been shown through experimental manipulations of population densities. This has been achieved by deploying conspecific decoys and broadcasting cues such as bird song in suitable or unsuitable habitats in an attempt to elicit dispersal into density-enhanced areas; birds that respond positively to these density cues are said to use conspecific attraction (e.g., Kress 1983; Ward and Schlossberg 2004; Nocera et al. 2006). Alternatively, settlement in response to conspecific behavioral cues pertaining to local reproductive success (public information, *sensu* Valone and Templeton 2002) has been demonstrated by manipulating reproductive parameters such as brood size and provisioning rates and tracking the subsequent dispersal and settlement into the “fitness enhanced” areas (e.g., Pärt and Doligez 2003; Parejo et al. 2007). Evidence of cues associated with conspecific density, or of reproductive success functioning to attract individuals to settle into particular areas, has begun to challenge the theoretical underpinnings of habitat selection behavior. Rather than conspecifics acting purely as competitors and repelling potential settlers (e.g., Fretwell and Lucas 1970), we must also now consider ways in which conspecific attraction and cueing in the settlement process can positively influence species distribution patterns (Stamps 1988; Wagner and Danchin 2003; Fletcher 2006).

Past studies of conspecific cues have generally focused on a narrow set of behaviors that are likely to serve as important sources of information about conspecific

density or reproductive success (e.g., brood size, Aparicio et al. 2007; male song frequency, Betts et al. 2008). Subsequent hypothesis tests have thus been limited to behaviors that researchers deem to be important to birds engaged in habitat assessment. However, the range of behaviors that could potentially be used as informational cues is largely unexplored. If social information cues are proximate measures used by birds to determine habitat quality, there should be a significant relationship between the level of reproductive activity in the vicinity and the frequency of particular behaviors (cues). In other words, some cues should increase in frequency when individuals are engaged in successful production of offspring (e.g., an increase in the number of provisioning females) whereas others should prevail in times of widespread failure, such as occurs after catastrophic storm events or widespread predation (e.g., increased frequency of display behaviors as birds seek to re-mate).

Many animals use a combination of environmental and social cues when deciding where to settle, but separating the importance of these influences can be difficult. By exploring these questions in the saltmarsh sparrow *Ammodramus caudacutus*, a non-territorial species in which males and females mate with multiple partners (Hill et al. 2010) and do not form pair bonds (Greenlaw and Rising 1994), we were able to concentrate on the relationship between sparrow nesting activity and social cue prevalence without the potentially complicating factors of territoriality or mate defense. Although the primary intent of our study was to look at the relationship between the frequency of different behaviors and measures of local reproductive activity, it is also necessary to understand how the occurrence of behaviors varies according to conditions unrelated to reproductive success as this could affect their usefulness as cues. Therefore,

an important secondary aspect of our study was to quantify the relationships between temporal/environmental variables and the prevalence of different sparrow behaviors. For example, a certain amount of variation in the frequency and occurrence of breeding behavior is expected to result from temporal factors such as the time of day and the phase of the breeding season, as well as changing environmental conditions such as temperature or precipitation.

In this study, we modeled the total number of nests, as well as the number of nests in the incubation and nestling phases, as explanatory variables in a series of models predicting different aspects of sparrow behavior and abundance. Using this approach, we sought to identify specific sparrow behaviors that might be useful cues of local nesting activity for prospecting sparrows. Although our study was designed to identify any and all possible associations between sparrow behaviors and nesting activity, we had several specific predictions about the possible ways in which reproductive activity might be related to sparrow behavior. Because tidal flooding associated with the lunar cycle is the primary cause of nest failure for saltmarsh sparrows (Gjerdrum et al. 2005; Shriver et al. 2007), and many nests never reach the nestling stage (Chapter 4), we predicted that the number of nests with chicks would determine the frequency of behaviors involving female care of nestlings, and would be negatively associated with male mate attraction behavior such as song rates and display. In addition, we expected sparrow behavior to vary in relation to the lunar tidal cycle, with birds becoming more active in the days following the new moon when many individuals are re-nesting (Shriver et al. 2007).

METHODS

Study System

The saltmarsh sparrow is an obligate saltmarsh specialist and nests in grassland-like stands of vegetation associated with the high marsh zone (Greenlaw and Rising 1994). Females are solely responsible for nest site selection and parental care, and place nests at random with respect to the placement of other nests (Bayard and Elphick 2010; Chapter 2). Although sparrow occurrence is closely tied to vegetation type (Greenlaw and Rising 1994; Gjerdrum et al. 2005), breeding season abundance varies considerably, both within and between marshes, and only a small portion of this variation can be attributed to habitat characteristics (Gjerdrum et al. 2005, 2008). Tidal flooding is a major cause of nest failure in this species regardless of nesting substrate (Gjerdrum et al. 2005; Shriver et al. 2007; Chapter 4), suggesting that even within marshes dominated by high-marsh habitat, there might be particular areas that are more or less favorable due to their propensity to flood. If differentiation among high-marsh vegetation types is an inadequate cue of flooding risk, social cues provide a reasonable alternative hypothesis for explaining how sparrows decide where to settle at the local level.

Behavioral research on saltmarsh sparrows is aided by the lack of visual barriers in the marsh; observation of behaviors such as flights, male sexual displays, singing, perching, chasing, and provisioning is straightforward, although ground level movement and interactions are frequently obscured by the dense marsh vegetation. Detection of nests is also relatively simple and most nests can be found early in the nesting cycle (Gjerdrum et al. 2008; Bayard and Elphick 2010; Chapter 4). Nesting by female sparrows often becomes synchronized with the approximately 28-day lunar tidal phase in

response to the widespread nest failure that occurs in association with the highest spring tides (Gjerdrum et al. 2005; Shriver et al. 2007). This synchrony has the potential to make detection of cues related to specific reproductive activities easier, at least analytically, as most individuals are engaged in similar phases of the nest cycle simultaneously, and the variety of behaviors that females are likely to be engaged in at any one time is reduced.

Study Sites

Field research on breeding saltmarsh sparrows was conducted from 21 May to 24 August 2007 at two salt marshes on the central Connecticut coast of Long Island Sound in the northeastern U.S. (Hammonasset State Park (SP), 41° 15' 47" N, 72° 32' 55" W, study area 31.5 ha; East River, 41° 16' 24" N, 72° 39' 12" W, study area 25.2 ha). These marshes were chosen because of their large sizes (209 ha and 289 ha, respectively), abundance of high-marsh habitat, and high densities of nesting sparrows relative to other sites (Gjerdrum et al. 2005; Elphick et al. 2009). We selected study areas of similar size within each marsh using natural features of the marshes – large channels, waterways and upland boundaries – to delineate the study area boundaries. The two marshes are approximately 8 km apart and are distinct marsh systems, lying within different watersheds and separated by non-saltmarsh (suburban/forest) habitat.

Social Cue Surveys

Because saltmarsh sparrow vocalizations are generally inaudible beyond 50 m (Greenlaw and Rising 1994), and females tend to limit their within-marsh movement to distances of

less than 100 m (Hill 2008), we selected social cue survey locations at random within each study area such that survey points were at least 50 m from the study area boundary and at least 100 m apart (ArcGis 3.2 random point generator; Environmental Systems Research Institute, Inc. 1999). This process yielded 16 survey points at the Hammonasset SP study area and 13 points at East River. Due to constraints in our ability to navigate all portions of the marsh, seven points were ultimately located less than 100 m from their nearest point: one pair of points at East River was located just 92 m apart and three pairs of points at Hammonasset SP were located 77 m, 80 m, and 93 m apart. . Social cue surveys were conducted at each survey location on a weekly basis from 28 May to 17 August between 0600 and 1100 hours. Survey points were visited in random order on each visit. Each social cue survey consisted of a 5-min unlimited radius count in which the behaviors and approximate distances to the observer (0-25 m, 25-50 m, >50 m) of all saltmarsh sparrows were recorded. Temporal and environmental variables noted for each survey included the date, time of day, day in lunar cycle, time since high tide, temperature, and average wind speed. Temperature was measured in the field; timing of the high tide was taken from the Tides and Currents website of the U.S. National Oceanic and Atmospheric Administration's National Ocean Service (NOAA 2009); average daily wind speed was taken from NOAA National Climatic Data Center (NOAA 2007). The specific behaviors recorded included the number of individuals engaged in song, flight, female-specific alarm calls, perching/standing, chasing, provisioning, and male sexual displays. Care was taken to avoid counting individual birds more than once within a given survey, though our population is largely unmarked and we cannot be certain of how successful we were in this regard. All social cue surveys were immediately followed by

an unlimited radius 15-min song survey. This survey was designed to provide a measure of song frequency within the environment rather than the number of singing males. Consequently, no attempt was made to determine the identities of singing males, and individual males could thus be counted multiple times.

Nest Monitoring

Each study area was partitioned into four contiguous plots of approximately 6 – 8 ha each to facilitate equal nest searching effort across all portions of the study area. Plots were systematically searched twice weekly, with additional searching during nest monitoring activities. Nest locations were recorded with a Garmin GPSMap76; a small flag was placed approximately 5 m from each nest to identify its location, while limiting the potential for the flag to act as a cue to predators. Care was also taken to avoid trampling the vegetation in the vicinity of nests and to avoid creating trails leading to and from nests. Nests were monitored every 2-5 days to track the outcome of the nesting attempts. Because the sparrows in our study population were not individually marked, the identity of the female associated with each nesting attempt was not known. Based on the timing of all nest attempts, however, we know that a minimum of 53 females at Hammonasset SP and 43 females at East River were engaged in nesting activity within our study areas during our study.

Analysis

We faced several statistical challenges in modeling the relationships among sparrow behaviors, local reproductive activities, and temporal and environmental conditions.

These included: 1) dependent variables that were non-normal and contained excess zeros, 2) high colinearity among our three metrics of reproductive activity, and 3) potential temporal auto-correlation due to the repeated sampling aspect of our study design. Our general approach, which is described in detail below, was to first separate correlated variables into separate models, then to reduce the number of zeros in our dependent variables and, when necessary, account for zero-inflated count data in our model structure. Finally, we identified and incorporated temporal dependence using an appropriate correlation structure. All diagnostic tests and exploratory data analyses were run for all models examined.

Dependent Variables

Although we had initially envisioned treating each of our eight behaviors as separate dependent variables, many of our variables were dominated by zeros. This occurred because we chose to include only birds that were within 50 m of the survey point to avoid overlap with data collected from adjacent survey points. In addition, some of the behaviors measured were quite rare. We addressed this issue by collapsing the behavioral data into four groups: 1) the number of individuals involved in intersexual or mating behavior (“mate acquisition”), defined as all individuals seen chasing, displaying, or singing, 2) the number of females identified (“females”), defined as those individuals engaged in provisioning or generating a female-specific “tic” call (Greenlaw and Rising 1994; C. Field, unpub. data), 3) the number of birds engaged in other activities (“active”), including flying and perching, 4) the total song count (“total songs”), defined as the total number of songs recorded in a 15-min period. A fifth group related to sparrow

abundance, defined as the total number of birds recorded during the survey (“total birds”), was also used. Using these categories, we were able to reduce the number of zeros and the total number of possible models to consider.

Initially we assessed the count histograms visually to determine whether our five dependent variables were candidates for zero-inflated models (Zuur et al. 2009). We then used the PSCL (Jackman 2009) and MASS (Venables and Ripley 2002) libraries in R (R Development Core Team 2009) to determine whether our dependent variables followed a Poisson or negative binomial distribution. We first ran each zero-inflated model using a negative binomial distribution; if the estimate of the dispersion parameter Log (theta) was significantly different from zero, we retained the negative binomial distribution; otherwise we used the Poisson distribution (UCLA 2010). We then performed two model comparisons. We first compared each model to the intercept-only model using a likelihood ratio test to determine if the model constituted a substantial improvement over the null model. We then compared the zero-inflated model to the relevant standard model using the Vuong test (Vuong 1989). This allowed us to determine whether incorporating zero-inflation resulted in a substantial improvement over the standard model. In all, we examined five sets of three models (three types of nesting models per behavioral variable; see below), comparing each set separately using information-theoretic model selection (Burnham and Anderson 2002). Significance of individual predictors was evaluated for $\alpha = 0.05$.

Zero-inflated models can account for excess zeros in one of two ways, depending on the investigator’s a priori knowledge of the cause of the zeros. Zeros can either be modeled in separate steps using a binomial model for the zeros and a truncated Poisson

(ZAP) or negative binomial model (ZANB) for non-zero count data, or the probability of measuring false zeros can be analyzed using a binomial model while the “true” zeros and count data are modeled using a Poisson (ZIP) or negative binomial (ZINB) general linear model (GLM) (Zuur et al. 2009). “False” zeros may occur due to sampling errors or observer error, i.e., the bird is present but remains undetected. The basic difference between ZIP/ZINB and ZAP/ZANB models is that the nature of the zeros is left undefined in ZAP/ZANB models. Because we had reason to believe that individual sparrows and sparrow behavior could go undetected during our surveys we used the ZIP/ZINB models.

Reproductive Activity

We quantified local reproductive activity as the number of nests that were active within a 50-m radius of each survey point at the time of observation. Nests that survived long enough to reach the nestling stage were presumably a more reliable indicator of successful reproduction than those that were still in the incubation phase; therefore we also quantified how many nests were in each stage at the time of the survey. Including all three measures of reproductive activity in the same model would introduce unacceptably high levels of collinearity; therefore, we incorporated the three measures of nest activity into each model of sparrow behavior separately and used model selection to determine which measure best explained the data.

Temporal Auto-Correlation

To explore the degree to which temporal dependence due to bird responses to seasonal or tidal cycles might violate assumptions of independence among model residuals, we calculated the mean and variance of each behavioral cue for each week. We used the auto-correlation function (ACF) (NLME library; Pinheiro et al. 2009) in R on the weekly mean and variance data to identify specific time lags for which the independence assumption was violated for a given behavioral model (Zuur et al. 2010). A related but separate statistical challenge was the potential lack of independence among the multiple observations collected at each survey point. To assess within-point temporal dependence we also plotted the ACF for each survey point individually.

Because our behavioral data were not normally distributed, the conventional practice of running generalized least square models with and without a correlation structure and then comparing the AIC values was not an additional option for judging whether auto-correlation was present (e.g., Pinheiro and Bates 2000; Zuur et al. 2009). Instead we used generalized estimation equations (GEE; Liang and Zeger 1986), which can account for response variables that are counts or otherwise non-normal, and can incorporate various correlation structures. Using the GEEPACK library in R (Højsgaard et al. 2005), we ran each model with two biologically plausible types of auto-correlation structures. The exchangeable correlation structure simply assumes that observations from a given survey point are correlated, while the autoregressive correlation structure assumes that the correlation between two sequential observations from the same point is greater than that of observations further apart in time (Zuur et al. 2009). All means are given \pm SD.

RESULTS

The number of nests active within a 50-m radius of our 29 survey points averaged 0.7 ± 1.0 nests (min-max: 0 – 5) per survey. When nests were categorized by nesting phase, there were an average of 0.4 ± 0.7 nests with eggs and 0.2 ± 0.6 nests with chicks present at each survey. The number of individuals observed in each of our behavior categories averaged 2.0 ± 1.7 active sparrows (min-max: 0 – 8) per survey, 0.6 ± 1.0 females (min-max: 0 – 6), 0.5 ± 0.9 individuals involved in mate acquisition (min-max: 0 – 6), 2.5 ± 3.3 songs per 15-min survey (min-max: 0 – 25), and 5.2 ± 4.1 total sparrows (min-max: 0 – 20). When the number of sparrows engaged in each behavior was plotted as a function of the number of nests present within 50 m, no clear patterns emerged (Appendix A). However, Spearman rank correlation tests detected significant relationships between the five behavioral measures and the three measures of nesting activity in nine of 15 cases (Spearman's $\rho < 0.2$ and $p < 0.01$ for all significant tests; Appendix A). The only behavioral measure that lacked a significant correlation with any type of nesting activity was the total number of songs.

Choosing the Appropriate Model

Our zero-inflated model comparisons indicated that the negative binomial distribution was better than the Poisson distribution (the dispersion parameter Log (theta) was significantly different from zero for $\alpha = 0.05$) for modeling all sparrow behaviors except the number of individuals engaged in mate acquisition. Zero-inflated models also provided a significant improvement over the standard Poisson or negative binomial models for all cases considered ($Z > 1.87$ and $p < 0.05$ for all tests).

The auto-correlation function plots revealed no evidence of significant temporal auto-correlation when the data were averaged across all survey points. When we plotted auto-correlation by point, there were 5220 possible time lags in which auto-correlation could have been detected (29 points x 15 models x 12 weeks). We found 42 lags in which auto-correlation was statistically significant, far fewer than one would expect based on chance alone ($\alpha = 0.05$; expected = 261 significant results). Moreover, there was no consistent pattern (i.e., clustering at particular time lags or for particular points) in where significant results were found within the set of tests, further suggesting a lack of biological relevance. Given the lack of evidence for temporal auto-correlation within the survey point data, we concluded that the GEE modeling approach incorporating a temporal correlation structure was unwarranted and the results of those models are not reported here.

Reproductive Activity Associations

Despite finding significant Spearman correlations between nest metrics and behavioral cues in nine comparisons (Appendix A), behavioral cues were not significantly correlated with reproductive activity in many of our models, whereas environmental (weather) conditions were more commonly related (Table 1; outputs for all models are included in Appendix B). This result suggests that the behavioral measures, such as song rates and female abundance, quantified in this study are not reliable indicators of nesting activity/success, and that neither birds nor researchers should depend on them to assess local breeding activity. For cases in which reproductive activity was a significant correlate of sparrow behavior, the type of behaviors predicted by nesting activity tended

to be more general measures of sparrow activity, such as the total number of sparrows observed and the number of active individuals, rather than behaviors specifically related to reproduction such as song totals or the number of females observed. One exception to this pattern was the model relating the number of nests in the nestling stage to the number of individuals involved in mate acquisition, which were inversely related (Table 1).

The total numbers of active nests and nests in the incubation phase were significantly associated with the total number of sparrows observed and the number of active birds, while the number of nests in the nestling stage was significantly associated with the number of sparrows involved in mate acquisition. To our knowledge it is not possible to compute pseudo- R^2 values for ZIP models, therefore the strength of these associations is not known. However, conversion of nest parameter estimates to odds-ratios (e^{β}) indicate that for every additional active nest present in the vicinity of a point count survey, the odds of observing an additional sparrow increased by a factor of 1.09 (equivalent to a 9% increase in odds), when all other variables were fixed, and the odds of observing additional sparrows involved in “active” behavior increased by a factor of 1.17 (17%). For every additional nest present in the incubation phase, the odds of observing an additional sparrow increased by a factor of 1.12 (12%) and the odds of observing sparrows engaged in “active” behavior increased by a factor of 1.19 (19%). Finally, for every additional nest present in the nestling phase, the odds of observing additional sparrows involved in mate acquisition behavior decreased by a factor of 0.37 (63%).

Environmental/Temporal Associations

Temperature and wind speed were both significant predictors of the number of active birds observed and the number of birds involved in mate acquisition; sparrow counts generally declined with increasing temperatures and wind speed while the number of individuals involved in mate acquisition increased in relation to these variables (Table 1; Appendix B). Average wind speed was also positively related to the total number of females observed, but inversely related to the total number of songs, confirming that sparrow vocalizations can be difficult for the human observer to hear (Greenlaw and Rising 1994). Temperature was inversely related to the total number of sparrows observed, which also supports anecdotal accounts of sparrows being less active during high temperatures.

Of the three temporal variables considered, the stage of the breeding season (week) was most commonly related to sparrow behavior, with counts declining as the season progressed. Both the number of days since the new moon and the amount of time elapsed since the most recent high tide emerged as significant predictors in the binomial portion of the zero-inflated models for total number of birds (days since new moon), and the number of birds involved in mate acquisition and the number of active birds (time since high tide). The binomial portion of the zero-inflated model tests whether a given variable is a significant predictor of false zeros, suggesting that the birds could have been engaged in these activities but eluded detection.

DISCUSSION

Variation in the prevalence of saltmarsh sparrow behaviors and abundance could provide conspecifics with information regarding local nesting activity, but the pattern of relationships we detected suggests that reproductive activity and the many behaviors we examined are largely unrelated, with a few notable exceptions. It appears that cues related to the total number of sparrows in the vicinity of a point (e.g. number of active individuals, total number of birds) are more strongly linked to nesting activity than are cues that specifically reflect local breeding activity, such as male song or female provisioning behavior. This result is perhaps surprising, but suggests that density related cues may serve as the better indicator of local reproductive activity and thus habitat quality.

The use of conspecific presence or density as a habitat selection cue has been documented in a range of avian species with diverse life histories, ranging from colonial seabirds (e.g., common terns (*Sterna hirundo*); Kress 1983, and Atlantic puffins (*Fratercula arctica*); Kress and Nettleship 1988) to songbirds as diverse as loggerhead shrikes (*Lanius ludovicianus*) (Etterson 2003) and house wrens (*Troglodytes aedon*) (Muller et al. 1997); the number of species for which conspecific attraction has been demonstrated is rapidly increasing (Chapter 3). If conspecific attraction occurs at the landscape level in saltmarsh sparrows, it would help explain evidence for area sensitivity in the species (Benoit and Askins 2002; Shriver et al. 2004; and see Fletcher 2009) and the absence of sparrows in seemingly suitable habitat (Montagna 1942; Gjerdrum et al. 2008).

Experimental manipulations of vocal cues have been particularly fruitful in demonstrating the importance of conspecific attraction in habitat selection decisions (e.g., Alatalo et al. 1982; Ward and Schlossberg 2004; Betts et al. 2008). Previous research on saltmarsh sparrows documented a significant increase in male song rate following the new moon high tides, when females are engaged in re-nesting (Shriver et al. 2007). In our study, however, we found no relationship between nesting activity and male song frequency. This was unexpected, given that the primary function of saltmarsh sparrow song is thought to be in attracting females – males do not need to sing for purposes of territory defense (Woolfenden 1956). We thus thought it logical to assume that if males are actively singing in an area, then female sparrows should also be present and possibly in receptive breeding condition as well. One possible reason that nesting activity does not predict male song activity is that males sing for reasons other than mate attraction (Kroodsma and Byers 1991). Previous mist-netting efforts have indicated that marshes sometimes have abundant males present, but few or no females (Elphick et al. 2009). Males have been observed singing in situations where females are not known to be present, or very few conspecifics are present (S. Meiman, unpub. data), suggesting that song could be important for non-mate attraction purposes such as male-male social relationships or in song development (Kroodsma and Byers 1991). This might in turn dilute any link between male song and the presence of females.

At the outset of this study, we had a conflicting set of expectations regarding the potential relationship between apparent female abundance and local breeding activity. Previous banding data suggests a lack of relationship between female abundance and nest density (Elphick et al. 2005), but since males do not participate in parental care, one

would expect that the number of females, rather than the total number of birds, should be an important cue of nesting activity. This discrepancy may be related, in part, to the difficulty involved in observing female sparrows in this study. Female saltmarsh sparrows are very secretive (Greenlaw and Rising 1994), and one can rarely be certain of distinguishing between males and females in the field unless they are uniquely marked or are actively engaged in sex-specific behavior. From the perspective of the human observer, females are at their most visible during the nestling stage when they are frequently engaged in provisioning flights - one of the few behaviors that can be reliably attributed to females alone. Saltmarsh sparrows presumably are not faced with the problem of differentiating between males and females, so attempting to relate female abundance as a cue of reproductive activity may always be limited by observer constraints unless the females are artificially, individually marked.

Environmental conditions such as temperature and average wind speed were frequent significant predictors of sparrow activity and behavior in our models (Table 1), suggesting that sparrows either limit certain kinds of activity (e.g., singing, general activity) during periods of high wind and high temperatures and increase others (e.g., provisioning, mate acquisition), or that our ability to detect sparrows engaged in different behaviors is affected by these conditions. Due to the cyclical nature of sparrow nesting activity, we expected singing and general activity to be greatest following high spring tides when many nests fail due to flooding and females are engaged in re-nesting attempts (Gjerdrum et al. 2005; Shriver et al. 2007). However, the number of days since the new moon was not a significant predictor of singing frequency in any of the models

considered. Rather, the survey week emerged as an important predictor, with song rates peaking at the onset of the breeding season and declining from that point forward.

In theory, prospecting birds should be most interested in cues that provide dependable information about local reproductive success (Doligez et al. 1999). In saltmarsh sparrows, flooding is the primary cause of nest failure and many nests never reach the nestling stage. Therefore, we expect prospecting females to use any cues that indicate the availability of high marsh habitat (e.g., vegetation composition) and select marshes that have a high proportion of this habitat type. This information may be gained from social cues such as conspecific density, ecological cues such as the relative composition of saltmarsh vegetation types, or both. Conversely, the needs of prospecting males are much less constrained; food, access to mates, and shelter are their primary requirements. Therefore, we expect males to settle any place where there are females and to cue in on female behavior and receptivity in relation to the tidal cycle. In this way, it is possible that female and male saltmarsh sparrows use social and ecological cues in different ways, and perhaps to varying degrees of importance. Further experimental tests of conspecific social cues will help us understand the relative importance of social cues in these types of settlement decisions.

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Table 1. Results of 15 models relating saltmarsh sparrow nesting activity to potential behavioral cues. Each measure of nest activity was regressed against the five dependent behavioral variables; the best performing model within each behavioral category is indicated in the Δ AIC and w columns. P -values for individual predictive variables are given for significant variables only; (+) and (-) indicate the nature of the relationship between the predictive variable and the dependent variable (i.e., positive or inverse). All zero-inflated models include two outputs; the probability of measuring the “true” zeros and count data, which are modeled using a truncated Poisson or negative binomial (NegBin) general linear model, and the probability of measuring false zeros, modeled using a binomial model. Full model outputs including parameter estimates are included in Appendix B.

Model type	Nest Variable Type	Nest Variable ^a	Temp. ^b	Wind speed ^c	Lunar ^d	High Tide ^e	Week	Log-likelihood	Δ AIC	w
Dependent variable: # of females										
NegBin truncated	# of nests			0.044 (+)			< 0.001 (-)	-355.4	0.78	0.29
NegBin binomial	# of nests			0.027 (+)			0.051 (-)			
NegBin truncated	# of nests (egg stage)						< 0.001 (-)	-355.0	0	0.44
NegBin binomial	# of nests (egg stage)			0.025 (+)						
NegBin truncated	# of nests (chick stage)			0.039 (+)			< 0.001 (-)	-355.6	1.02	0.26
NegBin binomial	# of nests (chick stage)			0.028 (+)			0.046 (-)			
Dependent variable: # of birds involved in mate acquisition										
Poisson truncated	# of nests			0.005 (+)			< 0.001 (-)	-317.6	12.10	< 0.01
Poisson binomial	# of nests			0.025 (+)						
Poisson truncated	# of nests (egg stage)			0.006 (+)			< 0.001 (-)	-317.0	10.87	< 0.01
Poisson binomial	# of nests (egg stage)			0.025 (+)						
Poisson truncated	# of nests (chick stage)	< 0.001 (-)		0.002 (+)		0.021 (-)	< 0.001 (-)	-311.5	0	0.99
Poisson binomial	# of nests (chick stage)	0.025 (-)		0.006 (+)						

Dependent variable: # of songs								
NegBin truncated	# of nests			0.044 (-)	< 0.001 (-)	-642.4	0.02	0.45
NegBin binomial	# of nests							
NegBin truncated	# of nests (egg stage)			0.042 (-)	< 0.001 (-)	-642.3	0	0.46
NegBin binomial	# of nests (egg stage)							
NegBin truncated	# of nests (chick stage)			0.021 (-)	< 0.001 (-)	-643.9	3.16	0.09
NegBin binomial	# of nests (chick stage)							
Dependent variable: # of active birds								
NegBin truncated	# of nests	< 0.001 (+)	0.008 (-)		0.049 (+)	-609.7	0	0.98
NegBin binomial	# of nests			0.043 (-)				
NegBin truncated	# of nests (egg stage)	0.011 (+)	0.005 (-)			-613.5	7.6	0.02
NegBin binomial	# of nests (egg stage)							
NegBin truncated	# of nests (chick stage)		0.008 (-)			-620.9	22.4	< 0.01
NegBin binomial	# of nests (chick stage)				0.022 (+) 0.028 (-)			
Dependent variable: total number of birds								
NegBin truncated	# of nests	0.024 (+)	0.009 (-)			-896.4	0	0.74
NegBin binomial	# of nests			0.015 (-)				
NegBin truncated	# of nests (egg stage)	0.047 (+)	0.007 (-)			-897.7	2.62	0.20
NegBin binomial	# of nests (egg stage)			0.011 (-)				
NegBin truncated	# of nests (chick stage)		0.011 (-)			-898.9	5.03	0.06
NegBin binomial	# of nests (chick stage)			0.025 (-)				

^a Nest Variable = # of nests, # of nests in incubation stage, or # of nests in the chick stage depending on the model.

^b Temp. = temperature, measured in the field at the time of the survey.

^c Wind = average wind speed observed the day of the survey.

^d Lunar = # of days since the most recent new moon.

^e High Tide = time elapsed since the most recent morning high tide.

CHAPTER 2: USING SPATIAL POINT PATTERN ASSESSMENT TO UNDERSTAND THE SOCIAL AND ENVIRONMENTAL MECHANISMS THAT DRIVE AVIAN HABITAT SELECTION

ABSTRACT

Understanding when species distribution patterns should be ascribed to patterns in the physical habitat, rather than the influence of social cues, remains a crucial step in understanding avian habitat selection. To distinguish between these mechanisms, we assessed the point pattern of 213 Saltmarsh Sparrow (*Ammodramus caudacutus*) nests and the spatial autocorrelation of vegetation characteristics at two separate study sites. Tests of aggregation at cumulative and discrete distance classes failed to detect any significant non-random pattern; consistent with the hypothesis that nest placement is random with respect to other nests. When the timing of nesting attempts was taken into account such that only previous or currently active nests were considered, there was still no evidence that female sparrows attempted to nest closer to other nests than expected given random site selection. The underlying spatial structure of the vegetation variables was somewhat patchy, but not in a way that was consistent between sites or that matched patterns in nest placement, suggesting that female Saltmarsh Sparrows do not distribute themselves within marshes according to these features. A lack of association between vegetation characteristics and the probability of nest flooding, which is the primary source of nest failure in this species, may explain the apparent lack of spatial structure.

INTRODUCTION

How animals select habitat and distribute themselves in space has fundamental consequences for their demography, ecology and evolution, yet our ability to predict species distributions remains mixed (Scott et al. 2002). Stamps (1994) and others (Reed 1999, Reed et al. 1999, Blumstein and Fernandez-Juricic 2004) have suggested that a greater understanding of behavioral processes is needed to improve our theoretical and practical understanding of habitat selection. If social cues are commonly used during habitat selection, then responses to these cues could drive species distribution patterns and would have significant implications for both habitat selection theory and conservation practice (Stamps 1988, Ahlering and Faaborg 2006).

Environmental parameters such as soil moisture, elevation, and slope can directly affect vegetation composition and structure, which in turn can drive faunal species occurrence (Fortin and Dale 2005). When biologically important resources are spatially autocorrelated, patterns in species distributions may occur in response to the underlying spatial structure of the environment. Such “induced” spatial patterns have quite different implications for species settlement behavior than do the “inherent” structured patterns arising from behavior such as conspecific attraction or competition (Fortin and Dale 2005). Thus, aggregated settlement patterns can occur when individuals select habitat based on the presence of conspecifics, or simply in response to clusters in resource distribution (Stamps 1988).

Although much progress has been made in addressing these types of questions in the plant and landscape ecology literature (Fortin and Dale 2005), spatial analysis of avian nest locations is much less common (Bourque and Desrochers 2006). Despite

widespread interest in quantifying the ecological features of avian breeding habitat, the influence of these features on habitat selection behavior is infrequently approached from an explicitly spatial perspective (but see Bourque and Desrochers 2006, Cornulier and Bretagnolle 2006) and few studies specifically address the influence of social cues in habitat selection via spatial pattern assessment (e.g., Brown and Brown 2000, Melles et al. 2009). Given the growing interest in the role of social cues in the process of avian habitat selection (e.g., Danchin et al. 1998, Ward and Schlossberg 2004, Ahlring and Faaborg 2006), these topics would benefit from being united by spatially explicit analyses.

In this study, we analyze the spatial pattern of Saltmarsh Sparrow (*Ammodramus caudacutus*) nests and assess potential mechanisms driving nest placement decisions. The Saltmarsh Sparrow is a non-territorial species in which females are the exclusive providers of parental care (Woolfenden 1956, Greenlaw and Rising 1994) and birds do not form pair bonds (Woolfenden 1956, Shriver et al. 2007, Hill et al. 2010). These behavioral attributes eliminate two major social constraints that most birds face and make *A. caudacutus* especially well suited to studies that seek to determine the role of social information cues. The breeding season distribution of female Saltmarsh Sparrows is not well understood at the local scale, but the current consensus from the literature is that nests are clustered. For example, nesting has been referred to as semi-colonial and as occurring in “hotspots” (Forbush 1929, Montagna 1942, Hill 1968, Murray 1969). Greenlaw and Rising (1994) suggested that sparrow aggregations in the marsh resulted from patchiness in nest microhabitat characteristics, while Murray (1969) speculated that aggregations result from social causes such as mate attraction. However, whether the

nests of this species are clustered has not been tested statistically, limiting inferences regarding putative mechanisms. Consequently, our main goal was to test the hypothesis that nests are distributed non-randomly; we also consider plausible explanations for non-random nest placement patterns.

Saltmarsh Sparrows occur in saltmarsh habitats that are dominated by vegetation such as Saltmarsh Hay (*Spartina patens*), Black Grass (*Juncus gerardii*), and Smooth Cordgrass (*Spartina alterniflora*) (Woolfenden 1956, Greenlaw and Rising 1994).

Although sparrow occurrence is closely tied to vegetation type, sparrow abundance varies considerably during the breeding season, both within and between marshes, and only a small portion of this variation can be attributed to habitat characteristics (Gjerdrum et al. 2005, 2008a). In addition, nest failure in the species is primarily attributed to tidal flooding associated with monthly high tides; individuals that are synchronized with the tide have a greater chance of successfully fledging young, regardless of nesting vegetation (Gjerdrum et al. 2005, Shriver et al. 2007). Nevertheless, establishing whether the vegetation features associated with Saltmarsh Sparrow occurrence are patchy in their distribution is an important component of understanding their nest placement decisions. If vegetation parameters are key determinants of settlement decisions, and the distribution of vegetation is patchy, one would expect that nest placement would correspond to patches of especially favorable habitat. Thus an additional aim of this study was to determine the spatial structure of the underlying saltmarsh vegetation.

Conversely, if sparrow settlement patterns are primarily a function of conspecific attraction, females may cluster around other nests with little regard to fine-scale habitat characteristics. Under this hypothesis, the scale and location of nest aggregations would

be unrelated to that of vegetation patches. Because non-random patterns in nest placement could result either from females using other nests as cues in their nest placement decisions, or because females are attracted to nest near other actively nesting females, we use information on the temporal sequence of nest activity to assess each possibility separately.

Under the scenario in which vegetation is patchy and nest placement is clustered, our null model of random nest placement would need to be modified to specifically control for patchiness in vegetation. If nests were still clustered compared to the null expectation, the hypothesis that birds are aggregating for social reasons would be supported. However, if the settlement pattern was consistent with the null expectation, the hypothesis that females respond to similar habitat cues, but not necessarily social cues, would be supported. If we found patchiness in the vegetation, but not clustered settlement patterns, the hypothesis that nest placement is random with respect to other females, and to the specific aspects of vegetation we measured, would be supported.

METHODS

Study System

Field research on breeding Saltmarsh Sparrows was conducted from 21 May to 24 August 2007 at two salt marshes located along Long Island Sound, USA: Hammonasset State Park (41°15' N, 72° 33' W), and East River (41° 16' N, 72° 39' W). These sites were chosen because of their large size (209 ha and 289 ha, respectively), availability of suitable habitat, and high density of nesting sparrows relative to other sites (Gjerdrum et al. 2005, Elphick et al. 2009). We selected study areas of similar size within each marsh

(Hammonasset SP: 31.5 ha, East River: 25.2 ha) using natural features of the marshes – large channels, waterways and upland boundaries – to delineate the sites. The two marshes are approximately 8 km apart and lie within different watersheds separated by non-saltmarsh (suburban/forest) habitat. Our banding data show that there are occasional movements between the two sites, but suggest that there is little within-season mixing of the populations (C. Elphick, unpubl. data).

Nest Monitoring

Each study area was partitioned into four contiguous plots of approximately 6-8 ha to facilitate equal nest searching effort across all portions of the study area. Plots were systematically searched twice weekly, with additional searching during nest monitoring activities. Nest locations were recorded with a Garmin GPSMap76; a small flag was placed approximately 5 m from each nest to identify the location, while limiting the potential for it to act as a cue to predators. Care was also taken to avoid trampling the vegetation in the vicinity of the nest or create a trail leading to and from the nest. Nests were monitored every 2-5 days to track the outcome of the nesting attempts; temperature data-loggers (Thermochron iButtons, Maxim, Sunnyvale, California) were used in 35 nests (16% of total) to track nest fate (cf. Gjerdrum et al. 2008b). Nests that fledged at least one chick were considered successful for the purposes of this analysis. Although we cannot be certain that all nests were found, most marsh vegetation is short (< 0.5 m) and easy to search; moreover, we found most nests (88%) in the building or incubation phase, suggesting that our nest searching was sufficiently thorough to detect most nest attempts early in the nesting cycle (see also Gjerdrum et al. 2008a). Because the majority of

sparrows in our study population were not individually marked, the identity of the female associated with each nesting attempt was not known. Because females may engage in multiple nesting attempts, some nests in some analyses represent re-nesting attempts (see Data Analysis below). Given that the statistical tests used in this study are designed to detect spatial dependence among nests (i.e., clustering), the potential lack of independence among these nests is not an issue (Fortin and Dale 2005). Based on the timing of all nest attempts, however, a minimum of 53 females at Hammonasset SP and 43 females at East River were sampled.

Vegetation Sampling

Vegetation sampling was conducted within one-meter square quadrats centered at each nest and at randomly located points selected using the ArcGis 3.2 (Environmental Systems Research Institute, Inc. 1999) random point generator. Data gathered included: maximum vegetation height at each quadrat corner, thatch depth (i.e., dead plant matter underlying the vegetation) at the center of the quadrat, stem density in five 10-cm² sub-quadrats, and species composition (see also Gjerdrum et al. 2005).

Data Analysis

To test the null hypothesis that Saltmarsh Sparrow nests are distributed randomly within the marsh, we used a combination of first and second-order point pattern tests. First-order tests are related to the mean number of events (i.e. nests) per unit area (intensity) and allow a crude assessment of clustering within a bounded study area. Second-order methods are concerned with the covariance structure of the number of events per unit

area and allow investigation of interaction among events (Perry et al. 2006). Because different statistical approaches can yield conflicting results (Fortin and Dale 2005), we used a combination of these tests to determine how robust our results were. All tests were computed in R (R Development Core Team 2008) using the SpatStat library (Baddeley and Turner 2005). Data from each marsh were analyzed separately.

We used two first-order nearest neighbor tests as a preliminary tool to assess whether the spatial distribution of sparrow nests differed significantly from the null hypothesis of complete spatial randomness (CSR). The Clark and Evans aggregation index R is calculated as the ratio of the mean nearest neighbor distance (NND) for all nests to the mean NND expected for a Poisson point process of the same intensity (Clark and Evans 1954). A value of R significantly < 1 suggests clustering while a value significantly > 1 suggests regularity and $R = 1$ is the expected value for spatial randomness. We also used the nearest neighbor distribution function (Diggle's G -function; Diggle 1979) to quantify the cumulative distribution function (i.e., the distance from a randomly chosen nest to the nearest other nest (Baddeley and Turner 2005). We used 499 Monte Carlo simulations of a Poisson point pattern process to generate a 99% confidence envelope of the function (Diggle 2003). The estimation of Diggle's G derived from the nest dataset was compared to the theoretical curve of the Poisson point pattern. Values of the empirical G function above the 99% confidence envelope indicate clustering, while those below the confidence envelope indicate regularity.

A central assumption of second-order pattern analysis is that the variable under consideration has an equal probability of occurring throughout the study area. To test this assumption of homogeneity, we used the Kolmogorov-Smirnov goodness-of-fit test to

compare the observed distribution of nest location x-coordinates (i.e., longitude) to the distribution expected under complete spatial randomness (Baddeley 2008).

Another important consideration in point pattern analyses is the possibility of edge effects, and how to select an appropriate edge correction. Edge effects arise because the points lying near the edge of the study area have fewer neighbors available in all directions than do points located in the middle. Many edge corrections exist, and the shape and extent of the study area can be used as a guide for choosing among them (Haase 1995, Lancaster and Downes 2004). For the sites considered here, the biological justification for using edge corrections was mixed. Some portions of the study area boundaries should be considered hard boundaries, because Saltmarsh Sparrows do not occur in the adjacent habitat (e.g., upland edges); hence no correction is needed. Other areas had softer boundaries such as river edges where we have regularly observed sparrows crossing en route to adjacent areas of marsh; in this situation it is ambiguous whether a correction is warranted. In yet other areas, study area boundaries were completely artificial and thus clearly necessitate an edge correction. Consequently, we ran all analyses with and without edge corrections for irregular polygonal study areas (when such a correction was available) and reported any differences between the two sets of results as a test of the sensitivity of the results to edge-related bias.

Ripley's K ($K(r)$), is a cumulative test that allows detection of clustered point patterns at successively larger spatial scales (Ripley 1979, 1981). We used this test with Ripley's isotropic edge correction (Ripley 1988) to test for the presence of clustering among nests at distance lags of r . We used the linearized form of K , $L(r) = (K(r)/\pi)^{0.5} - r$, to aid in interpretation and to stabilize the variance (Besag 1977, Haase 1995). Here,

the expected number of nests in a circle of radius r is subtracted from $(K(r)/\pi)^{0.5}$, the observed number of nests in a circle with radius r . Under complete spatial randomness, the number of nests in a circle follows a Poisson distribution and $L(r) = 0$ for all distances. Variability in user-defined distances for this test can affect the outcome of Ripley's L , so we ran each test using the default range as prescribed by SpatStat. The recommended range for the distance lags was 0 – 162.55 m for Hammonasset SP and 0 – 156.18 m for East River. We did not perform this test without an edge correction because the exclusion of a weighting factor causes the values for the observed and expected $L(r)$ to converge after very few distance lags (Lancaster and Downes 2004).

Using Monte Carlo simulation methods, we generated 499 simulations of a homogenous Poisson process of the same average density as that found at each study area. 99% confidence envelopes for the $L(r)$ function were defined by taking the lowest and highest values of the simulated $L(r)$ for each r . Values of $L(r)$ above the upper bounds of the confidence envelope indicate clustering while those below the lower bounds indicate regularity.

To supplement this analysis, we also used the pair-correlation function (PCF) recommended by Stoyan and Stoyan (1994), which tests for interactions between points (i.e., nests) separated by a distance r and is related to Ripley's K . Whereas the pair correlation function can be thought of as a circle centered at a given nest, where the only nests counted are those that lie on the circle boundary, Ripley's K function counts all nests that are contained within the circle. The PCF is the probability of observing a pair of nests separated by a distance r , divided by the corresponding probability for a Poisson

process (Baddeley 2008). Interpretation of the PCF is similar to that of Ripley's K , in that values above the upper bounds of the confidence envelope indicate clustering.

To assess the relative importance of vegetation in influencing female sparrow settlement, we investigated spatial autocorrelation in habitat features within the marsh. If vegetation parameters are key determinants of settlement decisions, one would expect that clusters of nests would correspond to patches of especially favorable habitat.

Saltmarsh Sparrows select nest sites where the vegetation has a greater maximum height, is denser, and has a higher proportion of *Spartina patens* compared to non-nest locations, though vegetation substrate type is not correlated with nest fate (Gjerdrum et al. 2005).

To understand how the spatial structure of marsh vegetation compares to the settlement pattern of nesting sparrows, we used Moran's I to test for spatial autocorrelation (Moran 1948) in these three vegetation features. Where multiple measurements were taken of vegetation characteristics at a point (e.g., maximum vegetation height, stem density), the mean values were used. Moran's I is used to test the null hypothesis of no systematic pattern, or spatial autocorrelation, in the distribution of a quantitative variable (Cliff and Ord 1981); positive autocorrelation (aggregation) is indicated by positive values of the coefficient, negative autocorrelation (segregation) is indicated by negative values and non-significant values (randomness) are close to 0.

To explore spatial autocorrelation at different scales, each vegetation parameter was tested using different distance classes (20, 50, 100) in the freely available software program, SAM (Rangel et al. 2006), with greater numbers of distance classes representing a finer scale analysis. Each distance class was defined such that an approximately equal number of pairs of points were considered in each distance class (T.

Rangel, pers. comm.). Significance of Moran's I was tested for each distance class using a randomization procedure (Fortin and Dale 2005). Vegetation data for nest locations and randomly located points were analyzed both separately and in a combined dataset. To account for non-independence among distance classes, significance for each class was assessed using a sequential Bonferroni correction ($\alpha = 0.05$, $k = 1-20, 1-50, 1-100$) (Legendre and Legendre 1998). Moran's I values were then plotted as a correlogram against k distance classes to aid in interpretation (Fortin and Dale 2005). Only those coefficient values that were significant at the α / k level were used to interpret spatial structure (Fortin and Dale 2005). A positive, significant Moran's I value was taken as an indication of a patch of similarly-structured vegetation, whereas a negative, significant value indicating dissimilar vegetation characteristics was interpreted as a space between patches (Amico et al. 2008).

The question of whether female sparrows use similar cues in their settlement decisions, irrespective of the exact nature of the cues used, was addressed in the tests of spatial randomness presented above. However, in these analyses, a focal nest's nearest neighbor could be a nest that was active before, during or after the focal nest was initiated, or even a female's previous nesting attempt. We therefore conducted further tests, taking into account the order of nest establishment. We used an iterative procedure of nearest neighbor tests to analyze the distribution of nests according to their initiation dates throughout the breeding season. We estimated initiation dates for each nest assuming 12 days of incubation, a 10-day nestling period, and using observations of laying, hatching or fledge dates (Greenlaw and Rising 1994). When hatching and fledge dates were unknown because of early nest failure, we used a modification of the formula

that Gjerdrum et al. (2005) used to determine when incubation started (originally from Martin et al. 1997):

$$\text{Initiation date} = ((\text{date found} - ((\text{incubation period} - \text{number of days observed}) \div 2))) - \text{number of eggs in clutch.}$$

We determined end dates for each nest using the following criteria: 1) the last date the nest was observed active prior to nest failure, 2) the last date the nest was active according to iButton temperature data (available for 35 nests), and 3) the estimated fledge date based on a 10-day nestling phase and positive evidence of fledging.

To test whether female sparrows build nests closer to previously established nests than expected under complete spatial randomness, we calculated the nearest neighbor distance for each nest, using only those nests that were initiated on or before the focal nest's initiation date as potential neighbors. Each nest's nearest neighbor distance was computed from a distinct dataset that included only those nests (number of neighbors = n) that could have served as a cue during nest placement (including, potentially, a female's own previous nesting attempt). We then simulated random placement of n points in the marsh, using the `nncross` and `runifpoint` commands in `SpatStat` (Baddeley and Turner 2005) to generate a unique, random simulation for each focal nest. The distance from each real nest to its nearest neighbor in the simulated point dataset was calculated. A paired t -test was used to compare the nearest neighbor distances from the previously active nest dataset to the nearest neighbor distances of the random point dataset.

Although testing whether females nest closer to previously active successful nests than previously active failed nests is an important indicator of the use of social cues in nest site selection (e.g., public information, *sensu* Valone and Templeton 2002), the

synchronous nature of nest activity in the species made this analysis unfeasible. The majority of nesting attempts in the early part of the season were failures, whereas a second round of nesting culminating in mid-July yielded many successful attempts. As a result, only the females nesting very late in the breeding season had both failed and successful nests to use as cues; this sample was too small for a separate analysis.

To test whether females are attracted to settle near simultaneously nesting females, we also calculated the nearest neighbor distance for each nest using only active nests as potential neighbors. We defined the active nest dataset for each nest as the set of nests that were initiated prior to the focal nest initiation date, and ended following the focal nest initiation date. Again, a distinct dataset of active neighbors was created for each nest (number of neighbors = q), and the nearest active neighbor distance was calculated. A simulation of randomly located points was performed for each nest, using the number of active neighbors, q , as the basis for the number of points to be simulated. The distance from each nest to its nearest neighbor in the simulated point dataset was calculated. Nearest neighbor distances from the active nest dataset were compared to the nearest neighbor distances of the random point dataset using paired t -tests.

RESULTS

A total of 130 and 83 Saltmarsh Sparrow nests were found and monitored at Hammonasset SP and East River, respectively (Figure 1). None of the first or second order tests conducted showed strong evidence for clustered nesting. Clark and Evans aggregation indices revealed mild aggregation at the global level for both marshes (Hammonasset SP $R = 0.89$; East River $R = 0.88$) when a cumulative distribution

function (CDF) edge correction was used. When no edge correction was applied, the results were even more suggestive of a random pattern (Hammonasset SP, $R = 0.97$; East River, $R = 0.98$). Consistent with the conclusion that there is little clustering, comparison of Diggle's G function to the 99% confidence limits of the Poisson point process null model failed to reveal a departure from complete spatial randomness at either study area (Figs. 2a, b). Finally, the assumption of homogeneity required for second-order analyses was met at both marshes (Kolmogorov-Smirnov: Hammonasset SP, $D: 0.08$, $P = 0.31$; East River, $D: 0.13$, $P = 0.12$). Comparison of the empirical $L(r)$ function to the 99% confidence intervals for the null hypothesis also revealed a lack of departure from spatial randomness at both study marshes, in all distance classes (Figure 2c, d), as did results from the pair correlation function test (Figure 2e, f).

The level of spatial autocorrelation detected in the three saltmarsh vegetation variables differed between marshes and among variables, and depended on the type of points considered (Table 1). Of the 54 tests of spatial autocorrelation conducted (2 sites x 3 vegetation variables x 3 distance classes x 3 point subsets), 44% (24/54) yielded no significant autocorrelation. The best support for patchiness in vegetation features was found for vegetation density (15/18 tests) while the least support was found for mean maximum vegetation height (4/18 tests). Significant spatial autocorrelation (i.e., patchiness) was detected at distances ranging from 15–90 m, depending on the number of classes and vegetation features considered. Although all point combinations yielded a similar number of significant tests (all points (9/18), nests only (10/18), random (8/18)), the nature of spatial autocorrelation detected in each dataset was sometimes inconsistent, e.g., spatial autocorrelation was strongest for maximum vegetation height at

Hammonasset SP and for % *S. patens* at East River. Vegetation features at East River tended to exhibit more patchiness than did those at Hammonasset SP, and this patchiness persisted under all combinations of distance classes, point types, and vegetation parameter considered, with the exception of vegetation height. Vegetation features at Hammonasset SP differed in their degree of patchiness depending on the number of distance classes used, and on whether nest locations, random locations or all locations were considered.

If female sparrows did build their nests close to other current or previously established nests, this could be due to shared preference for a habitat characteristic (possibly unmeasured) rather than social cues. Females, however, did not place their nests in relation to previously active nests in a way that is significantly different from random placement (Hammonasset SP: t -test = 0.24, $df = 127$, $P = 0.81$; East River: t -test = -1.29, $df = 80$, $P = 0.20$), nor did simultaneously nesting females show evidence of aggregation in their nest placement. The distances between actively nesting nearest neighbors were not significantly different from the distances expected under random nest placement (HM, t -test = 0.67, $df = 127$, $P = 0.50$, ER, t -test = 0.18, $df = 80$, $P = 0.86$).

DISCUSSION

Although quantitative analysis of species distributions is now common at the landscape scale (Scott et al. 2002), it remains an underused tool for understanding settlement patterns and mechanisms of habitat selection at the local scale (Melles et al. 2009). Similarly, as our understanding of the potential role of social cues in avian habitat selection grows (e.g., Ahlering and Faaborg 2006), many have come to realize the

importance of incorporating this information into models of species distributions, but lack the data to do so (Blumstein and Fernandez-Juricic 2004). Quantitative analysis of settlement patterns provides a tool to address these issues by allowing assessment of alternative hypotheses in advance of performing experimental tests.

Despite a long history of anecdotal references to the “patchy local distributions” of Saltmarsh Sparrows (Greenlaw and Rising 1994), tests of aggregation at cumulative and discrete distance classes failed to detect any significant non-random pattern in sparrow nests, consistent with the view nest placement is random with respect to other nests within suitable habitat. These tests addressed the similarity of nest placement choices made by individual females, rather than directly shedding light on the mechanisms behind those choices. When the timing of nesting attempts was taken into account such that only previous or currently active nests were considered, however, there was no evidence that female sparrows attempted to nest closer to other nests. Although some patchiness in the underlying vegetation features of Saltmarsh Sparrow breeding habitat was identified, there was no evidence that female sparrows aggregated in response to this patchiness and the degree of vegetation patchiness varied depending on the marsh and the variable considered. If we had detected aggregations in sparrow nests, incorporating vegetation patchiness into our null models would have been an essential step in determining whether aggregations were due to a shared preference for a habitat characteristic or use of social cues (e.g., Melles et al. 2009). Given the lack of evidence for aggregation, however, such tests were not warranted in our study.

Our findings are seemingly at odds with early studies of Saltmarsh Sparrows and indeed our own perception that sparrows aggregate in certain areas of the marsh.

Townsend (in Forbush 1929) and Murray (1969), among others, also thought that Saltmarsh Sparrows congregate in certain areas of the marsh, leaving seemingly suitable habitat unoccupied. It is difficult to compare these early anecdotal reports of aggregation to the patterns observed in this study, in part because we lack detailed information regarding sparrow populations and their habitat at the time of these historical studies. Whether or not early reports of sparrow aggregations reflect a truly alternative distribution pattern to that of today's sparrows is not clear. One possible explanation for this discrepancy is that changes in Saltmarsh Sparrow population density or habitat availability have resulted in a change in settlement patterns. Similarly, we cannot be certain whether the patterns observed at our study marshes in one breeding season are representative of most years or sites. Our study marshes contain large populations and are considered relatively high quality marshes; different patterns may occur in low quality marshes where suitable marsh habitat is limited and sparrow density is low. Annual changes in settlement patterns are unlikely, however, given that vegetation composition and hydrology are fairly consistent on a year-to-year basis. Moreover, our anecdotal observations in multiple years and in multiple marshes provide no reason to believe that there was anything atypical about the data used here. A final possibility, and the one that we find most plausible, is that it is simply difficult for humans to distinguish among spatial patterns without careful quantitative analysis. Sparrow nest densities differ considerably across marshes (Gjerdrum et al. 2008a), and it is possible that females nesting in proximity to one another are more noteworthy in our minds, especially if this behavior conforms to our expectation of clustered settlement patterns (i.e., confirmation bias, Nickerson 1998). These sensory weaknesses, coupled with biases in nest search-

image that field workers inevitably develop (Rodewald 2004), highlight the need to conduct quantitative analyses of point patterns, rather than relying on the subjective nature of human perception.

Despite the lack of evidence supporting the influence of conspecific cues in Saltmarsh Sparrow nest placement, it is plausible that some combination of social cues and habitat features are important factors in the habitat selection process at a larger spatial scale. Montagna (1942) reported that sparrow surveys in apparently suitable marshes sometimes yielded few or no individuals, yet sparrows were abundant in Long Island Sound marshes at the time of his research. More recently, Gjerdrum et al. (2008a) evaluated the performance of habitat-based Saltmarsh Sparrow distribution models using field data from 30 study plots. Although the habitat models did moderately well in explaining sparrow abundance and nesting activity within study plots, they were poor predictors of sparrow activity in cross-validation tests and at new sites, suggesting that habitat features alone are insufficient to explain Saltmarsh Sparrow distributions. Both of these studies point to the possibility that the cues operating at the landscape level could be more important for habitat selection in this species than are local nest placement cues. If the density of conspecifics in a potential habitat area is a critical factor for individual settlement decisions, conspecific attraction at the marsh level would be an important mechanism driving Saltmarsh Sparrow distributions. Exactly where females nest within a given marsh may be less important.

The nature of nest failure in this species is such that fine-scale differences in elevation and vegetation at nest locations may be largely irrelevant. Nest failure is primarily caused by flooding events associated with monthly high tides (> 60% of all

failures: DeRagon 1988, Shriver 2002, Gjerdrum et al. 2005); females that nest synchronously with the tide have a greater chance of successfully fledging young (Shriver et al. 2007), regardless of nest vegetation characteristics (Gjerdrum et al. 2005). Given these results, one would like to know whether nests that succeed (or fail due to flooding, predation, etc.) are more clumped than is expected by chance. For example, if nests that succeed are clustered, it would suggest that either the processes driving nest fate, such as predation or tidal flooding, do not act uniformly across the habitat, or that there is some benefit to nesting in groups. This analysis could be achieved by “marking” each nest in accordance with its fate and performing a bivariate, or multi-type version of the point pattern analyses outlined here (see Baddeley et al. 2008 for methods; Giesselmann et al. 2008). However, because such tests would need to be conducted for simultaneously nesting females (i.e., to detect spatial associations between temporally-coincident failures), rather than the entire nest dataset, we lacked the sample sizes necessary for each nest fate type to perform these analyses.

Animal ecologists often express concern about the degree to which habitat selection studies fail to predict species occurrence (Garshelis 2000, Jones 2001), and these failures have been attributed to a range of factors (Scott et al. 2002). The scale or extent of the study may be inappropriate (Maurer 2002, Trani 2002), behavioral interactions are often ignored (Stamps 1988, Smallwood 2002), and the failure to consider the hierarchical structure of the habitat selection process may play a role (Wiens 1989, Battin and Lawler 2006, Gjerdrum et al. 2008a). The spatially explicit approach presented here addresses the behavioral aspect of this issue, and allows researchers to generate and test specific hypotheses of habitat selection mechanisms using a commonly

collected type of data. Ultimately, understanding when Saltmarsh Sparrow absences at the landscape-level should be ascribed to a deficiency in the physical habitat, rather than a lack of social cues, remains a crucial step in understanding habitat selection in this and many other species.

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TABLE 1. Results of the Moran's I tests of spatial autocorrelation for three vegetation features associated with sparrow nests. Each variable was evaluated using 20, 50 and 100 distance classes and three subsets of point vegetation data: all points, nests only, and random points only. The significance of the Moran's I coefficients for each distance class was evaluated at the α/k level ($\alpha = 0.05$, $k = 1-20, 1-50, 1-100$). When significant spatial autocorrelation was detected at a given distance class, the median distance (m) of that class is reported; "NS" indicates that the result was not significant. When significant spatial autocorrelation was detected for multiple distance classes, the range of the median distance of the closest and furthest distance classes is reported, along with the maximum *P*-value associated with those classes.

TABLE 1

	Hammonasset SP						East River					
	All points		Nests only		Random points		All points		Nests only		Random points	
	Distance	<i>P</i>	Distance	<i>P</i>	Distance	<i>P</i>	Distance	<i>P</i>	Distance	<i>P</i>	Distance	<i>P</i>
	Vegetation height											
20 distance classes	NS		95	0.004	NS		NS		NS		NS	
50 distance classes	NS		23	0.018	NS		NS		NS		NS	
100 distance classes	15	0.020	15	0.034	NS		NS		NS		NS	
	% <i>Spartina patens</i>											
20 distance classes	NS		NS		37	0.046	33-80	<0.004	NS		34	<0.001
50 distance classes	NS		NS		NS		21-90	<0.030	NS		21-82	<0.010
100 distance classes	NS		NS		NS		14	0.002	12	0.023	36-58	<0.018
	Vegetation density											
20 distance classes	38	0.040	38	0.002	NS		33-150	<0.011	29	<0.001	34	<0.001
50 distance classes	23	<0.001	23	0.006	NS		21-90	<0.017	18-45	<0.002	21-52	<0.003
100 distance classes	NS		15	0.012	51	<0.001	14-46	<0.012	12-40	<0.014	14-58	<0.050

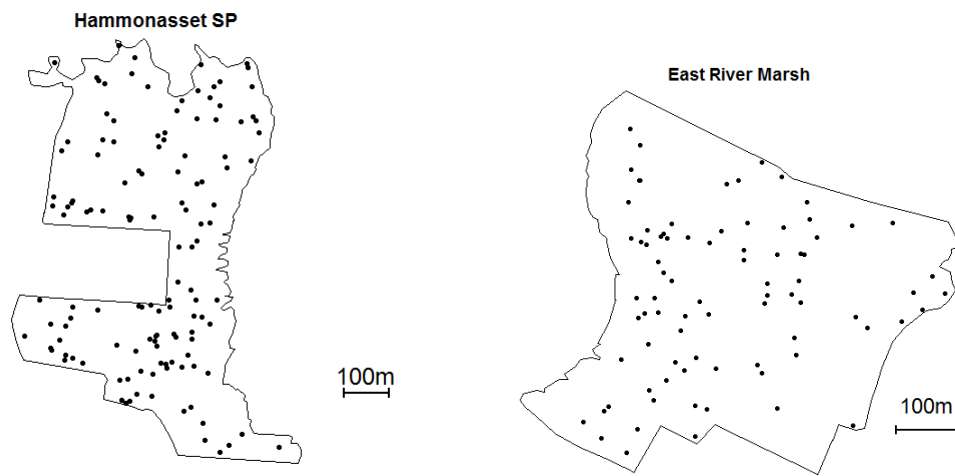


FIGURE 1. Map of Saltmarsh Sparrow nest locations used in point pattern analyses.

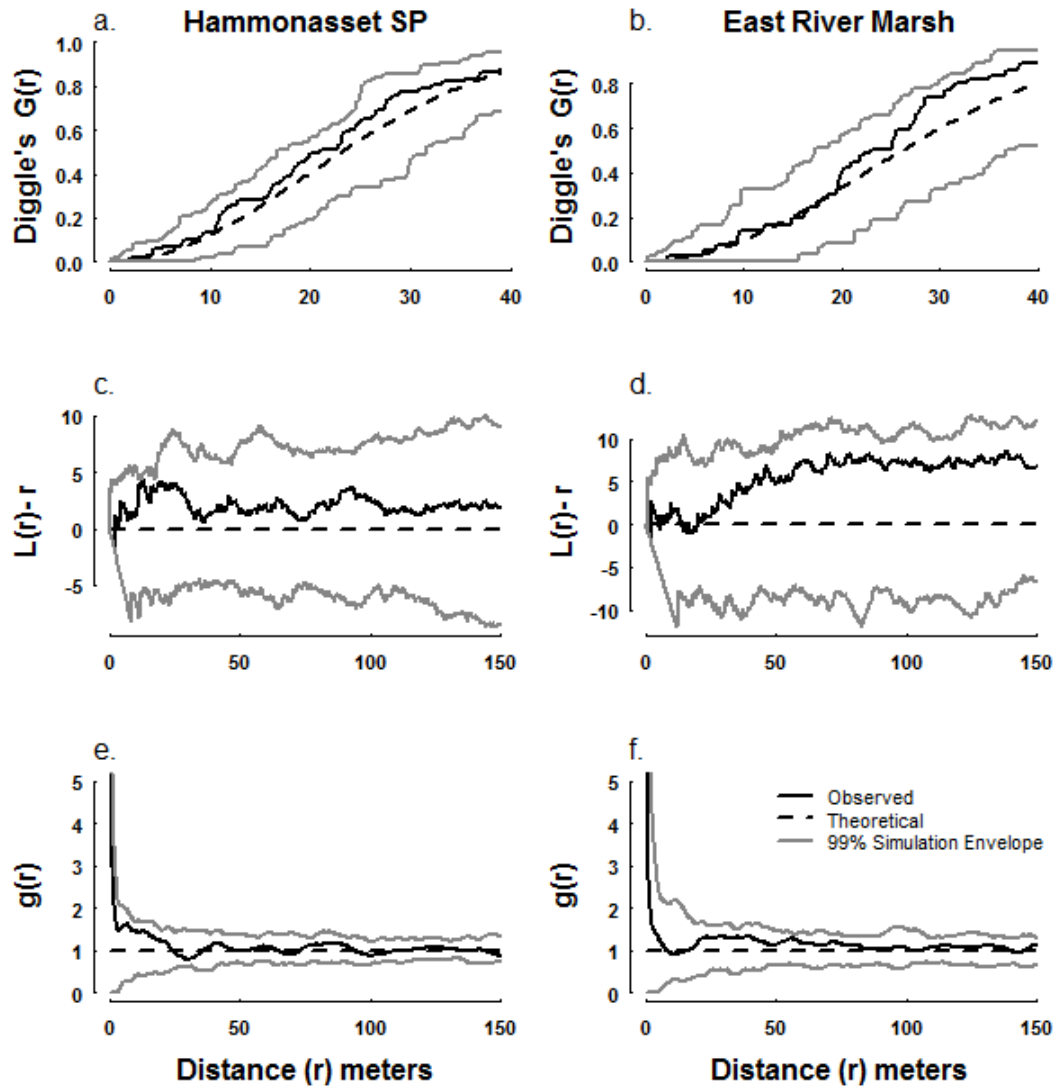


FIGURE 2. Comparison of Diggle's cumulative distribution function G (a, b), Ripley's K (transformed to L) (c, d) and the pair correlation function (e, f) for Saltmarsh Sparrow nests at two Connecticut salt marshes. Solid black lines represent values for the point patterns (observed), dashed black lines represent the expectation under complete spatial randomness (theoretical), and dotted gray lines represent the 99% confidence interval based on 499 randomizations of a Poisson point process. Values above the upper bounds of the confidence interval indicate clustering at distance r , while values below the lower bounds indicate regularity.

CHAPTER 3: TESTING FOR CONSPECIFIC ATTRACTION IN A NON-TERRITORIAL SONGBIRD

ABSTRACT

Audio broadcast experiments have been used to test social mechanisms of habitat choice in a growing number of songbird species, however little is known about the extent to which social mechanisms might influence settlement decisions in non-territorial songbird species. In this study, we tested whether the saltmarsh sparrow (*Ammodramus caudacutus*), a non-territorial, socially promiscuous species, uses conspecific attraction to make habitat selection decisions. We broadcast sparrow vocalizations in two distinct contexts: at occupied, high population density marshes and at apparently suitable but unoccupied or low-density marshes. Despite previous research indicating that sparrow density may be a useful cue of nesting activity, we found no evidence that saltmarsh sparrows respond to conspecific density cues at either the local or landscape level. Not only were sparrow numbers very similar in treatment and experimental plots and in pre-treatment and treatment plots, but the number of nests and fledglings produced were similar as well. The results of this study suggest that conspecific attraction is not an important component of habitat settlement decisions for this species.

INTRODUCTION

Selection of breeding habitat is a behavioral process that has powerful implications for fitness, yet the way in which individuals assess habitat quality is not well understood (Hildén 1965; Jones 2001). Recent work in behavioral ecology has explored the idea that birds, including those that are territorial, may use the presence of conspecifics as a cue of habitat quality and be attracted to settle near one another (e.g., Ahlering and Faaborg 2006). A key benefit of using conspecific cues to assess habitat quality is that the presence of conspecifics represents the net effect of many social and environmental factors, whereas ecological cues of habitat quality may change over the course of the breeding season (Brewer and Harrison 1975) or be difficult or time-consuming to sample (Stamps et al. 2005). Use of such an integrative cue can thus be an important time-saving measure, particularly for animals such as migratory birds that must commence breeding in a timely manner.

Audio broadcast experiments have been used to test social mechanisms of habitat choice in a growing number of songbird species (Alatalo et al. 1982; Ward and Schlossberg 2004; Ahlering et al. 2006; Hahn and Silverman 2006, 2007; Mills et al. 2006; Nocera et al. 2006; Fletcher 2007; Betts et al. 2008; Harrison et al. 2009). In these studies, conspecific vocalizations are broadcast at experimental plots in an attempt to elicit dispersal into these areas while control plots remain un-manipulated; birds that respond positively to these cues are said to use conspecific attraction. Although the implementation of broadcast experiments is seemingly straightforward, there are a number of ways in which their details have varied. For example, the suite of cues used (e.g., conspecific song, heterospecific song, model decoys), the density of playback

stations per plot, the number of unique vocalizations used in playback recordings, the timing of the experiment (breeding season, vs. pre- or post-breeding season), the duration of the experiment, the suitability of the habitat (e.g., habitat vs. non-habitat), prior population density (e.g., unoccupied, low, medium, high), the number and size of the plots, the type of data collected (e.g., presence/absence, prospecting behavior, settlement, territories, breeding pairs, age class composition), and whether additional treatments were implemented (e.g., brown-headed cowbird, *Molothrus ater* removal) are all potentially important ways in which these studies differ (Table 1). Nonetheless, a significant audio treatment effect has been found in seven of the nine songbird species for which playback studies have been published, indicating that conspecific attraction and other social information cues may be important factors in the habitat selection decisions for a range of songbird species.

Although conspecific attraction has been implicated in the evolution of colonial breeding (Shields et al. 1988; Boulinier et al. 1996) and has recently received more attention in territorial songbird species, little is known about the extent to which social mechanisms might influence settlement decisions in non-territorial songbird species. One might predict that species that are unconstrained by the territorial behavior of others would be more likely to be attracted to settle near conspecifics due to the potential fitness benefits of living in groups (Stamps 1988) and the lack of territorial aggression from other individuals. For example, individuals living in aggregations can access information about local resource quality and social relationships by observing the daily activities of neighbors. As conspecifics look for food, defend themselves against predators, and engage in mating and parental activities, they inadvertently produce information that can

be valuable to others (Galef and Giraldeau 2001; Valone and Templeton 2002). Valone and Templeton (2002) define this phenomenon as the generation of public information because it is available to all individuals in the vicinity of the activity. Clustered individuals may also reduce predation through anti-predator strategies (Hamilton 1971) or improve their mate selection choices (Allee 1951; Darling 1952).

Determining whether animals differ in their use of social information may be difficult if they are constrained in their access to certain sites due to territorial behavior or other social interactions. In order to accurately characterize use of social information in habitat selection decisions, a system in which individuals are not constrained in their choice of habitat by the territorial behavior of conspecifics provides a unique opportunity. The saltmarsh sparrow *Ammodramus caudacutus*, is an ideal species for testing the role of social cues because it is a non-territorial species in which males and females mate with multiple partners (Hill et al. 2010) and do not form pair bonds (Greenlaw and Rising 1994), thus avoiding limits imposed by social constraints. Females are solely responsible for nest site selection and parental care and select nest site locations randomly with respect to one another (Bayard and Elphick 2010; Chapter 2). Saltmarsh sparrows are also obligate saltmarsh specialists and nest in grassland-like stands of tidal marsh vegetation, making detection of nests relatively straightforward. Although sparrow occurrence is closely tied to vegetation type (Greenlaw and Rising 1994; Gjerdrum et al. 2005, 2008), breeding season abundance varies considerably, both within and between marshes, and only a portion of this variation can be attributed to habitat characteristics (Benoit and Askins 2002; Shriver et al. 2004; Gjerdrum et al. 2005, 2008). These

components of saltmarsh sparrow breeding biology suggest that social cues may play an important role in habitat selection.

Given the variety of approaches taken in other broadcast experiments, we designed our study to be as expansive as possible in order to cover the range of ways in which sparrows may respond to conspecific cues. For example, we broadcast over the entire breeding season (including pre- and post-breeding periods), monitored nesting attempts and reproductive success (which are infrequently assessed in other studies), and tested for within-year and subsequent-year effects. In addition, we carried out experiments in two distinct contexts: within suitable, occupied habitat at marshes known to support relatively high numbers of sparrows, and at smaller marshes with low densities or zero sparrows that represent seemingly suitable, but unoccupied habitat (i.e., a mix of native high marsh vegetation similar to that found in occupied marshes). The first experiment was designed to address settlement decisions at the within-marsh scale, whereas the second experiment allows us to address whether conspecific attraction occurs in marsh-level selection decisions, i.e., when sparrows select among salt marshes.

Tidal flooding is the primary cause of nest failure for saltmarsh sparrows, regardless of differences in the underlying nest vegetation (Gjerdrum et al. 2005; Shriver et al. 2007; Chapter 4). Nonetheless, some of the variation observed in sparrow abundance within the marsh is associated with the presence of high marsh vegetation (Gjerdrum et al. 2008), suggesting that there might be particular areas within the marsh that are more or less favored due to their propensity to flood. If differentiation among high marsh vegetation types is an inadequate cue of the risk of flooding events within the marsh, conspecific attraction is one reasonable hypothesis for explaining how sparrows

decide where to settle within the marsh. If conspecific attraction is important at this scale, we predict that sparrows will be attracted to settle in density-enhanced (i.e., audio broadcast) plots at our occupied study areas. A lack of response at this scale could indicate that the habitat is either filled to capacity, that conspecific attraction is not an important strategy for nest-site selection at this scale, or that our experimental design or cues were lacking in some fundamental aspect.

Alternatively, saltmarsh sparrows may make their primary habitat selection decisions at the landscape scale – when deciding which marshes to settle in. Where they nest within a given marsh may be less significant in terms of fitness, perhaps because when tidal flood waters are great enough to inundate high marsh habitat, all nests, regardless of their exact location, have a good chance of being lost to flooding (Bayard and Elphick 2010; Chapters 2 and 4). In which case, unoccupied marshes may be uninhabited because, a) they flood frequently enough to preclude a complete nesting cycle and sparrows can detect through social or environmental cues that the marsh is unsuitable, or b) because prior fragmentation and stochastic events led to local extirpation at these sites and they now lack the conspecific cues necessary to attract individuals (cf. Kress 1983). If conspecific cues are important during marsh-level selection decisions, we predict that increasing the apparent density of sparrows will cause an increase in sparrows at seemingly suitable sites that are otherwise unoccupied or have had low sparrow densities. Furthermore, if sparrows occur and nest in these habitats and achieve reproductive success equivalent to that of established populations, the inherent suitability of these unoccupied marshes would be demonstrated. Alternatively, a lack of response would provide support for the hypotheses that the habitat at these marshes is unsuitable,

that conspecific cues are not an important component of habitat selection at this scale, or that our experimental approach does not test the right cues.

Use of conspecific attraction can lead to patch size effects, wherein population density varies in relation to patch size, in fragmented landscapes (e.g., Fletcher 2006, 2009). Both experiments may shed light on why area sensitivity is seen in the species (Benoit and Askins 2002; Shriver et al. 2007), the mechanisms for which are currently unclear (e.g., Bayard and Elphick 2010b). In addition, for species of conservation concern such as the saltmarsh sparrow that are vulnerable to climate change and sea-level rise (Chapter 4), assisted colonization and habitat creation/restoration are likely to become important management considerations in the future (e.g., Hunter 2007; McLachlan et al. 2007). Understanding whether conspecific attraction is an important component of habitat selection and settlement is thus an important concern for future conservation efforts.

METHODS

Study Sites

We conducted field research on the effects of conspecific attraction on sparrow settlement behavior in two separate experiments. For the within-marsh settlement study we selected two salt marshes located on the central Connecticut coast of Long Island Sound in the northeastern U.S.: Hammonasset State Park (41° 15' 47"N, 72° 32' 55"W), and East River (41° 16' 24"N, 72° 39' 12"W). Hammonasset SP and East River are approximately 8 km apart, are distinct marsh systems lying within different watersheds, and are separated by non-saltmarsh (suburban/forest) habitat. These marshes were

chosen because of their large sizes (209 ha and 289 ha, respectively), abundance of suitable habitat, and high density of nesting sparrows relative to other sites (based on field data from 2002-2007: Gjerdrum et al. 2005; Elphick et al. 2009). Prior research at these marshes also indicates that sparrow abundance varies considerably within each marsh and that only a relatively small portion of this variation can be attributed to habitat characteristics (Gjerdrum et al. 2005, 2008). We did not conduct pre-treatment density surveys, but we used data on past sparrow presence at both marshes as evidence of their suitability (Bayard and Elphick 2010; Chapter 2; C. Elphick unpub. data). Ten 100 x 200 m (2 ha) plots were established at each marsh such that all plots were a minimum of 100 m apart (Appendix C). Due to constraints in marsh size, plots were located in a somewhat uniform pattern to maximize the number of plots sampled per marsh. Five plots at each marsh were randomly selected to receive the audio broadcast treatment (see *Audio treatment*).

For the landscape-scale marsh settlement study we selected 11 salt marshes that contained seemingly suitable high marsh habitat but had either low sparrow numbers (< 5 individuals) or no sparrows present in prior years. These marshes were selected based on data collected as part of an unrelated saltmarsh sparrow study (Elphick et al. 2009). Three to five point-count surveys were conducted at randomly placed 1 ha plots at these sites in 2004 (two marshes, five surveys), 2006 (six marshes, three surveys), 2007 (one marsh, five surveys) or 2008 (two marshes, five surveys). We used data from three surveys from each study plot as a baseline, pre-treatment basis for comparison in the current study. Three point count surveys at a given site has been estimated to yield a > 90% chance of detecting sparrows when they are present (S. Meiman pers. comm.). The

marshes sampled in this portion of our study included: Farm River State Park, Branford (6 ha, 41° 15' 18"N, -72° 51' 29"W), Indian Neck, Branford (36 ha, 41° 15' 22"N, -72° 48' 53"W), Stony Creek, Branford (24 ha, 41° 16' 28"N, -72° 45' 37"W), Jarvis Creek, Branford (28 ha, 41° 15' 47"N, -72° 44' 24"W), Hoadley Creek, Branford/Guilford (18 ha, 41° 15' 57"N, -72° 43' 48"W), Long Cove, Guilford (15 ha, 41° 15' 38"N, -72° 41' 10"W), Fence Creek, Madison (12 ha, 41° 16' 31"N, -72° 35' 7"W), upper Oyster River, Old Saybrook (30 ha, 41° 17' 33"N, -72° 23' 19"W), Groton Long Point Marsh, Groton Long Point (17 ha, 2 plots, 41° 19' 5"N, -72° 0' 35"W, 41° 19' 2"N, -72° 0' 18"W), and Cottrell Marsh, Stonington (21 ha, 41° 20' 30"N, -72° 57' 13"W).

Audio Treatment

For the within-marsh experiment, two broadcast stations were placed at the boundary of each 2-ha plot such that they were 100 m apart, with speakers aimed towards the center of the plot. For the marsh-level experiment, one broadcast station was placed at the boundary of each 1-ha plot such that the unit was oriented towards the center of the plot. Consideration of how prospecting sparrows might enter the marsh was also used to determine callbox placement at these plots, i.e., broadcast units were placed so that they faced away from upland boundaries where sparrows do not occur and towards open water or other marsh areas.

The design for our audio broadcast units was based on the prototype conceived by Ward and Schlossberg (2004). We worked with Modern Outpost (www.modernoutpost.com) to select the appropriate electronic and solar components for a 100% solar-powered, waterproof broadcast unit. We used iPod® 2nd generation 2G

Nano mp3 players, coupled with Pürtek amplified speakers (Lei Electronics, Inc.) that were powered by Powerfilm 12 v solar panels, and all electronic components were housed in a waterproof plastic box. These components were mounted on PVC piping and installed in the ground at a height of approximately 1.2 m to ensure no loss of equipment from tidal flooding. Although our broadcast stations were positioned above the surrounding vegetation, male saltmarsh sparrows sing from a variety of positions, including song posts and in flight.

Each station broadcast a playlist consisting of 5.5 hours of sparrow songs and calls on a daily basis between 26 May and 27 August 2008 and 11 May and 29 July 2009 at Hammonasset and East River, and from 6 May to 7 August 2009 at the unoccupied/low-density sites. Male saltmarsh sparrows generally arrive on the breeding grounds in early to mid-May and females arrive later in the month; breeding tapers off significantly in early August with fall migration occurring from September through mid-October (Greenlaw and Rising 1994). The importance of pre-breeding versus post-breeding season cues appears to vary by species (e.g. Nocera et al. 2006; Fletcher 2007); therefore we designed our broadcast schedule to provide both breeding and post-breeding season cues in 2008 and pre-breeding and breeding season cues in 2009. Only pre-breeding and breeding season cues were provided in the 2009 marsh-level study. Saltmarsh sparrows sing sporadically throughout the day (T. Bayard, unpub. data; C. Field, unpub. data); therefore daily broadcasts were initiated using the iPod[®] alarm/playlist function at 7 a.m. to achieve morning to mid-day coverage and take advantage of the increased solar energy available following sunrise.

Recordings of saltmarsh sparrow songs from the local region were obtained from the Borror Laboratory of Bioacoustics, the Stokes Field Guide, and the personal bird song libraries of Judy Fieth (“Watching Sparrows” video) and Chris Field. Because saltmarsh sparrows are not territorial and sing a quiet complex whisper song on an intermittent basis (Greenlaw and Rising 1994), obtaining quality recordings of their vocalizations is extremely difficult. This constraint limited us to seven individuals in our broadcast repertoire. Saltmarsh sparrow song was interspersed with periods of silence and occasional vocalizations from other heterospecific birds of the salt marsh, including seaside sparrows (*Ammodramus maritimus*), willets (*Catoptrophorus semipalmatus*) and red-wing blackbirds (*Agelaius phoeniceus*). Call notes from female sparrows and chicks were also included. Sparrow song rate was programmed to match natural song rates observed in the field (2.5 ± 3.3 SD songs per 15 min, T. Bayard, unpub. data) and vocalizations were audible from a distance of 50 m, which is similar to natural levels.

Sparrow Surveys

Sparrow abundance and activity at each plot were quantified using 5-min unlimited radius point counts. Point count surveys were located at the center of each plot. Sparrow presence, behavior, and distance from the center of the plot were noted at each survey and care was taken to avoid counting the same individuals multiple times within a given survey. Sparrow sex was identified through vocalizations or provisioning behavior when possible. Point count surveys were conducted at Hammonasset SP and East River on a weekly basis throughout the breeding season in 2008 (from 26 May to 27 August) and through the peak of the breeding season in 2009 (from 25 May to 19 July). Point count

surveys were conducted at the unoccupied marshes at 2-week intervals from 27 May to 13 August in 2009.

Nest Monitoring

Each plot was systematically searched two to three times weekly. Plots at the low density/unoccupied marshes were searched four separate times, which was consistent with pre-treatment survey efforts. Nests were found by traversing the plot on foot and carefully searching the vegetation when birds were flushed. Behavioral signs of breeding activity, e.g., alarm calls and females carrying food, were also used to locate nests. Nest locations were recorded with a Garmin GPSMap76; a small flag was placed approximately 5 m from each nest to identify the nest location, while limiting the potential for it to act as a cue to predators. Care was also taken to avoid trampling the vegetation in the vicinity of the nest and to avoid creating a trail leading to and from the nest. Nests were monitored every 2-5 days to track the outcome of the nesting attempts; nests that fledged at least one chick were considered successful for the purposes of this analysis. The number of fledglings was based on the number of chicks observed in the nest at the final nest check prior to the expected fledging date.

Analysis

Weekly point count estimates of sparrow abundance from the occupied marshes were analyzed using repeated measures ANOVA. In addition to testing for the effect of the experimental broadcast treatment, we were interested in how sparrow response might differ in the first year of the study, when breeding and post-breeding season cues were

provided, versus the second year, when sparrows may have reacted to either the post-breeding cues provided during the previous 2008 season, or to the pre-breeding cues provided prior to settlement in 2009. We were also interested in how sparrows responded to the experimental treatment at different points of the breeding season and in relation to the number of weeks since the new moon. Sparrows that initiate breeding within a few days of the highest monthly spring tide have a higher chance of success (Shriver et al. 2007) and sparrows often become synchronized with the lunar cycle in response to the devastating flood tides that occur approximately every 28 days. Sparrow activity could thus vary based on the progression of the breeding season (i.e., week) or in synchrony with the approximately 28-day lunar cycle (i.e., lunar week). The two temporal covariates were compared in alternative models. Treatment (broadcast vs. control), year (2008, 2009), site identity (Hammonasett SP, East River), week (1 - 12), lunar week (weeks since the new moon; 1 - 4) were examined. To test how sparrow responses might vary within the breeding season, e.g., if sparrow response was heightened during certain parts of the breeding cycle, we included the interactions between treatment and both week and lunar week. We also included the interaction between treatment and year of the study to test how sparrow response might differ in relation to different timing of cues. The interactions between both week and lunar week and year were included to test whether sparrow responses varied according to both the year of the study and the timing of the survey within the breeding season. We calculated the total nest abundance observed in each plot across the entire breeding season and assessed the effect of treatment and site for each year separately because of unequal sampling effort between years (nests were monitored for 12 weeks in 2008 and 8 weeks in 2009) using ANOVA.

Pre- and post-treatment sparrow and nest abundance at our 11 low-density/unoccupied marshes were compared using paired *t*-tests.

RESULTS

The number of sparrows observed in our within-marsh settlement study ranged from 0 – 13 per survey in control plots and 0 – 11 in audio treatment plots; the number of nests per plot ranged from 0 – 10 nests in both treatments (Table 2). High nest failure rates due to tidal flooding contributed to extremely low fledging rates in both treatment and control plots in 2009 (Table 2). There were no detectable differences in sparrow abundance ($F_{1,17} = 0.13, p = 0.73$), nest abundance (2008: $F_{1,17} = 0.46, p = 0.51$; 2009: $F_{1,17} = 0.20, p = 0.66$), or the number of young fledged (2008: $F_{1,17} = 0.36, p = 0.56$; 2009: $F_{1,17} = 0.07, p = 0.80$) between audio treatment plots and control plots (Tables 3, 4; Figure 1).

Significantly higher densities of sparrows were found at Hammonasset SP (Table 3).

However, nest and fledgling numbers did not differ between the two sites (Table 4), indicating that differences in abundance at the two sites did not mean that there were population level reproductive differences. Additionally, more birds were observed in 2009 than 2008 (Table 2, 3) but there was no interaction between year and treatment as would be expected if the conspecific attraction response lagged by a year. Finally, bird numbers changed over the course of the breeding season, with the greatest number observed five weeks into the sampling period, but there was no evidence for variation in response to the lunar cycle (Table 3). We used the mean number of birds detected in our control plots to calculate the statistical power achieved under two hypothetical outcomes. We achieved 74% power to detect a mean difference of 2.0 birds (equivalent to effect

size = 0.38), and 26% power to detect a mean difference of one (1.0) bird (effect size = 0.19).

Before-treatment observations at our low-density marshes averaged 0.15 sparrow sightings per survey (five sightings in 33 surveys) at the 11 plots, versus 0.24 sightings per survey (eight sightings in 33 surveys) during the broadcast treatment of 2009. Nest detection was also low; two nests at two marshes were found during pre-treatment surveys in 2006 and 2007 and two nests were found at two marshes during the 2009 treatment season, only one of which was at a previously unoccupied marsh (Table 2). The number of birds and nests did not differ between pre-and treatment-period samples (birds: $t\text{-test}_{10} = 0.41$, $p = 0.69$; nests: $t\text{-test}_{10} = 0$, $p = 1.0$; Tables 2, 4).

DISCUSSION

We found no evidence that saltmarsh sparrows respond to conspecific density cues in our experiments, which suggests that conspecific attraction is not important to this species' settlement decisions at either the local or landscape scales. Not only were sparrow numbers very similar in treatment and experimental plots, and in pre-treatment and treatment plots, but the number of nests and fledglings produced were similar as well. Given the results of our previous work relating sparrow nesting activity to the frequency of different types of sparrow behavior (Chapter 1), the unexplained variability in sparrow densities in and among marshes (Benoit and Askins 2002; Shriver et al. 2004; Gjedrum et al. 2005, 2008), and both the lack of territoriality and the extremely promiscuous mating system of the species (Hill et al. 2010), this lack of response is at odds with our expectation of how conspecific density cues would affect sparrow behavior. Specifically,

we had determined previously that the number of active nests and nests in the incubation phase are positive and significant predictors of the total number of sparrows in the vicinity (Chapter 1), suggesting that the relative abundance of sparrows within the marsh could potentially be a useful cue of local breeding activity and thus habitat quality. Furthermore, Hill et al. (2010) demonstrated that the number of male partners per female increased with male density; therefore it would make sense for females to be attracted to places where conspecifics are abundant, assuming it is advantageous for females to mate with multiple males, or that there are other advantages to living in groups (Allee 1951). If this were the case, one would expect sparrows to be attracted to experimentally enhanced plots.

Although unexplained variance in sparrow abundance within and among marshes (Benoit and Askins 2002; Gjerdrum et al. 2005, 2008) initially led us to suspect that social cues such as conspecific attraction might be an important factor driving saltmarsh sparrow distributions, more recent work on the spatial distribution of nesting sparrows does not support this line of reasoning. Contrary to previous accounts of semi-colonial aggregations and clustered nesting by saltmarsh sparrows (e.g., Townsend in Forbush 1929; Murray 1969), spatial analyses of sparrow nest locations indicate that females nest randomly with respect to the location of other breeding females and to prior nest locations (Bayard and Elphick 2010; Chapter 2). Thus our spatial analyses supports the view that females are not attracted to settle near one another and that where they settle within the marsh may not be fundamentally important for their fitness. This may be due, in part, to the reproductive biology of the species; most nest failures can be attributed to tidal flooding, which affects nests regardless of differences in nesting substrate

(Gjerdrum et al. 2005; Shriver et al. 2007; Chapter 4). After a certain point, minor elevation differences gained by nesting within particular areas of the marsh are likely inconsequential in the face of the high spring tides that inundate much of the high marsh plane. On average, the difference between the maximum tide height that successful versus failed nests can withstand without flooding is only 5 cm (Chapter 4). The lack of experimental evidence for conspecific attraction at the local level is thus consistent with our spatial analyses of nesting patterns.

Our statistical power to detect a mean increase of two birds across the treatment plots was high, suggesting that the lack of effect was not due to insufficient sample size. It is possible that our results may be attributable to factors unrelated to conspecific attraction, e.g., the habitat could have already been saturated and/or otherwise unsuitable (in the marsh-scale study); song rates may have already been above an asymptote beyond which additional cue intensity provides no additional information (within-marsh study); or our broadcast cues may have been insufficient or inappropriate to elicit a response. However, as was noted previously, we designed our study to encompass a range of possible responses, from cues operating at different spatial scales to marshes known to support sparrows versus those with low densities. We broadcast pre- and post-breeding cues, in addition to breeding-season cues, and we measured reproductive parameters such as nest and fledgling abundance in order to document the demographic consequences of our broadcast treatment. Given the complete lack of evidence for conspecific attraction in our study, and our use of a study design that broadly spanned the range of conditions that might elicit a response, we consider our results to support the conclusion that conspecific attraction does not operate at the local or landscape level for this species.

In contrast to our results, audio playback experiments in other (territorial) songbird species have detected conspecific attraction with audio broadcasts as infrequent as every other day for 18 days (Brewer's sparrow *Spizella breweri breweri*, Harrison et al. 2009) and with as few as seven experimental plots (e.g., black-capped vireo *Vireo atricapilla*, Ward and Schlossberg 2004). Some researchers have even succeeded in attracting individuals into completely unsuitable sites (e.g., bobolink *Dolichonyx oryzivorus*, Nocera et al. 2006). Of the conspecific attraction studies published to date, seven of nine species have shown a significant, positive response to the audio broadcast treatment (Table 1). Of the two species that failed to show an effect, both were *Ammodramus* species: Baird's sparrow *A. bairdii* (Ahlering et al. 2006) and the Acadian subspecies of Nelson's sparrow *A. nelson subvirgatus* (Nocera et al. 2006). Although the sample size for the Baird's sparrow study was low, it seems unlikely that differences in study design account for the lack of effect found in what is now three *Ammodramus* species. The wide range of approaches taken across all conspecific attraction studies lends credibility to the possibility that conspecific attraction may not be an important component of the habitat selection process in this genus.

It should be noted that of the ten experimental studies of conspecific attraction in songbirds we found in the literature (Table 1) most lasted for just one to two years, including our own. Parameters relating directly to reproductive output, such as nest success and the number of breeding pairs, were measured in only two studies other than ours (Ward and Schlossberg 2004; Harrison et al. 2009, respectively); most studies looked primarily at male settlement. Given the substantial investment in equipment and monitoring effort that is needed to implement audio broadcast studies, more information

is needed on both the short and long term demographic consequences of these manipulations and on how patterns of conspecific social cue use vary across life history strategies and taxonomic groups. The need for such information is especially important if we are to promote the use of the broadcast methods implemented in these studies for applied songbird conservation and restoration efforts, as is frequently done (e.g., Ward and Schlossberg 2004; Hahn and Silverman 2007). For example, in attempting to restore a species to an unoccupied or restored area, the extent and duration of audio broadcast treatments necessary to elicit a response would be a critical piece of information. Likewise, if males respond to broadcast treatments but are unable to subsequently attract mates to these areas, or if breeding success is low, the utility of implementing audio broadcast treatments is lost. Although the long-term effects of artificial social attraction techniques are better understood for colonial seabirds (e.g., Kress 1983, Kress and Nettleship 1988, Parker 2007), the applicability of these results for songbird species is not certain. Only when we have a better understanding of how fitness is affected by the use of artificially simulated social cues can the feasibility of audio broadcast treatments for songbird restoration efforts be adequately assessed.

In light of the many efforts that are underway to restore ecosystem function to threatened habitats such as coastal salt marshes, understanding the mechanisms that promote colonization by target species is critical (Reed 2004; Gilroy and Sutherland 2007). Even when pre- and post-restoration monitoring is achieved in restoration projects, the lack of experimental controls often precludes an understanding of what specific elements promoted the success or failure of a particular project (e.g., Seigel et al. 2005). This deficiency is further fueled by our basic lack of understanding of the

relative importance of social versus ecological cues in animal settlement decisions. The current debate on assisted colonization also places a premium on information that allows us to understand how animals respond to cues pertaining to habitat suitability (e.g. McLachlan et al. 2007; Ricciardi and Simberloff 2009). For species that are unable to respond to rapid changes in their habitats due to climate change, our ability to promote habitat use at new or restored sites will be directly related to our knowledge of the mechanisms driving habitat selection. Clearly experimental studies of conspecific attraction will continue to advance our understanding of the role of social cues in the habitat selection process, as well as begin to shed light on larger questions pertaining to species distribution patterns and colonization behavior.

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Table 1. Summary of published experimental results of conspecific attraction experiments on songbird species.

Species	Plots ^a	Plot Size	Treatment	Timing/ Duration	Season ^b	Parameters measured	Effect?	Citation
Least flycatcher <i>Empidonax minimus</i>	5	8 ha	Conspecific decoy, songs and calls	10 hrs/day 14 days	Settlement (1)	Male visitation	N/A (no analysis performed, but effect is suggested)	Mills et al. 2006
Least flycatcher <i>Empidonax minimus</i>	7	0.79 ha	Local conspecific song	6 hrs/day ~65 days	Settlement (2) Breeding (2)	Density	Yes	Fletcher 2007
Black-capped vireo <i>Vireo atricapilla</i>	7	15-71 ha	Cowbird removal, local conspecific song and decoy, heterospecific song	6.5 hrs/day ~115 days	Settlement (2) Breeding (2)	Density Nest Success	Yes – density Yes – breeding success (cowbird control plots only)	Ward & Schlossberg 2004
Pied flycatcher <i>Ficedula hypoleuca</i>	4	50 x 50 m	Conspecific song	~ 7 hrs/day 21 days	Settlement (1)	Occupancy	Yes	Alatalo et al. 1982
Nelson's sharp-tailed sparrow <i>Ammodramus nelsoni subvirgatus</i>	20-22	50 m radius circle	Conspecific song and decoy	6 hrs/day 10-12 days	Settlement (2) Post-season 2)	Male settlement	No	Nocera et al. 2006
Baird's Sparrow <i>Ammodramus bairdii</i>	6	9 ha	5 local conspecific songs, heterospecific song	6 hrs/day 75 days	Breeding (1)	Density	No	Ahlering et al. 2006
Brewer's sparrow <i>Spizella breweri breweri</i>	44	100 m radius circle	Local conspecific song	6 hrs every other day 18 days	Settlement (1) Breeding (1)	Male visitation Territory occupancy	Yes – male visitation No – breeding pairs	Harrison et al. 2009
Black-throated blue warbler <i>Dendroica caerulescens</i>	8	800 m transect	12 local conspecific songs	9.5 hrs/day 31 days	Settlement (1)	Male abundance/ territories	Yes	Hahn & Silverman 2007
Black-throated blue warbler	36	N/A	Local conspecific songs,	10 hrs/day 10-12 days	Post-breeding (1)	Prospecting Male settlement	Yes – prospecting Yes – male	Betts et al. 2008

<i>Dendroica caerulescens</i>			fledgling/female, decoys			Female settlement	settlement Yes – female settlement	
American redstart <i>Setophaga ruticilla</i>	12	9 ha	Local conspecific song (75 individuals)	9.5 hrs/day 31 days	Settlement (2)	Male density	Yes	Hahn & Silverman 2006
American redstart <i>Setophaga ruticilla</i>	7	0.79 ha	Local conspecific song	6 hrs/day ~65 days	Settlement (2) Breeding (2)	Density	Yes	Fletcher 2007
Bobolink <i>Dolichonyx oryzivorus</i>	20-22	50 m radius circle	Conspecific song Decoy	6 hrs/day 10-12 days	Settlement 2) Post-season (2)	Male settlement	Yes	Nocera et al. 2006

^a Number of experimental plots (controls not included)

^b Number of seasons in which cues were broadcast in parentheses.

Table 2. Mean number of saltmarsh sparrows, nests, and chicks fledged per plot \pm SD (N = 20) at high-density, occupied study marshes and at low-density/unoccupied study marshes (N = 11). Min – max in parentheses.

		Control (N = 10)	Treatment (N = 10)
<i>High-Density Marshes</i>			
# Birds	2008	4.3 \pm 2.9 (0 - 13)	3.7 \pm 2.5 (0 - 11)
	2009	4.7 \pm 2.5 (0 - 10)	4.9 \pm 2.3 (0 - 11)
# Nests ^a	2008	3.2 \pm 2.4 (0 - 8)	2.7 \pm 2.2 (0 - 8)
	2009	6.1 \pm 3.1 (1 - 10)	5.5 \pm 3.2 (1 - 10)
# Fledged	2008	6.1 \pm 4.7 (0 - 14)	4.6 \pm 6.1 (0 - 16)
	2009	0.5 \pm 0.8 (0 - 2)	0.4 \pm .0 (0 - 3)
<i>Low-Density Marshes</i>		Pre-Treatment ^b	Treatment
# Birds		0.9 \pm 1.8 (0 - 5)	0.7 \pm 1.8 (0 - 6)
# Nests		0.2 \pm 0.4 (0 - 1)	0.2 \pm 0.4 (0 - 1)
# Fledged		0	0

^a Nest searching/monitoring occurred for 12 weeks in 2008 and eight weeks in 2009.

^b Pre-treatment surveys took place in 2004, 2006 – 2008, depending on the site.

Table 3. Results of repeated measures ANOVA relating saltmarsh sparrow abundance to audio treatment effect using “week” (top) and the number of weeks since the new moon, “lunar week” (bottom) as the temporal covariate. The between subjects test results were identical for both models.

	DF	SS	MS	F	<i>p</i>
Between subjects (<i>Both Models</i>)					
Treatment	1	2.23	2.23	0.13	0.73
Site	1	184.53	184.53	10.30	0.005
Residuals	17	304.38	17.91		
Within subjects (<i>Week Model</i>)					
Week	7	154.77	22.11	4.53	<0.001
Year	1	48.83	48.83	10.01	0.002
Treatment*Week	7	34.45	4.92	1.01	0.43
Treatment*Year	1	10.15	10.15	2.08	0.15
Week*Year	7	92.90	13.27	2.72	0.01
Residuals	277	1350.97	4.88		
Within subjects (<i>Lunar Model</i>)					
Lunar	3	7.53	2.51	0.45	0.72
Year	1	48.83	48.83	8.76	0.003
Treatment*Lunar	3	1.61	0.54	0.10	0.96
Treatment*Year	1	10.15	10.15	1.82	0.18
Lunar*Year	3	13.81	4.60	0.83	0.48
Residuals	289	1610.13	5.57		

Table 4. Results of ANOVA relating 2008/2009 saltmarsh sparrow nest abundance (top) and fledgling abundance (bottom) to audio treatment and site. Years were analyzed separately due to unequal sampling effort between years.

	DF	SS	MS	F	P
<i>Nest Abundance</i>					
2008					
Treatment	1	5	5	0.46	0.51
Site	1	16.2	16.2	1.48	0.24
Residuals	17	186.0	10.94		
2009					
Treatment	1	1.8	1.8	0.20	0.66
Site	1	24.2	24.2	2.69	0.12
Residuals	17	153.2	9.01		
<i>Fledging Abundance</i>					
2008					
Treatment	1	11.25	11.25	0.36	0.56
Site	1	1.25	1.25	0.04	0.84
Residuals	17				
2009					
Treatment	1	0.05	0.05	0.07	0.80
Site	1	2.45	2.45	3.35	0.09
Residuals	17	12.45	0.73		

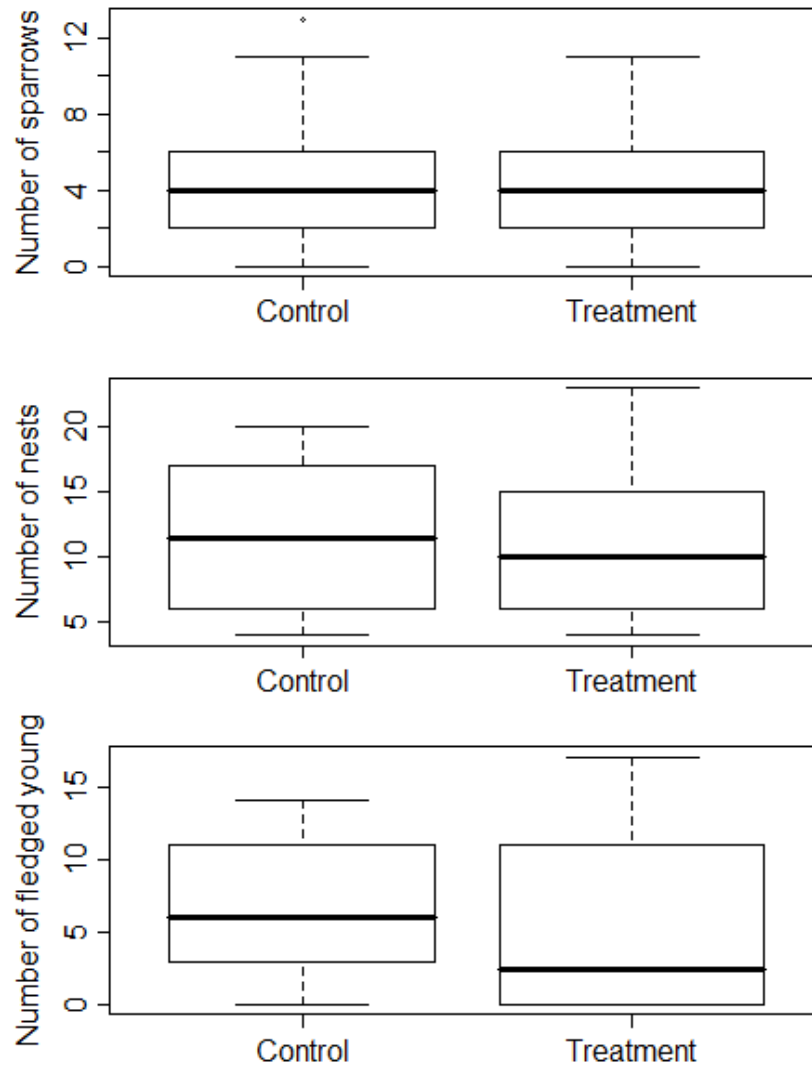


Figure 1. The number of saltmarsh sparrows (top), sparrow nests (middle), and sparrow fledglings (bottom) observed in control plots versus audio treatment plots in 2008-2009. The maximum and minimum values observed for each variable are represented by the whiskers, the 25th and 75th quartiles are represented by the lower and upper lines of the box, and the dark shaded lines represent the median values. Outliers are symbolized with a *. No significant differences between control and treatment groups were detected.

CHAPTER 4: PLANNING FOR SEA LEVEL RISE: QUANTIFYING PATTERNS OF SALTMARSH
SPARROW NEST FLOODING UNDER CURRENT SEA LEVEL CONDITIONS

ABSTRACT

Climate change and sea-level rise pose an imminent threat to the survival of coastal ecosystems and the species associated with them, but the mechanisms by which terrestrial animals inhabiting these areas may be affected by these changes are not well studied. During 2007-2009, we quantified the frequency and duration of nest flooding events at two salt marshes located in the Northeast United States that are of global importance to saltmarsh sparrow *Ammodramus caudacutus* conservation. Although nest flooding is a major cause of nest failure for this species, the difference between the tide heights at which sparrow nests experience lethal vs. non-lethal flooding is not documented, nor is it known how frequently nests are inundated. We tested whether variables associated with the timing of nest initiation, tide height and the number of flooding events can be used to estimate three aspects of nest fate; the probability of nest success, the probability of nest failure due to flooding, and the number of offspring lost to flooding, using logistic and zero-inflated Poisson models. Only 28 of 191 nests did not experience flooding and just 35 nests were successful; 103 failed due to flooding and 53 failed for other reasons. The mean (\pm SD) number of flooding events observed was 2.8 ± 2.1 (min-max: 0 – 10) and on average, the difference between the maximum non-flood height for successful and failed flooded nests was just 5 cm. The top performing model for each measure of nest fate included variables related to tidal metrics, but model composition among the three model types differed in regards to the importance of particular tidal variables and the timing of nest initiation. These results highlight the extreme vulnerability of saltmarsh sparrows to

even slight increases in sea level and demonstrate the importance of making clear distinctions about which aspects of nest fate are of interest when studying the mechanisms driving nest fate.

INTRODUCTION

The International Panel on Climate Change (IPCC) estimates that global mean sea level will rise at a rate of 1.5 to 9.7 mm/yr throughout the 21st century, resulting in an increase of 0.18 to 0.59 m by 2100 (IPCC 2007). More recent estimates predict greater sea-level rise, of 0.5 to 2.0 m by 2100 (e.g., Rahmstorf 2007; Pfeffer et al. 2008). The current acceleration of global sea-level rise is apparent from records taken in the 20th century; sea-level rise averaged between 1 and 2 mm/year in this period, a rate ten times that of the past 3000 years (IPCC 2001). The most significant processes contributing to the acceleration of sea-level rise at the global scale are the thermal expansion of sea water and the melting of continental ice sheets due to global warming (Parmesan and Matthews 2006). At the local scale, processes such as post-glacial land rebound, changes in climatic and meteorological patterns, and groundwater extraction produce variation in the extent of sea-level rise observed at any one location (Valiela 2006).

Sea-level rise, along with increases in temperature and changes in precipitation (IPCC 2007), poses an imminent threat to the survival and persistence of coastal ecosystems and their associated species (e.g., Erwin et al. 2006; Craft et al. 2009; Gedan and Bertness 2009). Coastal marshes are particularly vulnerable to climate change due to their sensitivity to alterations in the frequency and magnitude of tidal inundation (Reed 1990; Morris et al. 2002) and climate (Bertness and Pennings 2000). Changes in vegetation zonation, food web dynamics, and the frequency of tidal inundation are just a few ways in which climate change and sea-level rise may particularly affect avian species occupying these habitats (Hughes 2004; Erwin et al. 2006). However, few studies to date have focused on exactly how these mechanisms will affect species persistence and as a

result, their relative importance is not well documented. An understanding of the extent to which the species that rely on these ecosystems for foraging, breeding, stopover, or overwintering habitat have the capacity to respond or adapt to the ecosystem changes wrought by climate change, given their life history requirements, is critical for establishing conservation priorities and actions.

Here, we focus on a species inhabiting the high marsh zone of the Atlantic coast of North America. The saltmarsh sparrow (*Ammodramus caudacutus*, family: Emberizidae) occurs exclusively in salt marshes and as such is among the group of marsh-nesting birds most threatened by sea level rise along the Atlantic coast (Erwin et al. 2006). It is currently considered a species of conservation concern both globally (IUCN: *Vulnerable*; BirdLife International 2009) and nationally (*Redlist*; American Bird Conservancy 2007), and has been identified by Partners in Flight (an international cooperative partnership for bird conservation efforts) as a species in need of immediate conservation action (Rich et al. 2004). The entire global breeding range of this species is contained within the narrow band of tidal marsh present from coastal Maine to Virginia; up to half of the global breeding population is estimated to breed in southern New England (Dettmers and Rosenberg 2000). A lack of comprehensive surveys throughout the species' range makes estimation of global population size difficult; however, recent preliminary estimates put the population size in the range of ~ 30,000 – 50,000 individuals (Elphick et al. 2009).

Even more so than other saltmarsh birds, saltmarsh sparrow breeding success is intimately tied to the lunar tidal cycle (Greenberg et al. 2006). Successful nests are characterized by a close synchronization to the tidal cycle such that the 22-27 day nesting

period (egg laying, incubation, and care of nestlings) falls within the approximately 28-day lunar cycle; females that initiate breeding within 2.9 ± 0.6 SD days after a flood tide have a greater chance of successfully fledging young, regardless of nesting substrate vegetation type or elevation (Gjerdrum et al. 2005; Shriver et al. 2007). It is thought that extreme flooding events during spring tides, which occur during the new and full moons, synchronize nesting activity by flooding nests and forcing simultaneous re-nesting (e.g., Shriver et al. 2007). Nest flooding also occurs in association with large storm events that increase water flow in the marshes' watersheds. In recent decades, nest fate analyses indicate that approximately 60% of all nest failures occur as a result of nest flooding (DeRagon 1988; Gjerdrum et al. 2005; Shriver et al. 2007) and even nests that succeed in fledging young sometimes experience partial losses due to flooding (Humphreys et al. 2007; Gjerdrum et al. 2008).

Previous studies have examined the role of domed nest architecture in reducing risk of egg loss due to flooding (Humphreys et al. 2007), and shown that eggs can survive nest inundation if they do not float out of the nest (Gjerdrum et al. 2008). Even nestlings may withstand short periods of nest inundation, as is evidenced by partial losses within a given nest, although the exact mechanisms by which nestlings avoid drowning are not known (Gjerdrum et al. 2008). The frequency, duration and timing of nest flooding in relation to tide height are not well understood, however, and it is unclear to what extent most nests experience inundation under current climatic conditions. Similarly, the effects of multiple flooding events and the potential consequences of nest flooding at different phases of the nest cycle are unknown. For example, although we know that nests sometimes experience partial losses due to flooding, the tide height at which sparrow

nests experience lethal vs. non-lethal flooding is not known. To understand how even small changes in sea level can be expected to affect saltmarsh sparrow breeding success, it is necessary to understand the mechanisms currently causing nest flooding and failure.

In this study, we used temperature data loggers to explore the relationship between nest flooding events and nest fate in a large sample of nests at two sites thought to be of considerable importance for the species' conservation (Elphick et al. 2009). We quantified the frequency and duration of flooding events and determined the relative tide heights associated with flooding versus non-flooding, and with lethal flooding versus non-lethal flooding. We also tested whether variables associated with the timing of nest initiation and high tide height can be effectively used to model the probability of nest success, the probability of nest failure due to flooding, and the number of offspring lost to flooding.

METHODS

We collected data on nest fates between 21 May and 24 August 2007 in study areas at two marshes located along the central Connecticut coastline of Long Island Sound in the northeastern U.S. (Hammonasset State Park, 41°15'47"N, 72° 33'55"W, study area 31.5 ha; East River, 41°16'24"N, 72°39'12"W, study area 25.2 ha), and in 20 2-ha plots located in the vicinity of these study areas from 6 May to 5 August 2008 and 25 May to 24 July 2009. The Hammonasset and East River salt marshes were chosen because of their large size (209 ha and 289 ha, respectively), the presence of high-marsh habitat used by breeding saltmarsh sparrows, and high densities of nesting sparrows relative to other sites (Gjerdrum et al. 2005). The two sites are approximately 8 km apart and are distinct

marsh systems, lying within different watersheds and separated by non-saltmarsh (suburban/forest) habitat.

Nest Monitoring

Both study areas were sampled such that nest searching effort was consistent across all portions of the two sites. Study areas were systematically searched twice weekly, with additional nest searching occurring during nest monitoring activities. Nest locations were recorded with a Garmin GPSMap76; a flag was placed approximately 5 m from each nest to identify the nest location, while limiting the potential for the flag to act as a cue to predators. Nests were monitored every 2-5 d to track the outcome of the nesting attempts. We used temperature data-loggers (Thermochron iButtons, Maxim, Sunnyvale, California) to track the exact timing of flooding events and nest failure or fledging (cf. Gjerdrum et al. 2008) in an opportunistic selection of nests each year. The iButtons were programmed to collect nest temperature data at 15 minute intervals; additional iButtons were deployed in empty nests to measure the corresponding ambient temperatures. The timing of iButton deployment at each nest was dependent on when the nest was found, therefore the onset of temperature sampling relative to nest initiation varied among nests. Because nests that did not receive iButtons lacked reliable measurements of the timing and duration of flooding events or of the exact timing of fledging or failure, we excluded these nests from this study.

Nest Fate and Flooding

Nests that fledged at least one chick were considered to be successful for the purposes of this analysis, whereas nests that failed to fledge at least one chick and showed evidence of flooding were considered to have failed due to tidal flooding. Nests that experienced partial flooding (one or more eggs or dead chicks observed outside of the nest cup following a high tide) prior to a lethal predation event were considered to have failed due to predation (i.e., nest failure was taken to be the point at which the last egg or chick was lost from a nest). For a nest to be considered to have failed due to flooding, the following conditions were both required:

- 1) Nest temperature data had to indicate at least one flooding event, defined as a rapid drop in temperature corresponding to the timing of a high tide (cf. Gjerdrum et al. 2008) such that nest temperatures dropped to below 26.7°C for more than one 15-minute sampling period. The average temperature of active saltmarsh sparrow nests ranges from a mean (\pm SD) of $33.6 \pm 1.4^{\circ}\text{C}$ to $37.2 \pm 1.4^{\circ}\text{C}$, depending on nest stage and time of day, versus a mean minimum of $24.1 \pm 1.7^{\circ}\text{C}$ during flooding (Gjerdrum et al. 2008).
- 2) Regardless of how many flooding events occurred prior to nest failure, the ultimate timing of nest failure had to correspond with a flooding event. Nests that failed within 12 hours of a flooding event and had additional evidence that the failure was due to flooding (see below), rather than subsequent predation, were also considered failed due to flooding.

The following nest conditions were also used to determine failure due to flooding:

- 1) if the nest was observed to be underwater during a high tide and a subsequent nest check confirmed that the nest was empty;
- 2) if the nest was observed with intact eggs outside the nest (presumably after floating out) following a high tide;
- 3) if the nest was observed with dead chicks inside or close to the nest following a high tide;
- 4) if the nest was observed to be intact with eggs that were cold, wet, and dirty following a high tide.

The timing and duration of flooding events were determined for each nest by examining nest temperature data in relation to ambient temperatures and local tide heights. Raw data on observed tide heights and timing came from the Tides and Currents website of the U.S. National Oceanic and Atmospheric Administration's National Ocean Service (NOAA 2009). Tide data were retrieved from the New Haven Station (#8465705, 41°17'N, 72°54.5'W), the closest tide station to our study areas (approximately 20 - 30 km from East River and Hammonasset SP, respectively), where the timing of tides is approximately 15 minutes delayed relative to our study sites (www.ctdep.gov). We used the mean lower low water (MLLW) tidal datum and the local standard/local daylight savings time. MLLW refers to the average height of the lower of the two low tide heights of each tidal day observed over the National Tidal Datum Epoch (NOAA 2009). Although the specific tide heights associated with various aspects of nest flooding are included in our study, information on how the tide heights at our study marshes vary in relation to that of New Haven Station is not available. As a result, we do not assume that the tide measurements are equivalent at the three sites, rather, the tide

data provided in this study serve as a basis for comparison when assessing the differences among tide heights associated with nest fate and flooding.

The onset of each flooding event was taken to be the time at which the nest first experienced a sudden drop in temperature to less than 26.7°C; the duration was calculated from this point until the time at which the nest temperature rose above 26.7°C. Low nest temperatures or other temperature fluctuations that did not coincide with the timing of a high tide were not considered flooding events. In these cases, it is likely that the iButton was positioned within the nest in such a way that it was exposed to ambient conditions.

In 54 of our 191 nests, flooding events were logged at least once wherein the nest temperatures cooled to the threshold flooding temperature more than an hour before the high tide, or remained depressed long after flood waters would have receded (< 8% of all events). Because these nests subsequently remained viable, it was difficult to discern the exact duration of the flooding event or determine whether the cool temperatures were due to submersion rather than female or nestling behavior at the nest. For example, early in the nestling phase when chicks are small, they could be positioned in the nest cup in such a way that they have no contact with the iButton. As a result, the subsequent temperature readings would reflect only the ambient air temperature for those periods. Alternatively, when the chicks are more developed, they may climb in and out of the nest, also leaving the iButton exposed. Other explanations such as females moving the iButtons to the edge of the nest cup, or leaving the nest unattended for prolonged periods of time are also possible. To assess whether the prolonged low temperatures observed in 42 flood events lasting more than 300 min could possibly be attributed to nestling behavior, we determined when in the nest cycle each event happened. Only 14 of these prolonged

events occurred during the nestling stage, however, so other possible explanations such as female behavior are likely. Because, physiologically, it is the prolonged low temperature that affects the viability of eggs or chicks, all flood durations were ultimately retained; however, there are a number of possible reasons why nest temperatures might remain depressed. Given the uncertainty associated with determining the precise duration of flooding events, this variable was not examined in our statistical analyses.

Analysis

Summary statistics were calculated for the frequency and mean duration of nest flooding events observed at each nest, the maximum tide height that the nest withstood without flooding, and the maximum tide height experienced both during temperature sampling at the nest and during the nest's entire active period. Sampling metrics for each nest were determined, including the number of days for which temperature data were collected, the stage at which the nest was first found (day 1 of incubation = day 1 of the nesting cycle), and the stage in which the iButton was deployed at the nest. To assess how the probability of nest flooding and failure due to flooding varied throughout the nesting cycle, we standardized the data from all years by nest phase such that the first day of incubation equaled day one of the nest phase. We then calculated the proportion of sampled nests that flooded or failed due to flooding on each day of the nesting cycle.

Prior to our analysis of nest fate, we grouped 11 explanatory variables into three categories, based on our expectation that (a) the timing of nest initiation relative to the tidal cycle ("timing" variables), and (b) the magnitude and frequency of high tides ("tide" variables) would likely be important in explaining nest fate, and that (c) various sampling

effects related to the timing and duration of iButton deployment (“sampling” variables) could complicate interpretation of the data (Table 1). Because sampling parameters do not actually affect nest fate, we began by selecting the best performing sampling model from six combinations of four sampling variables using information-theoretic model selection (Burnham and Anderson 2002). This model was then used as a baseline to which all other combinations of tidal and timing variables were added (e.g., Nordby et al. 2009). Ten candidate models related to timing (five models) and the tide (five models) were created based on our understanding of the biology of nest fate in this system; a post-hoc model (“pooled model”) was also created by combining the best performing timing model with the best performing tide model to determine whether doing so further improved model fit. All models were estimated for three aspects of nest fate: (1) nest success vs. failure (Nest Success models), (2) nest failure due to flooding vs. all other fates (Flooding Failure models), and (3) number of eggs/chicks lost to flooding (Fitness Loss models). Although nests that failed due to flooding were a subset of all failed nests, we were interested in modeling nest fate in a way that specifically addressed how flooding events lead to nest failure. In addition, because simple binary outcomes such as “failure” or “success” do not capture the magnitude of fitness losses due to flooding, we considered it important to include the fitness loss model. Pairwise correlations and variance inflation factors (Zuur et al. 2010) for all covariates indicated that collinearity was not an issue (all VIF < 3; with the exception of maxtide and maxtideib, which were never used in the same model) and all variables were retained in our models. All analyses were computed in R (R Development Core Team 2009)

Although the binary dependent variables for the Nest Success and Flooding Failure models were suitable for logistic regression analysis, the dependent variable for the Fitness Loss model was a count of the total number of offspring (eggs and/or chicks) lost to flooding at each nest. Because of the excessive number of zeros observed for this count, we modeled fitness loss using a zero-inflated Poisson model (Zuur et al. 2010). Zero-inflated models account for excess zeros in one of two ways. The zeros can either be modeled in two separate steps using a binomial model to model the probability that a positive count is observed and a truncated Poisson model for non-zero count data (ZAP model), or, the probability of measuring false zeros can be analyzed using a binomial model while the “true” zeros and count data are modeled using a Poisson general linear model (GLM) (ZIP model) (Zeileis et al. 2008; Zuur et al. 2009). The basic difference between ZIP and ZAP models is that the nature of the zeros is left undefined in ZAP models. For our purposes, we had no prior reason to distinguish between true or false zeros in our analyses; therefore we ran both types of models to check for consistency, but report only the results of the ZAP models.

The two sets of 10 models were compared separately using information-theoretic model selection (Burnham and Anderson 2002) and the significance of individual predictors in the top performing models was evaluated at the $\alpha = 0.05$ level. All means are given \pm SD.

RESULTS

We collected temperature data from a total of 191 nests ($n = 33$, 2007; $n = 68$, 2008; $n = 90$, 2009). On average, iButtons were deployed on day 5.7 ± 3.3 d of the nesting cycle

(day 1 = first day of incubation; most nests have 3-5 eggs). Thirty-five nests (18%) were successful, fledging an average of 2.5 ± 1.1 chicks, while losing an average of 0.6 ± 1.0 offspring to flooding. One hundred and three nests (54%) failed due to flooding, losing an average of 3.5 ± 0.9 offspring to flooding, and 53 (28%) failed due to predation or undetermined reasons, losing an average of 0.3 ± 0.6 offspring to flooding. Overall, 56% of all eggs and chicks were lost to flooding. Only 28 nests (15%) experienced no flooding events during the time in which they were sampled; 133 nests (70%) flooded at least two times. The average number of flooding events observed across all nests was 2.8 ± 2.1 (min–max: 0–10; Figure 1) and the average duration of depressed nest temperatures, including the 42 prolonged events, was 140 ± 106 min (Figure 2). The mean maximum tide height occurring during all observed flood events was 2.31 ± 0.12 m above MLLW (min–max: 1.71–2.76 m), while the mean maximum tide height was 2.29 ± 0.10 m above MLLW for non-lethal flood events (which flood the nests, but do not cause complete nest mortality) and 2.30 ± 0.13 m above MLLW for lethal flood events. The mean maximum tide height that nests experienced without flooding was significantly lower than that of all flood events (maximum non-flood height: 2.19 ± 0.07 m above MLLW, min–max: 1.98–2.40 m, $t_{189} = -5.14$, $p < 0.001$).

Sampling

The mean day in the nesting cycle on which nests were found was similar for failed and successful nests (successful: 4.6 ± 4.0 d, failed: 4.1 ± 3.2 d; $t_{189} = -0.77$, $p = 0.45$) and for nests that failed due to flooding and other nests (fail-flood: 3.8 ± 2.8 d, other: 4.6 ± 3.9 d; $t_{189} = 1.62$, $p = 0.11$), although nests that were successful were

unsurprisingly sampled over longer periods than were those that ultimately failed (successful: 14.5 ± 4.0 d, failed: 7.0 ± 4.4 d; $t_{189} = -9.29$, $p < 0.001$). The stage at which iButtons were deployed at nests also was similar for failed and successful nests (successful: 6.6 ± 4.0 d, failed: 5.5 ± 3.2 d; $t_{189} = -1.69$, $p = 0.09$) but occurred slightly earlier in nests that failed due to flooding than for other nests (fail-flood: 5.2 ± 3.1 d, other: 6.3 ± 3.6 d, $t_{189} = 2.23$, $p = 0.03$). Nest timing and tidal flooding varied among years; in 2009, nests were initiated later relative to the new moon than in other years (2007: 8.5 ± 6.7 d, 2008: 6.1 ± 5.0 d, 2009: 11.9 ± 5.3 d; $F_{2,188} = 21.98$, $p < 0.001$) and experienced higher maximum tide heights (2007: 2.33 ± 0.07 m, 2008: 2.39 ± 0.07 m, 2009: 2.40 ± 0.11 m; $F_{2,188} = 8.98$, $p < 0.001$). The mean duration of flooding events was greatest in 2008 (2007: 116 ± 99 min, 2008: 158 ± 120 min, 2009: 136 ± 94 min; $F_{2,188} = 5.22$, $p = 0.01$).

Nest Flooding

Successful nests withstood higher tides without flooding, on average, than did failed nests (successful: 2.23 ± 0.07 m, failed: 2.17 ± 0.09 m; $t_{189} = -3.69$, $p < 0.001$), indicating that successful females either selected locations at higher elevations or placed their nests higher in the vegetation. When nests that failed due to flooding were compared to all other nests, flooded nests clearly had a lower tide height at which they began to flood (fail-flood: 2.16 ± 0.11 m, others: 2.21 ± 0.06 m; $t_{189} = 3.69$, $p < 0.001$), although the difference, on average, was only 5 cm. In addition, they were subjected to higher maximum tides over the period in which they were active (fail-flood: 2.39 ± 0.11 m, others: 2.37 ± 0.09 m; $t_{189} = -1.96$, $p = 0.05$) and experienced more flooding events

than nests of other fates (fail-flood: 3.2 ± 1.8 events, other: 2.3 ± 2.2 events; $t_{189} = -3.20$, $p = 0.002$). When nest data across all years were standardized by nest phase to assess daily survival, the proportion of nests that experienced flood events peaked on day two of the incubation period and again on day eight of the 10 day nestling phase (i.e. day 20 of the nesting cycle), whereas the proportion of nests that failed due to flooding peaked on day six of the nestling phase (Figure 3).

Nest Fate Models

In addition to the clear differences found in the timing and extent of flood events observed between failed and successful nests, and between nests that failed due to flooding and nests of other fates, our model selection process indicated that the best performing models included several variables related to tidal metrics. The best performing logistic model for Nest Success consisted of the base sampling model (Sampled + Dayfound + Dayibut) plus the number of flooding events experienced during temperature sampling (Table 2). The Akaike weight for this model ($w = 0.25$) suggests that it performed moderately well in predicting nest success relative to all other models. Conversion of parameter estimates to odds-ratios (e^{β}) indicates that for each additional flooding event experienced, the odds of success decreased by a factor of 0.68 (32%), though the 95% confidence interval for this variable included the value 1.0, indicating that it is not a strong predictor of nest success (Table 3). When each variable was considered at the $\alpha = 0.05$ level, only the number of days sampled and day of iButton deployment remained significant predictors of nest success (Table 3). Pooling the top performing models from both the top timing and top tide models resulted in no

improvement in the model variance explained (Pseudo- R^2 of 0.75 for both models) and the model weight was lower ($w = 0.14$).

In contrast to the Nest Success model, the best performing logistic model for Flooding Failure was composed of the base model, plus the maximum tide height experienced during iButton sampling, the maximum tide height withstood without flooding, the number of flood events, and the year. This model, however, had a low weight ($w = 0.09$) and model fit was much improved in the pooled model, which included an additional timing variable describing the number of days between the new moon and nest initiation (Table 2). The Akaike weight for this model suggests that it performed much better than all other models in predicting failure due to flooding ($w = 0.83$), however, the low Pseudo- R^2 value (0.26) indicates that a substantial amount of variance remains unexplained.

When each variable was considered at the $\alpha = 0.05$ level, only three variables were significant in explaining failure due to flooding: the maximum tide height at which nests did not flood, the number of days initiated post new moon, and the number of days on which temperature data were collected (Table 4). The odds of failing due to flooding rose for each additional day the nest was initiated after a new moon. Conversely, for every additional centimeter increase in the maximum tide height that the nest could withstand without flooding, the odds of failing due to flooding fell by a factor of 0.92 (8%), when all other variables are fixed.

The selection process for the best Fitness Loss model identified the base model with two tide variables added – the maximum tide height experienced during iButton sampling and the maximum tide height a nest withstood without flooding – as the best

performing model ($w = 0.79$) (Table 2). Comparison of Akaike weights for all fitness loss models suggests that model performance was not improved in the pooled model ($w = 0.16$). For the top Fitness Loss model, only the number of days the nest was sampled was significant in explaining the number of offspring lost in the truncated Poisson model ($p = 0.03$). Both tide variables were significant in explaining the probability of nests losing one or more offspring to flooding ($p < 0.001$, both variables; Table 5). The probability of losing offspring to flooding decreased by a factor of 0.90 (10%) for every centimeter increase in the maximum tide height withstood without flooding and increased by a factor of 1.14 (14%) for every centimeter increase in the maximum tide experienced during iButton deployment (Table 5).

DISCUSSION

Our study of flooding in saltmarsh sparrow nests indicates that inundation due to tidal flooding is not simply a sporadic event, nor does it always lead to nest failure. Instead, it appears to be a regular and frequent feature of the species' reproductive biology. Only 15% of the nests evaluated in this study did not experience a single flooding event during our temperature sampling, and even these nests may have flooded before iButtons were deployed. Whether this pattern is typical of the species' evolutionary history, or we are already observing the effects of sea-level rise, is not known. Regardless, given that the two salt marshes sampled in this study are thought to be among the most important in the species' breeding range (Elphick et al. 2009) and the extremely high rate of nest failure observed in this study, our findings have serious implications for the prospects of saltmarsh sparrows under current sea-level rise projections.

Gjerdrum et al. (2008) first noted the tendency of saltmarsh sparrow females to resume incubation after nest flooding, a behavior that was confirmed in our study by the large number of nests in which the female continued to attend the nest following tidal inundation. Exactly how female behavior in response to nest flooding is determined is not known, but the duration and timing of the flood event in relation to the stage of egg development would seem to have important physiological implications (Webb 1987). Experimental work by Olson et al. (2006) indicates that zebra finch *Taeniopygia guttata* embryos exposed to frequent cooling periods experience reduced growth efficiency and impaired growth rates compared to control embryos kept at constant incubation temperatures. Tests of the physiological effects of prolonged depressed temperatures combined with saltwater submersion on embryo and chick development are lacking, however. In our study, we were unable to determine if eggs that had been subject to tidal submersion and subsequently failed to hatch failed because of the flooding, or for other reasons such as female abandonment. Interestingly, nests containing chicks sometimes experienced only partial losses due to drowning. In these cases, we speculate that surviving individuals climbed out of the nest and clung to higher vegetation until flood waters receded. Chicks within a nest sometimes differ noticeably in their rates of physical development (T. Bayard, pers. obs.), suggesting that some offspring might be at an advantage if temporary evacuation of the nest is an option. Video recording at the nest would be a helpful future step in determining exactly how nestlings behave during flooding events.

Our data suggest that the maximum high tide a nest experiences is correlated with the number of eggs and chicks lost to flooding. Nests that are capable of withstanding

higher tides without flooding also tend to have a better chance at success. On average, however, the maximum tide height withstood without flooding for successful nests was just 5 cm higher than that for failed flooded nests, indicating just how precarious the species' situation is. When these tide variables were incorporated into our models of nest success and nest flooding, they were sometimes outperformed by variables related to the magnitude of sampling effort. This result is in some ways unsurprising; sampling effort has long been recognized to have an important influence on the apparent level of nest success observed in a study population (Mayfield 1961). Conventional wisdom holds that successful nests are more likely to be discovered than are nests that ultimately fail, simply because they exist for a longer period of time. In our dataset, most nests were found early in the nesting cycle and there was no difference in the timing of initial nest discovery for failed and successful nests. Not surprisingly, however, nests that were ultimately successful had significantly more days for which temperature data were sampled. IButtons were deployed marginally (on average 1 d) earlier in nests that failed due to flooding than in nests with other fates, a result that we attribute to the earlier deployment of iButtons in 2008 and 2009 than 2007, a year in which the proportion of nests that failed due to flooding was low relative to other years.

Although the best model for each measure of nest fate included variables related to tidal metrics, the specific variables differed among models. The Flooding Failure and Fitness Loss models included the maximum tide height experienced during iButton sampling and the maximum non-flood tide height, whereas the top Nest Success model included the number of flooding events experienced. Although we find all of these models to be biologically plausible, this discrepancy highlights how the commonly used

approach of modeling nest fate simply as success versus failure, where success can imply as few as one offspring has fledged or as many as a complete brood, can influence our understanding of the biology of nest fate in ways that are not always apparent. We chose to examine models of fitness loss because this measure isolates the effect of within-nest mortality from variation in egg production and thus emphasizes reductions from an individual's reproduction potential, whatever that may be. But, the converse (number of young fledged) could be modeled instead. Because these metrics are directly related to fitness, we contend that whenever possible, counts of fitness loss or gain are better than a simple binary measure of success when identifying important factors that influence nest fate in breeding birds.

Previous studies have documented the importance of nest timing and synchrony with the lunar tidal cycle in predicting saltmarsh sparrow nest success (e.g., DeRegon 1988; Shriver et al. 2007; Gjerdrum et al. 2008). In our study, the timing of nest initiation relative to the new moon was significant in the best Flooding Failure model only, and was not included in the top models for Nest Success or Fitness Loss. One possible explanation for this result may be the extremely high rate of nest failure due to flooding that we observed in our 2009 nests, which constituted 47% of our overall sample. Daily high tides averaged 19.8 cm and 18.6 cm higher than predicted during June and July of 2009, versus tide heights that were only 9.8 cm higher than predicted in July 2007, and 11.3 cm and 9 cm higher than predicted in June and July of 2008 (NOAA 2009). The high tides of 2009 were at least partially related to higher than normal rainfall. Based on Connecticut State data for the period 1895 – 2009, precipitation was 5.7 cm greater than normal in June 2009 and 6.8 cm greater than normal in July (NRCC

2009). In contrast, precipitation registered 5.5 cm lower in July 2007 compared to July 2009, while 2008 precipitation levels were 3 cm lower than 2009 in June and 2 cm lower in July.

The fact that daily high tides were on average higher than predicted in each of the peak breeding months sampled across the three years of our study, and that precipitation was greater than normal in four out of the five peak breeding months sampled, suggests that our data either come from three worse-than-normal years, or that sea-level rise and climate change are already having an effect on nesting saltmarsh sparrows. Although climate models suggest that an increase in global precipitation is likely under increased global temperatures, changes in the New England region may involve longer, drier, warmer summers with periodic heavy rainstorms (Frumhoff et al. 2007). If this is the case, an understanding of how drier, hotter temperatures will affect saltmarsh ecosystem function is critical. Alternatively, should a long-term increase in precipitation levels in the northeastern U.S. occur along with increases in sea level, the prognosis for saltmarsh sparrow persistence is especially grave. Failure due to flooding comprised 66% of all failures during our study period, compared to 60% of failed nests ($N = 80$) at the same study sites in 2002-2003 (Gjerdrum et al. 2005) and nest success rates (i.e., at least one fledgling produced) dropped from around 41% of all nests in 2002-2003 to 18% in 2007-2009.

In southern New England, which is thought to support a substantial portion of the global population of saltmarsh sparrows (Elphick et al. 2009), salt marshes are already an imperiled ecosystem. In Connecticut, approximately 30% of salt marshes were lost in the last century (Rozsa 1995) and comparisons of the current extent of salt marsh acreage to

historical records from the early 19th century indicate that Rhode Island has lost 53% of its salt marshes (Bromberg and Bertness 2005). In addition, the rate of sea-level rise in Connecticut during the 20th century was greater than the global mean. During 1964-1999, tide gauge data indicate that sea-level rise ranged from 2 mm/yr in the eastern portion of the state (New London) to 2.5 mm/yr in the more westerly portion of the state (Bridgeport) (Peltier 2001). This high rate is partially attributable to the geological history of the state; during the last glaciation event 20-25,000 yr ago, the weight of the ice sheet caused the land to warp and uplift the Earth's crust (Gornitz et al. 2004). After the ice sheet began to retreat around 18,000 years ago, the land responded by slowly sinking at a rate of approximately 0.76-0.89 mm/yr (Gornitz et al. 2004), a process known as glacial isostatic adjustment. Saltmarsh accretion, whereby marshes maintain or build vertical elevation, is not expected to keep pace with both isostatic adjustment and accelerated sea-level rise in this part of Long Island Sound (Donnelly and Bertness 2001). Saltmarsh migration into upland areas is a possibility (Pethick 2001), but the sheer density of human settlement along the northeast Atlantic coast makes it unlikely that natural processes will provide sufficient habitat within the timescale necessary for relatively short-lived organisms such as sparrows to persist. Furthermore, while state and private entities are currently discussing the possibility of managing conversion of upland habitats to salt marsh, the feasibility and effectiveness of this approach for salt marsh ecosystem conservation is completely unknown.

In other parts of the saltmarsh sparrow range, the outlook for the high saltmarsh community is similarly poor. Early estimates suggested that around 50% of coastal New England salt marshes were lost to human alteration and settlement between 1886 and

1976 (Nixon 1982), and more recent estimates suggest average losses of 37% across Maine, New Hampshire, Massachusetts and Rhode Island since European colonization (Bromberg and Bertness 2005). Although accretion rates in New England salt marshes have generally kept pace with or exceeded rising sea level over the past century (Warren and Niering 1993; Kennish 2001), the projected rate of sea-level rise is expected to overcome accretion rates, generating an accretion deficit (Donnelly and Bertness 2001). Salt marshes along the mid- and southern Atlantic coast are already failing to achieve accretion rates that exceed subsidence and sea-level rise rates, and thus will continue to be lost as sea-level rise increases (e.g., Delaware Bay, Phillips 1986; Chesapeake Bay, Wray et al. 1995, Kennish 2001; North Carolina, Hackney and Cleary 1987). A wide variety of anthropogenic impacts, including subsidence caused by subsurface extraction of water, oil and gas (Kennish 2001), and ecosystem changes, such as saltmarsh die-back in response to altered coastal food webs (Silliman et al. 2005), are also major factors currently driving the degradation of saltmarsh communities along the Atlantic seaboard.

If sea-level rise increases the frequency, duration and magnitude of tidal flooding in high saltmarsh habitats, an important question to consider is whether or not any type of physical intervention to reduce the magnitude of tidal flooding (e.g., tide gates) is warranted and/or desired. Tide gates have been used to establish the desired hydrological pattern in restored coastal marshes (Boumans et al. 2002), but the feasibility of financing and achieving widespread installation of these structures to combat salt marsh submergence is not known. Ultimately, it may be the potential loss of the ecosystem services provided by salt marshes and other coastal habitats (e.g., storm surge protection,

ecological productivity, waste treatment; Craft et al. 2009) that provide the incentive necessary to spur action on mitigating the effects of sea-level rise on coastal habitats.

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Table 1. Variables used in models of saltmarsh sparrow nest fate. Variable names are given in parentheses.

Variable	Description
Tide Variables	
Maximum tide height (maxtide*)	The maximum tide height recorded during the time the nest was active.
Maximum tide height iButton (maxtideib)	The maximum tide height recorded during the time temperature data was collected at the nest.
Maximum non-flood height (maxnonflood)	The maximum tide height the nest withstood without flooding.
# of flood events (events)	The number of flooding events observed at the nest, including the event resulting in failure.
Timing Variables	
Days post new moon (dayspstnm)	The timing of nest initiation (first egg) in relation to the most recent new moon.
Day in breeding season (dbs)	The day in the breeding season the nest was initiated, where Day 1 = first day of incubation for first nest of year.
Year (year)	The year the nest was sampled.
Baseline Model Variables	
# of days sampled (sampled)	The number of days nest temperature data were collected (nests were often monitored several times before iButtons were added).
Day iButton added (dayibut)	The day in the nesting cycle that temperature sampling began, standardized so that day 1 of incubation = Day 1.
Day nest found (dayfound)	The day in the nesting cycle that nest monitoring began, standardized so that day 1 of incubation = Day 1.
Site identity (site)	HM = Hammonasset State Park ER = East River

* Maxtide and maxtideib were never used in the same model.

Table 2. Model comparison results for three types of nest fate models, ranked in order by model performance, within groups. All models include the same top performing base model consisting of Sampled, Dayibut, and Dayfound. The pooled model for each group consists of the base model plus the top tide model and the top timing model. Ranking is based on the smallest AIC value; k is the number of parameters in the model; w is the Akaike weight. Variables are defined in Table 1.

Model variables	Log-likelihood	k	Pseudo R^2	ΔAIC	w
NEST SUCCESS MODELS					
Tide variables added					
(C) events	-23.1	4	0.75	0	0.25
(D) maxtide	-24.3	4	0.73	2.54	0.07
(E) maxnonflood	-24.7	4	0.73	3.22	0.05
(B) maxtide + maxnonflood	-24.2	5	0.73	4.35	0.03
(A) maxtide + maxnonflood + events + year	-22.0	7	0.76	5.83	0.01
Timing variables added					
(I) dbs	-23.7	4	0.74	1.39	0.12
(H) dayspstnm	-23.8	4	0.74	1.44	0.12
(F) dayspstnm + dbs + year	-22.1	6	0.76	4.14	0.03
(G) dayspstnm + year	-23.5	5	0.74	4.88	0.02
(J) year	-24.6	4	0.73	5.11	0.02
BASE MODEL: sampled + dayibut + dayfound	-24.7	3	0.73	1.24	0.13
POOLED MODEL: model C + model I	-22.6	5	0.75	1.09	0.14
NULL MODEL: intercept only	-91.0	0	0	127.84	< 0.01
FLOODING-FAILURE MODELS					
Tide variables added					
(A) maxtideib + maxnonflood + events + year	-100.5	7	0.24	4.38	0.09
(B) maxtideib + maxnonflood	-103.7	5	0.21	4.82	0.07
(C) events	-108.6	4	0.18	12.61	< 0.01
(D) maxtideib	-111.8	4	0.15	18.86	< 0.01
(E) maxnonflood	-114.7	4	0.13	24.70	< 0.01
Timing variables added					
(G) dayspstnm + year	-109.7	5	0.17	18.78	< 0.01
(F) dayspstnm + dbs + year	-108.8	6	0.17	18.95	< 0.01
(H) dayspstnm	-113.7	4	0.14	22.72	< 0.01
(J) year	-115.4	4	0.12	28.14	< 0.01
(I) dbs	-117.1	4	0.11	28.14	< 0.01

BASE MODEL: sampled + dayibut + dayfound	-117.3	3	0.11	27.99	< 0.01
POOLED MODEL: model A + model G	-97.3	8	0.26	0	0.83
NULL MODEL: intercept only	-131.80	0	0	50.94	< 0.01
FITNESS LOSS MODELS					
Tide variables added					
(B) maxtideib + maxnonflood	-301.6	5	N/A	0	0.79
(A) maxtideib + maxnonflood + events + year	-298.5	7	N/A	5.82	0.04
(C) events	-308.1	4	N/A	9.16	0.01
(D) maxtideib	-317.6	4	N/A	28.04	< 0.01
(E) maxnonflood	-321.6	4	N/A	36.10	< 0.01
Timing variables added					
(H) dayspstnm	-319.3	4	N/A	31.56	< 0.01
(G) dayspstnm + year	-317.5	5	N/A	35.91	< 0.01
(I) dbs	-321.7	4	N/A	36.33	< 0.01
(F) dayspstnm + dbs + year	-316.0	6	N/A	36.79	< 0.01
(J) year	-322.1	4	N/A	41.00	< 0.01
BASE MODEL: sampled + dayibut + dayfound	-323.1	3	N/A	35.08	< 0.01
POOLED MODEL: model B + model H	-301.2	6	N/A	3.25	0.16
NULL MODEL: intercept only	-331.9	0	N/A	40.74	< 0.01

Table 3. Parameter estimates for the top saltmarsh sparrow Nest Success model.

Variables are defined in Table 1.

Variable	Estimate	Std. Error	Z-value	<i>p</i>	Odds-ratio	95% CI	
Intercept	-26.76	6.16	-4.35	< 0.001			
Sampled	1.53	0.36	4.29	< 0.001	4.62	2.63	10.94
Dayibut	1.46	0.35	4.14	< 0.001	4.29	2.41	9.81
Dayfound	-0.33	0.18	-1.87	0.062	0.72	0.50	1.00
Events	-0.39	0.23	-1.70	0.089	0.68	0.41	1.03

Table 4. Parameter estimates for top saltmarsh sparrow Flooding Failure model. Variables are defined in Table 1.

Variable	Estimate	Std. Error	Z-value	<i>p</i>	Odds-ratio	95% CI	
Intercept	8.35	6.13	1.36	0.173			
Sampled	-0.17	0.06	-2.86	0.004	0.84	0.74	0.94
Dayibut	-0.14	0.08	-1.61	0.107	0.87	0.74	1.03
Dayfound	-0.05	0.07	-0.67	0.505	0.95	0.82	1.10
Maxtideib	0.05	0.03	1.71	0.087	1.05	0.99	1.11
Maxnonflood	-0.09	0.03	-2.63	0.009	0.92	0.86	0.96
Events	0.21	0.14	1.51	0.129	1.24	0.94	1.65
Year2008	0.78	0.59	1.33	0.185	2.19	0.69	7.15
Year2009	-0.55	0.54	-1.01	0.315	0.58	0.19	1.66
Dayspstnm	0.11	0.05	2.42	0.016	1.12	1.02	1.23

Table 5. Parameter estimates for top saltmarsh sparrow ZAP Fitness Loss model. In this modeling approach a truncated Poisson model is used to model all non-zero count data and a binomial model is used to model the probability that a positive count is observed. Variables are defined in Table 1.

Truncated Poisson with log link							
Variable	Estimate	Std. Error	Z-value	<i>p</i>	Odds-ratio	95% CI	
Intercept	2.82	1.18	2.39	0.017			
Sampled	-0.03	0.01	-2.16	0.031	0.97	0.94	0.99
Dayibut	-0.03	0.02	-1.25	0.211	0.97	0.92	1.02
Dayfound	< 0.01	0.03	0.12	0.905	1.00	0.95	1.05
Maxtide iButton	< -0.01	<0.01	-0.07	0.946	1.00	0.99	1.01
Maxnonflood	< -0.01	0.01	-1.09	0.277	0.99	0.98	1.00
Binomial with logit link							
Variable	Estimate	Std. Error	Z-value	<i>p</i>	Odds-Ratio	95% CI	
Intercept	-6.15	5.86	-1.05	0.294			
Sampled	-0.09	0.04	-2.32	0.030	0.91	0.84	0.99
Dayibut	-0.13	0.8	-1.70	0.089	0.88	0.76	1.02
Dayfound	-0.01	0.07	-0.11	0.911	0.99	0.87	1.14
Maxtide iButton	0.13	0.03	5.36	<0.001	1.14	1.09	1.20
Maxnonflood	-0.10	0.03	-3.49	<0.001	0.90	0.85	0.96

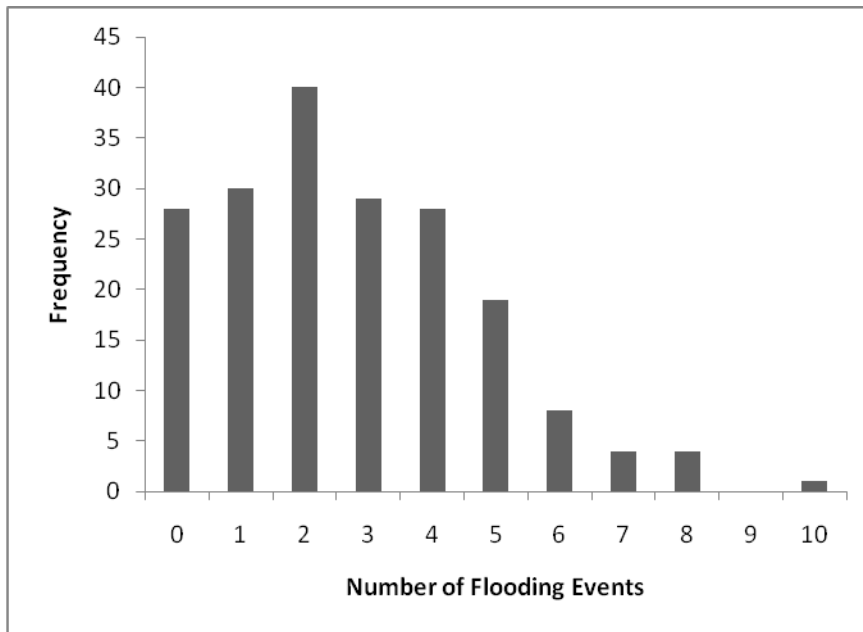


Figure 1. The frequency of tidal flooding events observed in 191 saltmarsh sparrow nests.

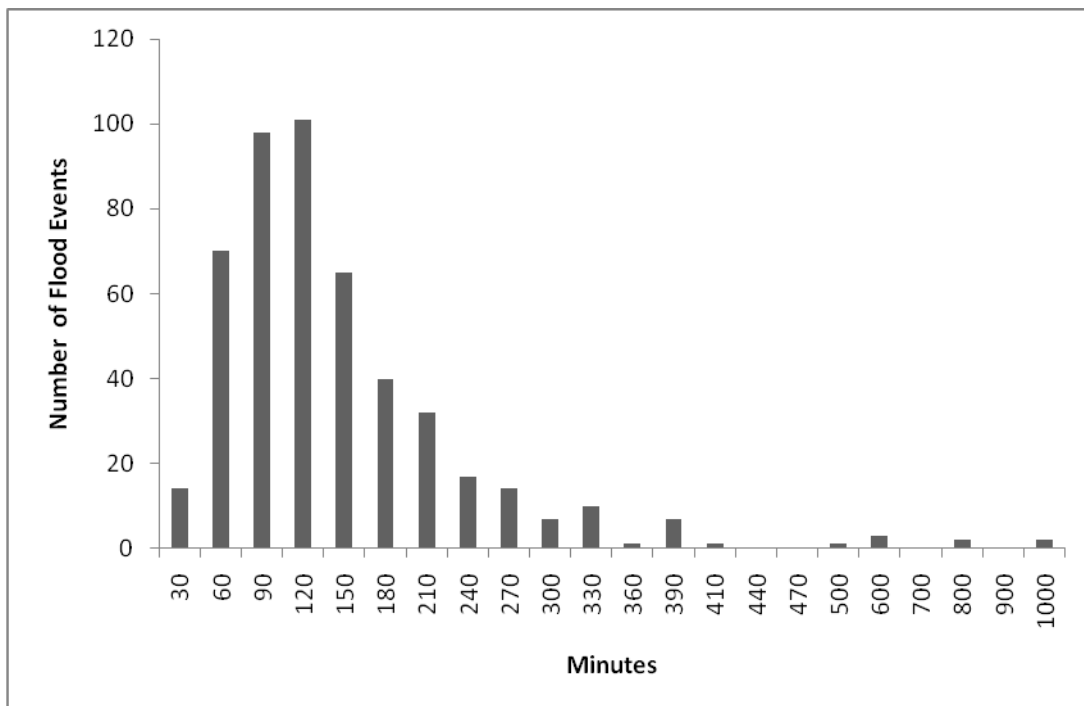


Figure 2. The duration of tidal flooding events observed in 191 saltmarsh sparrow nests (N = 485 events).

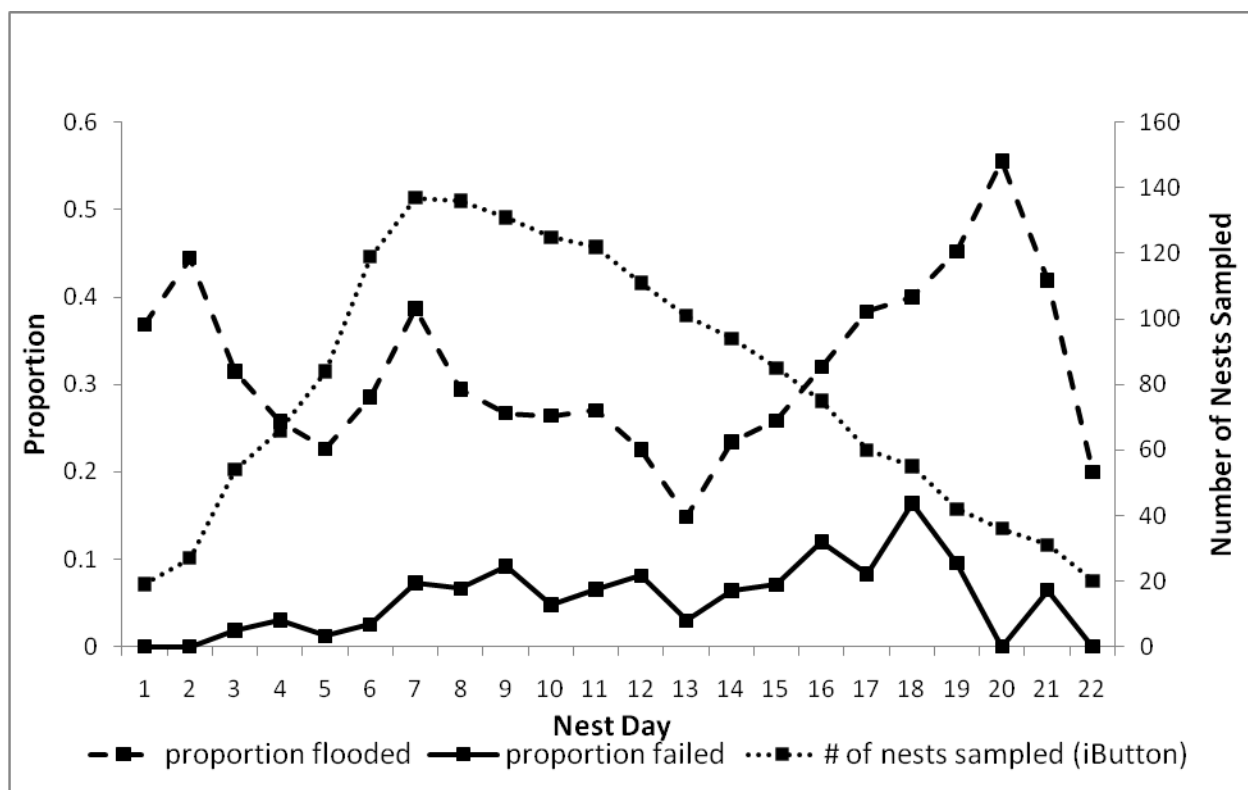


Figure 3. The proportion of saltmarsh sparrow nests ($N = 191$) that flooded or failed due to tidal flooding on each day of the 22-day nest cycle. Day 1 = day 1 of incubation; day 12 = day 0 of the nestling phase.

CONCLUSIONS

In my research on saltmarsh sparrow *Ammodramus caudacutus* habitat selection behavior I have addressed the possible use of conspecific social cues at multiple levels. I began by characterizing a number of behaviors that could serve as cues of habitat quality and explored the relationship between these behaviors and nesting activity to determine their relative importance. I then explored the possibility that saltmarsh sparrows use conspecific cues in their assessment of breeding habitat using both spatial analyses of nesting patterns and experimental manipulations of apparent sparrow densities at the local and landscape scales. Based on the results of this work, it appears that cues related to the total number of sparrows in the vicinity (e.g. number of active individuals, total number of sparrows) are more strongly related to nesting activity than are cues that specifically reflect local breeding activity, such as male song or female provisioning behavior. This suggests that density related cues could serve as an indicator of local reproductive activity and thus habitat quality. However, saltmarsh sparrows did not respond to conspecific density cues in the experimental broadcast study indicating that conspecific attraction is not important at either the local, within-marsh scale, or the larger landscape scale. Not only were sparrow numbers similar in both treatment and experimental plots, and in pre-treatment and treatment plots, but the number of nests and fledglings produced were extremely similar as well. In addition, tests of aggregation at cumulative and discrete distance classes failed to detect any evidence for a non-random pattern in nest placement; consistent with the hypothesis that nest placement is random with respect to other nests. When the timing of nesting attempts was taken into account such that only previous or currently active nests were considered, there was still no

evidence that female sparrows attempted to nest closer to other nests than expected given random nest site selection.

The lack of social cue use observed in this study may be related to the evolutionary life history of saltmarsh sparrows. At the landscape scale, prior studies suggest that saltmarsh sparrows are area sensitive (Benoit and Askins 2020) at least in some contexts (Shriver et al. 2004) and that some variation in sparrow abundance can be explained by the presence of high marsh vegetation (Gjerdrum et al. 2005, 2008a). These observations suggests that the size of the marsh, as well as the abundance of high marsh habitat, may be among the primary cues that sparrows pay attention to in determining marsh suitability. In addition, if site fidelity is moderate to high, as recent studies suggest (Post and Greenlaw 1982; DiQuinzio et al. 2001), many sparrows may simply return to the same marshes year after year, rendering habitat selection and social cue use at the marsh landscape scale largely irrelevant for most individuals in most years.

At the within-marsh scale, the variation in sparrow abundance and nest density observed in past studies (Gjerdrum et al. 2005, 2008a) would suggest that certain areas of marsh represent better quality nesting habitat than others, or at least have different uses. My spatial analyses of nest patterns, however, indicates that contrary to common perception, nesting sparrows are not clustered in certain areas of the marsh (Bayard and Elphick 2010; Chapter 2). Furthermore, given that nest failure is primarily caused by flooding events associated with monthly high spring tides (>60% of all failures: DeRagon 1988; Shriver 2007; Gjerdrum et al. 2005; Chapter 4); and females that nest synchronously with the tide cycle have a greater chance of successfully fledging young (Shriver et al. 2007), regardless of nest vegetation characteristics (Gjerdrum et al. 2005),

exactly where sparrows nest within the marsh may not matter in years of especially high tides. This means that social cues related to sparrow presence, abundance, or reproductive success may not necessarily be correlated with future reproductive success for a particular area within a marsh.

Although nest failure due to flooding has long been documented as a regular feature of saltmarsh sparrow breeding biology (Lewis 1920; Hill 1968; DeRagon 1988; Greenlaw and Rising 1994; Gjerdrum et al. 2005, 2008b; Shriver et al. 2007), the degree of nest failure due to flooding documented in this study, coupled with new information on the frequency of multiple flood events, is alarming (Chapter 4). Only 15% of the nests evaluated did not experience a single flooding event during temperature sampling, and even these nests may have flooded before iButtons were deployed. Whether this pattern is typical of the species' evolutionary history, or we are already observing the effects of sea-level rise, is not known. However, given that the difference in tide heights between successful nests and nests that failed due to flooding was on average, just 5 cm, it appears that saltmarsh sparrow population persistence is under imminent threat due to even incremental changes in sea-level or precipitation patterns. To fully understand the implications of future sea-level rise on saltmarsh sparrow populations, more information on their annual survival and re-nesting rates is urgently needed. In addition, although site fidelity has been investigated on a limited basis in both Rhode Island and New York, and appears to be relatively high (Post and Greenlaw 1982; DiQuinzio 2001), further study is needed across other parts of the species' range to verify this finding. Taken together, information on survival rates, individual productivity, and site fidelity will allow us to

determine the rate at which we can expect saltmarsh sparrow populations to decline under the current known threats.

Saltmarsh sparrows are just one of the many species of conservation that are faced with multiple threats to their persistence, the greatest of which now includes fundamental changes to their habitat due to climate change and sea-level rise (Parmesan and Yohe 2003; Root et al 2003; Thomas et al. 2004). Knowing whether such species are capable of responding to changes in their habitat or moving to new habitat areas, if available, is critical for promoting targeted conservation efforts (e.g., assisted colonization; Hunter 2007; McLachlan et al. 2007). Studies of the feasibility of marsh migration into upland areas, whether natural or artificial, are needed if we are to plan for saltmarsh sparrow persistence, as this is the only current solution for the expected loss of saltmarsh habitat to sea-level rise. In addition, although we know that changes in temperature and precipitation will likely cause substantial changes to the ecology of saltmarsh ecosystems; how this might play out among trophic levels is uncertain. A recent study of experimental warming of saltmarsh vegetation indicates that *Spartina patens*, a plant species commonly used by nesting saltmarsh sparrows, will be favored under increased temperature conditions, but that overall vegetation diversity will decline (Gedan and Bertness 2009). What this would mean for sparrows is unclear. Finally, careful analysis and documentation of the economic value of the ecosystem services provided by salt marshes (e.g., Craft et al. 2009) will be instrumental in garnering public support for saltmarsh preservation.

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APPENDIX A. Each of the five behaviors considered in our saltmarsh sparrow social cue models is plotted in relation to the number of nests (top panel), number of nests in the incubation phase (middle panel), and number of nests in the nestling phase (bottom panel). Spearman correlations are given for all pairs.

Figure A.1. Spearman correlations between the total number of females versus: number of nests, $Rho = 0.12$, $p = 0.03$; number of nests in the incubation phase, $Rho = 0.13$, $p = 0.01$; number of nests in the nestling phase, $Rho < 0.01$, $p = 0.75$.

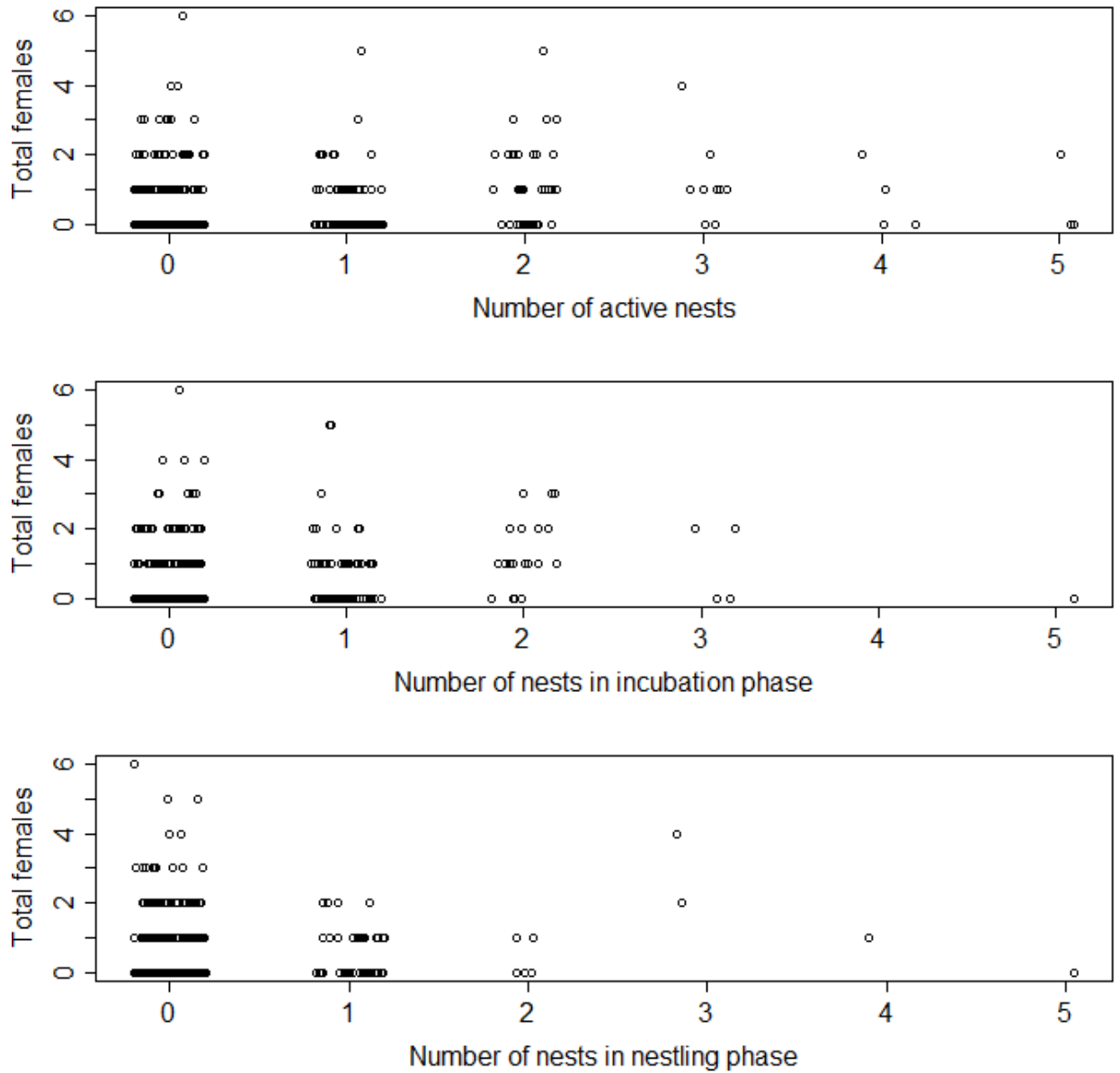


Figure A.2. Spearman correlations between the total number of individuals involved in mate acquisition versus: number of active nests, $Rho = 0.08$, $p = 0.14$; number of nests in the incubation phase, $Rho = 0.15$, $p = 0.01$; number of nests in the nestling phase, $Rho = -0.12$, $p = 0.03$.

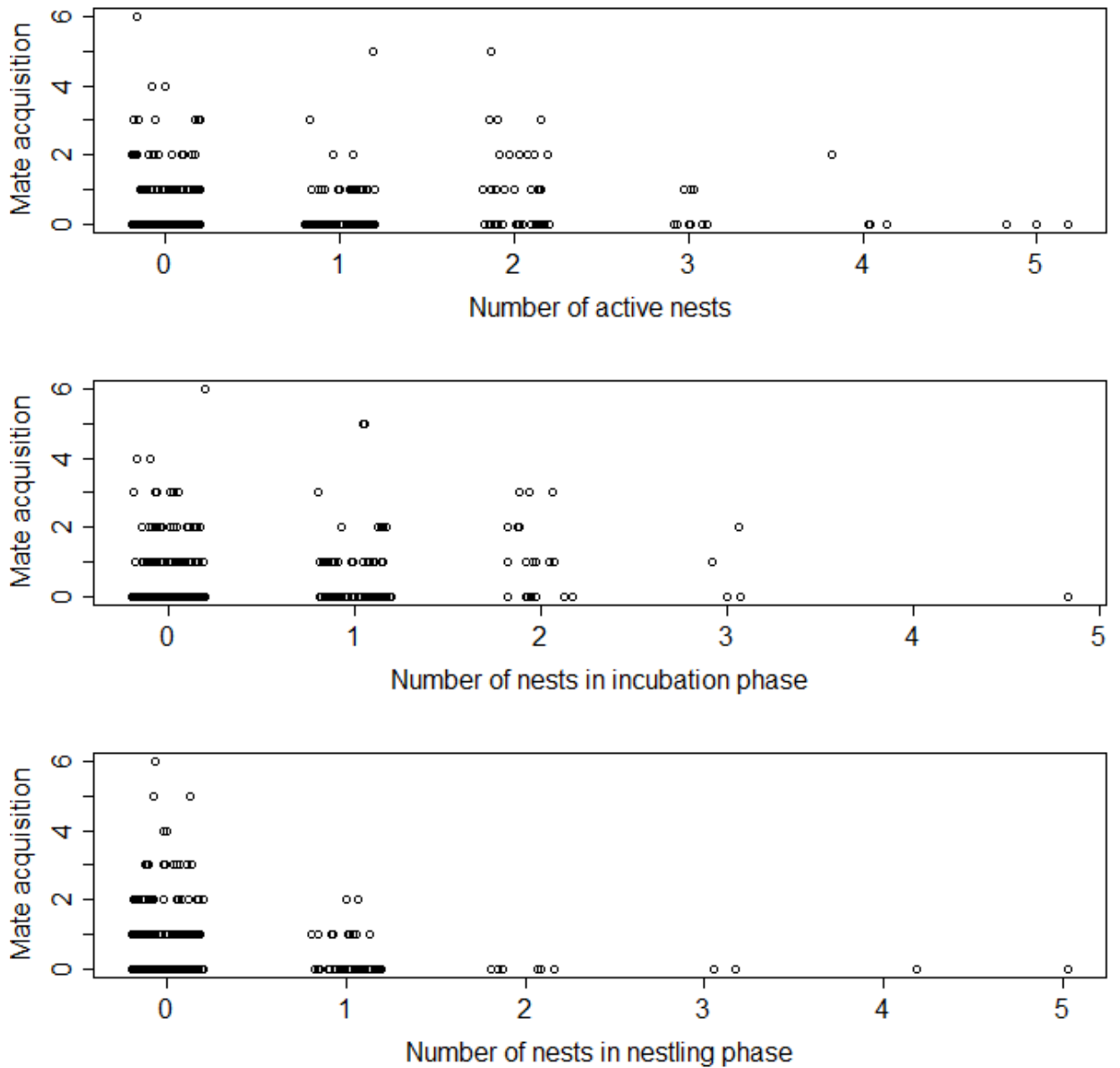


Figure A.3. Spearman correlations between the total number of songs versus: number of active nests, $Rho = 0.08$, $p = 0.13$; number of nests in the incubation phase, $Rho = 0.08$, $p = 0.14$; number of nests in the nestling phase, $Rho = -0.04$, $p = 0.50$.

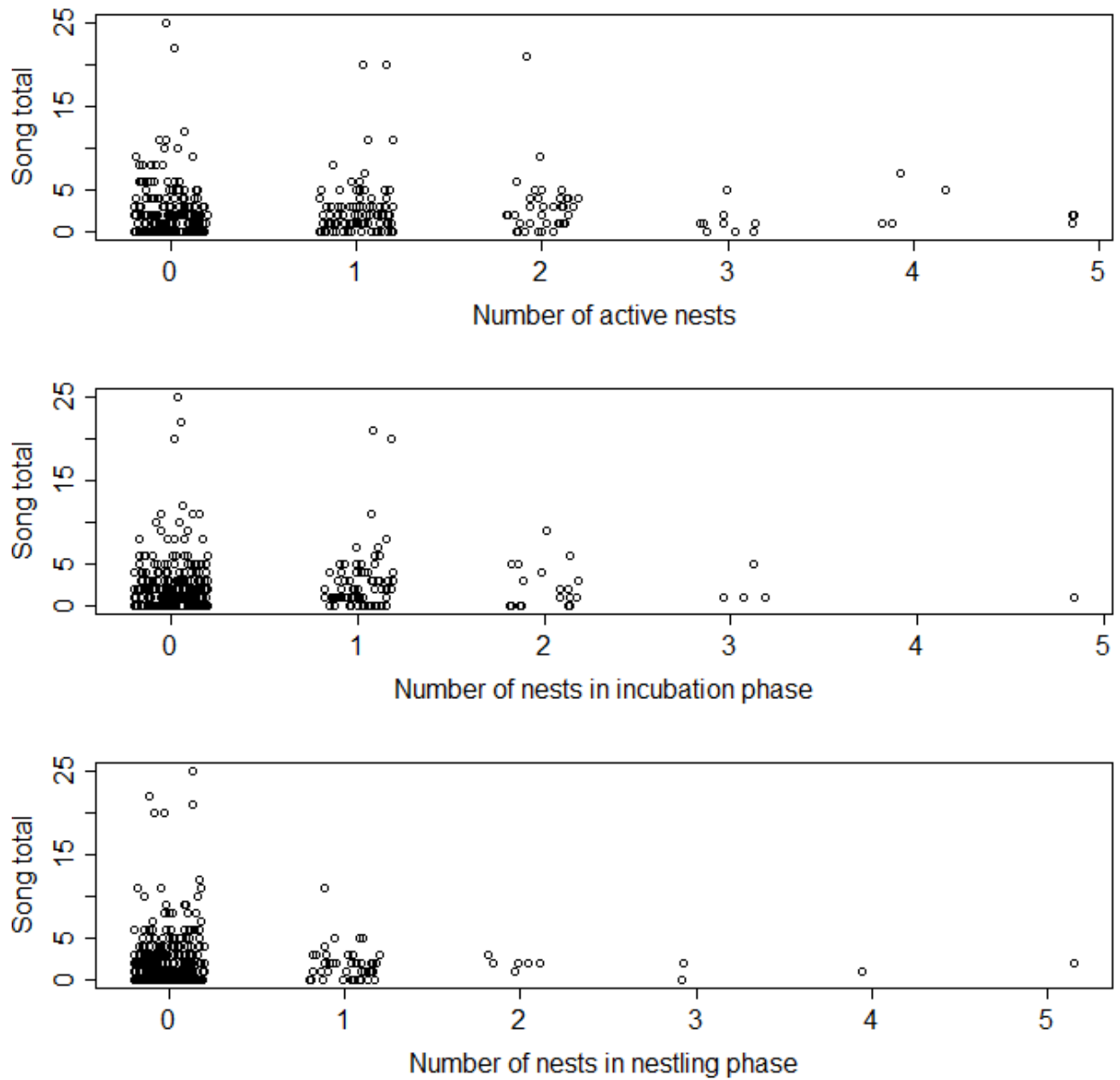


Figure A.4. Spearman correlations between the total number of active individuals versus:
number of active nests, $Rho = 0.18$, $p < 0.01$; number of nests in the incubation phase,
 $Rho = 0.14$, $p < 0.01$; number of nests in the nestling phase, $Rho = 0.12$, $p = 0.03$.

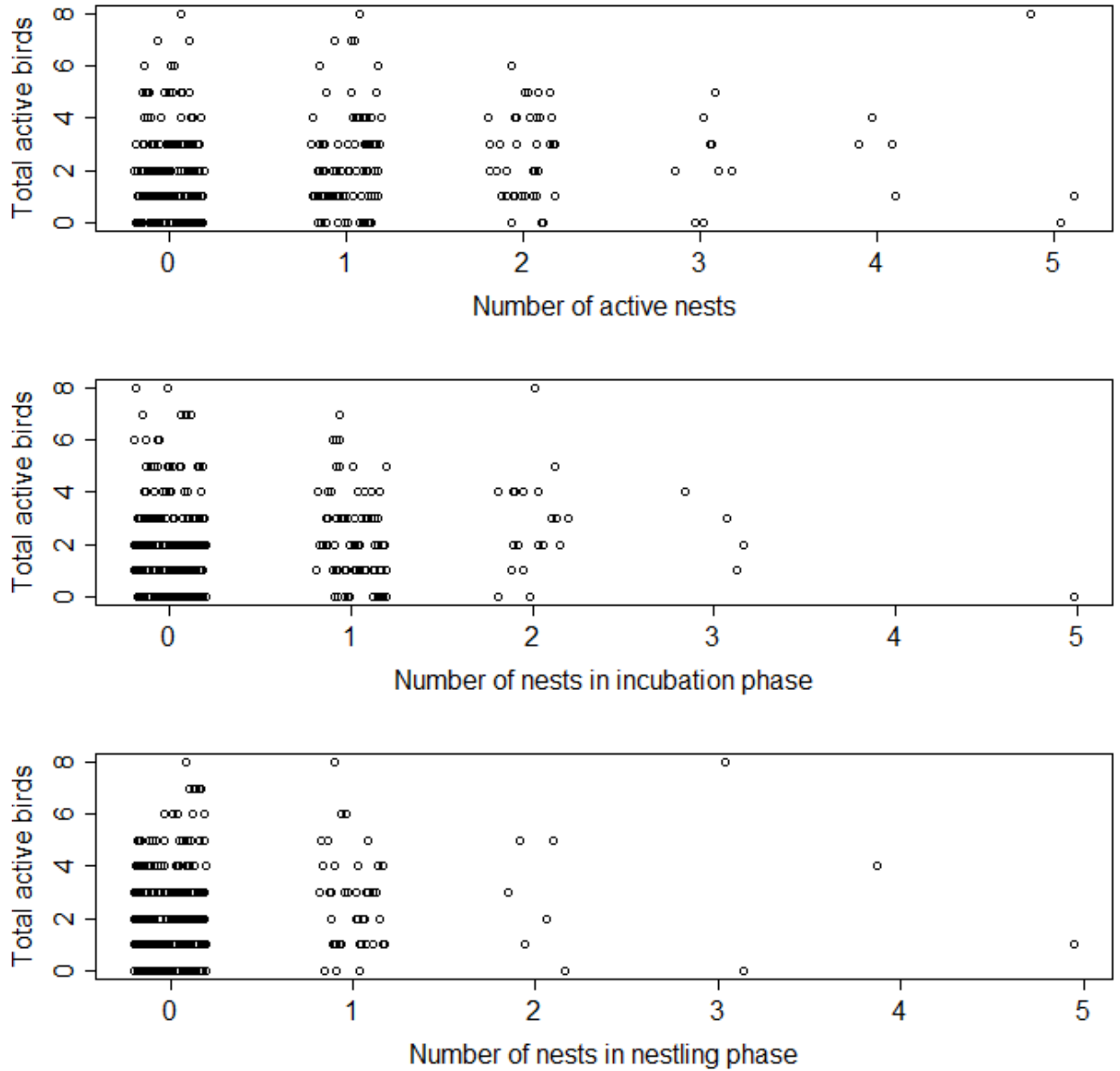
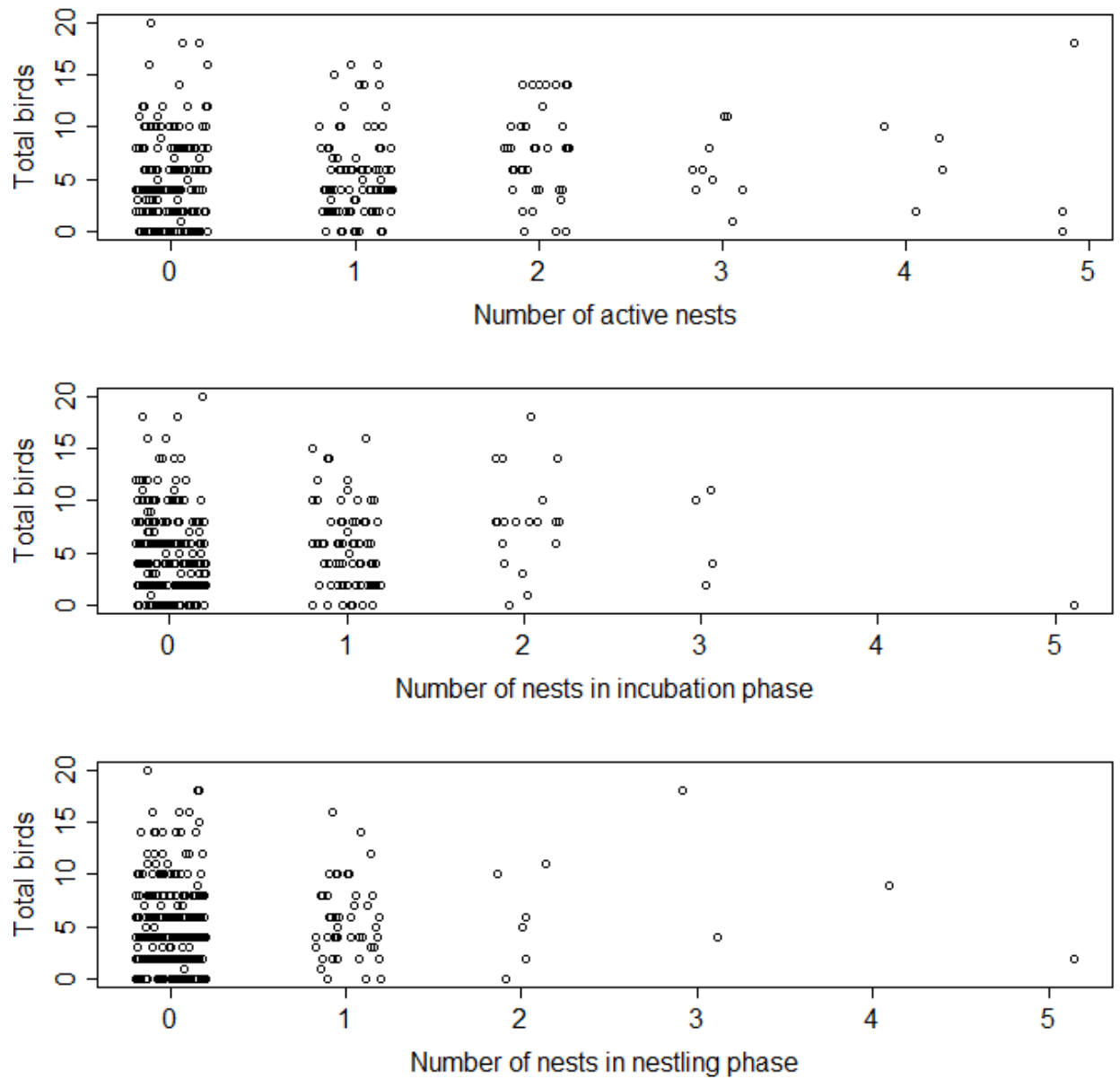


Figure A.5. Spearman correlations between the total number of birds versus: number of active nests, $Rho = 0.19$, $p < 0.01$; number of nests in the incubation phase, $Rho = 0.17$, $p < 0.01$; number of nests in the nestling phase, $Rho = 0.09$, $p = 0.09$.



APPENDIX B. Model outputs for the five potential saltmarsh sparrow cues considered in our study versus three measures of nesting activity (Chapter 1). The probability of measuring false zeros was analyzed using a binomial model while the “true” zeros and count data are modeled using a Poisson or negative binomial general linear model in a zero-inflated framework. Variable codes are as follows: Temp = temperature, measured in the field at the time of survey; Wind = average daily wind speed; DaysNM = number of days since the most recent new moon; TimeHT = time elapsed since the most recent high tide; Week = week of survey (1-12).

Table B.1. Number of female saltmarsh sparrows versus the total number of nests.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-0.46	1.08	-0.43	0.669
Nest	0.06	0.08	0.80	0.427
Temp	<0.01	0.01	0.07	0.943
Wind	0.12	0.06	2.01	0.044
DaysNM	0.02	0.01	1.58	0.114
TimeHT	-0.04	0.02	-1.75	0.080
Week	-0.13	0.03	-3.92	<0.001
Log(theta)	1.06	0.51	2.07	0.039
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-15.09	8.39	-1.80	0.072
Nest	0.13	0.09	1.34	0.166
Temp	0.13	0.09	1.39	0.166
Wind	1.46	0.66	2.22	0.027
DaysNM	0.04	0.09	0.45	0.098
TimeHT	-0.29	0.18	-1.65	0.098
Week	-1.28	0.66	-1.95	0.056

Table B.2. Number of female saltmarsh sparrows versus the number of nests in the incubation phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-0.42	1.08	-0.39	0.695
NestEgg	0.14	0.11	1.23	0.217
Temp	< -0.01	0.01	-0.02	0.984
Wind	0.11	0.06	1.90	0.057
DaysNM	0.02	0.01	1.78	0.076
TimeHT	-0.04	0.02	-1.78	0.076
Week	-0.12	0.03	-3.65	<0.001
Log(theta)	1.07	0.52	2.06	0.039
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-15.77	8.30	-1.90	0.058
NestEgg	0.02	0.81	1.57	0.118
Temp	0.13	0.08	1.57	0.118
Wind	1.50	0.67	2.25	0.025
DaysNM	0.05	0.08	0.57	0.568
TimeHT	-0.31	0.19	-1.65	0.099
Week	-1.32	0.69	-1.91	0.056

Table B.3. Number of female saltmarsh sparrows versus the number of nests in the nestling phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-0.42	1.08	-0.39	0.696
NestChick	0.05	0.14	0.34	0.731
Temp	< 0.01	0.01	0.08	0.934
Wind	0.124	0.06	2.07	0.039
DaysNM	0.02	0.01	1.55	0.121
TimeHT	-0.04	0.02	-1.78	0.076
Week	-0.13	0.03	-4.09	<0.001
Log(theta)	1.07	0.52	2.03	0.042
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-15.63	8.37	-1.87	0.062
NestChick	1.53	1.01	1.51	0.132
Temp	0.13	0.08	1.55	0.122
Wind	1.56	0.71	2.20	0.028
DaysNM	0.04	0.08	0.50	0.619
TimeHT	-0.29	0.19	-1.56	0.119
Week	-1.39	0.70	-2.00	0.046

Table B.4. Number of saltmarsh sparrows involved in mate acquisition versus the total number of nests.

Truncated Poisson with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	0.56	1.28	-0.44	0.663
Nest	-0.11	0.10	1.15	0.250
Temp	0.01	0.02	0.35	0.726
Wind	0.19	0.07	2.80	0.005
DaysNM	0.01	0.01	0.84	0.404
TimeHT	-0.05	0.03	1.77	0.077
Week	-0.19	0.04	-4.24	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-6.46	4.19	-1.54	0.123
Nest	-0.38	0.39	-0.98	0.327
Temp	0.05	0.05	1.14	0.255
Wind	0.54	0.24	2.24	0.025
DaysNM	0.03	0.03	0.98	0.329
TimeHT	-0.12	0.08	-1.41	0.16
Week	-0.23	0.15	-1.49	0.137

Table B.5. Number of saltmarsh sparrows involved in mate acquisition versus the number of nests in the incubation phase.

Truncated Poisson with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-0.85	1.26	-0.68	0.498
NestEgg	0.04	0.12	0.33	0.739
Temp	0.01	0.02	0.47	0.640
Wind	0.19	0.07	2.73	0.006
DaysNM	0.01	0.01	1.01	0.315
TimeHT	-0.05	0.03	-1.72	0.085
Week	-0.18	0.04	-4.91	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-7.06	4.26	-1.66	0.098
NestEgg	-0.48	0.41	-1.18	0.240
Temp	0.06	0.05	1.27	0.205
Wind	0.56	0.25	2.24	0.025
DaysNM	0.55	0.25	2.24	0.025
TimeHT	-0.12	0.08	-1.49	0.137
Week	-0.21	0.14	-1.53	0.127

Table B.6. Number of saltmarsh sparrows involved in mate acquisition versus the number of nests in the nestling phase.

Truncated Poisson with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-1.26	1.25	-1.01	0.313
NestChick	-.99	0.29	-3.47	<0.001
Temp	0.02	0.02	0.99	0.321
Wind	0.20	0.06	3.14	0.002
DaysNM	0.01	0.01	0.85	0.395
TimeHT	-0.06	0.03	-2.31	0.021
Week	-0.18	0.03	-5.51	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-10.77	4.81	-2.24	0.025
NestChick	-12.93	382.54	-0.034	0.973
Temp	0.11	0.06	1.92	0.055
Wind	0.70	0.25	2.77	0.006
DaysNM	0.02	0.03	0.50	0.614
TimeHT	-0.16	0.09	-1.82	0.068
Week	-0.33	0.18	-1.82	0.069

Table B.7. Total number of songs versus the total number of nests.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.19	0.77	2.85	0.004
Nest	-0.08	0.06	0.20	0.841
Temp	<0.01	0.01	0.20	0.841
Wind	-0.08	0.04	-2.02	0.044
DaysNM	-0.01	0.01	-1.59	0.112
TimeHT	0.01	0.01	0.60	0.547
Week	-0.13	0.02	-6.08	<0.001
Log(theta)	0.64	0.14	4.47	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-1840.5	1810.6	-1.01	0.312
Nest	86.92	88.89	0.98	0.328
Temp	-2.37	2.91	-0.82	0.415
Wind	5.78	5.83	0.99	0.322
DaysNM	-2.26	2.77	-0.82	0.414
TimeHT	28.58	28.94	0.98	0.323
Week	158.22	157.47	1.00	0.315

Table B.8. Total number of songs versus the number of nests in the incubation phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.19	0.77	2.86	0.004
NestEgg	-0.13	0.08	-1.52	0.128
Temp	<0.01	0.01	0.24	0.813
Wind	-0.08	0.04	-2.03	0.042
DaysNM	-0.01	0.01	-1.74	0.082
TimeHT	0.01	0.01	0.55	0.581
Week	-0.13	0.02	-6.15	<0.001
Log(theta)	0.64	0.14	4.49	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-624.45	609.25	-1.03	0.305
NestEgg	36.38	38.84	0.94	0.349
Temp	-0.45	0.86	-0.52	0.604
Wind	1.27	1.31	0.97	0.333
DaysNM	-0.36	0.66	-0.54	0.592
TimeHT	9.35	8.38	0.94	0.345
Week	52.23	52.20	1.00	0.317

Table B.9. Total number of songs versus the number of nests in the nestling phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.19	0.76	2.88	0.004
NestChick	-0.15	0.10	-1.48	0.139
Temp	<0.01	0.01	0.16	0.871
Wind	-0.09	0.04	-2.31	0.021
DaysNM	-0.01	0.01	-1.34	0.180
TimeHT	0.01	0.01	0.64	0.520
Week	-0.12	0.02	-5.86	<0.001
Log(theta)	0.64	0.14	4.43	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-1062.2	2034.3	-0.52	0.602
NestChick	29.73	144.65	0.21	0.837
Temp	-1.54	5.12	-0.30	0.764
Wind	1.46	12.38	0.12	0.906
DaysNM	-3.71	8.03	-0.46	0.644
TimeHT	26.71	55.46	0.48	0.630
Week	91.01	176.60	0.52	0.606

Table B.10. Number of saltmarsh sparrows involved in active behavior versus the total number of nests.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.06	0.57	3.61	<0.001
Nest	0.16	0.04	3.63	<0.001
Temp	-0.02	0.01	-2.64	0.008
Wind	-0.04	0.03	-1.47	0.142
DaysNM	<0.01	0.01	0.37	0.715
TimeHT	<-0.01	0.01	-0.08	0.936
Week	0.03	0.02	1.96	0.050
Log(theta)	2.15	0.41	5.28	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-9.96	6.46	-1.54	0.122
Nest	13.25	8.31	1.59	0.111
Temp	<0.01	0.15	0.01	0.996
Wind	-2.74	1.35	-2.03	0.043
DaysNM	-0.62	0.36	-1.73	0.084
TimeHT	0.80	0.48	1.65	0.098
Week	9.15	5.87	1.56	0.119

Table B.11. Number of saltmarsh sparrows involved in active behavior versus the number of nests in the incubation phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.22	0.58	3.84	<0.001
NestEgg	0.17	0.07	2.55	0.011
Temp	-0.02	0.01	-2.83	0.005
Wind	-0.04	0.03	-1.48	0.139
DaysNM	<0.01	0.01	0.77	0.444
TimeHT	<-0.01	0.01	-0.32	0.752
Week	0.03	0.02	1.92	0.055
Log(theta)	2.03	0.37	5.47	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-120.80	219.00	-0.55	0.581
NestEgg	18.65	33.06	0.56	0.573
Temp	0.005	0.19	0.03	0.980
Wind	-2.41	2.07	-1.17	0.244
DaysNM	-0.81	1.21	-0.67	0.502
TimeHT	0.43	0.63	0.69	0.492
Week	11.00	18.47	0.60	0.551

Table B.12. Number of saltmarsh sparrows involved in active behavior versus the number of nests in the nestling phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.27	0.58	3.94	<0.001
NestChick	0.13	0.07	1.87	0.062
Temp	-0.02	0.01	-2.63	0.008
Wind	-0.03	0.03	-0.96	0.336
DaysNM	0.01	0.01	1.46	0.145
TimeHT	<0.01	0.01	0.28	0.702
Week	-0.02	0.02	-1.24	0.215
Log(theta)	2.01	0.38	5.32	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	14.45	10.48	1.38	0.168
NestChick	-6.79	111.88	-0.06	0.952
Temp	-0.29	0.17	-1.68	0.092
Wind	-0.72	0.47	-1.54	0.125
DaysNM	-0.03	0.07	-0.36	0.721
TimeHT	0.89	0.39	2.29	0.022
Week	-0.066	0.30	-2.19	0.028

Table B.13. Total number of saltmarsh sparrows versus the total number of nests.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	3.02	0.47	6.41	<0.001
Nest	0.08	0.04	2.25	0.024
Temp	-0.02	0.01	-2.62	0.009
Wind	-0.02	0.02	-0.81	0.416
DaysNM	0.003	0.004	0.68	0.494
TimeHT	<0.01	0.01	0.09	0.925
Week	-0.02	0.01	-1.17	0.243
Log(theta)	1.63	0.17	9.36	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	-1.78	2.49	-0.72	0.474
Nest	-0.27	0.25	-1.10	0.272
Temp	<0.01	0.03	0.11	0.913
Wind	-0.04	0.11	-0.36	0.720
DaysNM	-0.06	0.02	-2.44	0.015
TimeHT	0.08	0.06	1.46	0.144
Week	0.03	0.07	0.41	0.680

Table B.14. Total number of saltmarsh sparrows versus the number of nests in the incubation phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	2.06	0.47	6.49	<0.001
NestEgg	0.11	0.06	1.98	0.047
Temp	-0.02	0.01	-2.72	0.007
Wind	-0.02	0.02	-0.84	0.400
DaysNM	<0.01	<0.01	0.96	0.337
TimeHT	<0.01	0.01	0.03	0.976
Week	-0.01	0.01	-1.00	0.316
Log(theta)	1.62	0.17	9.29	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>P</i>
Intercept	-1.72	2.46	-0.70	0.485
NestEgg	-0.15	0.30	-0.51	0.609
Temp	<0.01	0.03	0.02	0.984
Wind	-0.05	0.11	-0.41	0.681
DaysNM	-0.06	0.02	-2.54	0.011
TimeHT	0.09	0.06	1.55	0.120
Week	0.040	0.07	0.59	0.555

Table B.15. Total number of saltmarsh sparrows versus the number of nests in the nestling phase.

Negative binomial with log link				
Variable	Estimate	Std. Error	Z-value	<i>p</i>
Intercept	3.08	0.47	6.50	<0.001
NestChick	0.06	0.06	0.91	0.362
Temp	-0.02	0.01	-2.54	0.011
Wind	-0.01	0.02	-0.61	0.544
DaysNM	<0.01	<0.01	0.54	0.591
TimeHT	<-0.01	0.01	-0.15	0.878
Week	-0.02	0.01	-1.70	0.090
Log(theta)	1.60	0.17	9.31	<0.001
Binomial with logit link				
Variable	Estimate	Std. Error	Z-value	<i>P</i>
Intercept	-1.83	2.47	-0.74	0.460
NestChick	-0.48	0.58	-0.84	0.403
Temp	<0.01	0.03	0.04	0.971
Wind	-0.05	0.11	-0.43	0.668
DaysNM	-0.05	0.02	-2.24	0.03
TimeHT	0.08	0.06	1.48	0.138
Week	0.05	0.06	0.72	0.471

APPENDIX C. Location of experimental and control study plots used in saltmarsh sparrow conspecific attraction experiment 2008-2009 (Chapter 3).

Figure C.1. Hammonasset State Park, Madison, CT.

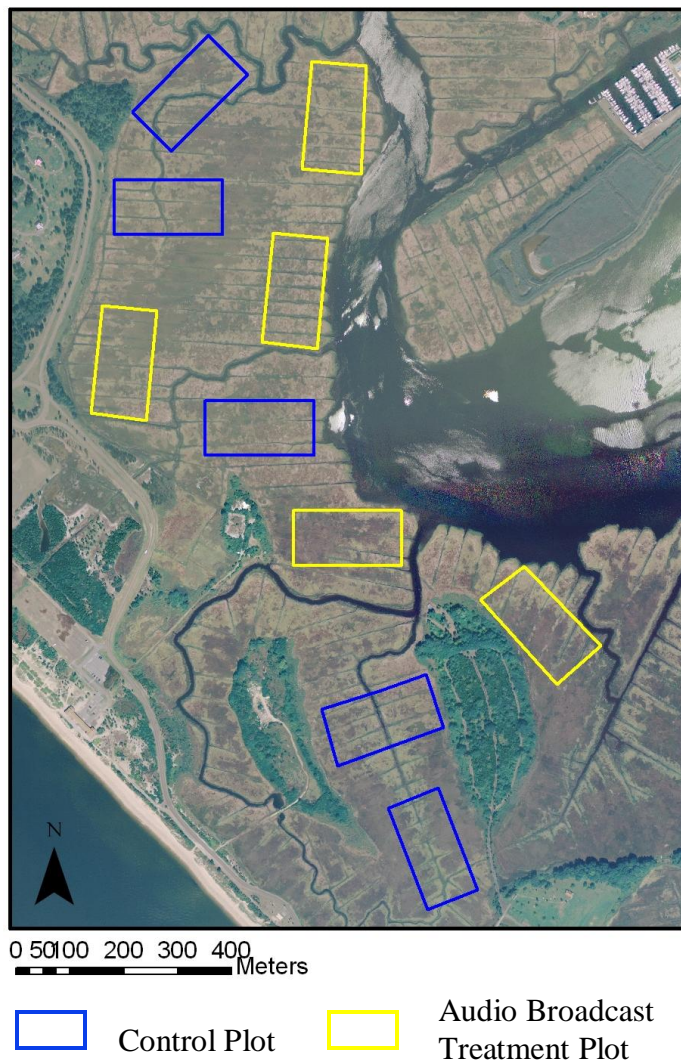


Figure C.2. East River Marsh, Guilford/Madison, CT

