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Factors that influence vital rates of Seaside and Saltmarsh sparrows in coastal New Jersey, USA

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ABSTRACT. As saltmarsh habitat continues to disappear, understanding the factors that influence the population dynamics of saltmarsh breeding birds is an important step in the conservation of these declining species. Using 5 yrs (2011–2015) of demographic data, we evaluated and compared apparent adult survival and nest survival of Seaside (*Ammodramus maritimus*) and Saltmarsh (*A. caudacutus*) sparrows at the Edwin B. Forsythe National Wildlife Refuge in New Jersey, USA. We determined the effect of site management history (unditched vs. ditched marshes) on adult and nest survival to aid in prioritizing future management or restoration actions. Apparent adult survival (61.6%, 95% CI: 52.5–70.0%) of Seaside Sparrows averaged > 1.5 times greater than that of Saltmarsh Sparrows (39.9%, 95% CI: 34.0–46.2%). Nest survival and predation and flooding rates did not differ between species, and predation was the primary cause of nest failure for both species. Apparent adult survival and nest survival did not differ between unditched and ditched marshes for either species, indicating that marsh ditching history may not affect the quality of breeding habitat for these species. Because predation was the primary cause of nest failure for both species in New Jersey, we suggest that future studies should focus on identifying predator communities in salt marshes and the potential for implementing predator-control programs to limit population declines.

RESUMEN. Factores que influyen las tasa vitales de *Ammodramus maritimus* y *A. caudacutus* en las costa de New Jersey, USA

Los hábitats de marismas de agua salada continúan desapareciendo, entender los factores que afectan la dinámica poblacional de las aves que anidan en las marismas de agua salada en un paso importante en la conservación de estas especies que están en declive. Usando cinco años (2011–2015) de datos demográficos, evaluamos y comparamos sobrevivencia aparente de adultos y nidos de *Ammodramus maritimus* y *A. caudacutus* en el refugio de vida silvestre nacional de Edwin B. Forsythe en New Jersey, USA. Determinamos el efecto de la historia del manejo del lugar (marismas de agua salada con y sin diques) sobre la supervivencia de adultos y nidos, para ayudar a la priorización de futuras acciones de manejo y restauración. La supervivencia aparente de los adultos (61.6%, 95% CI: 52.5–70.0%) de *A. maritimus* en promedio es > 1.5 veces mas grande que la de *A. caudacutus* (39.9%, 95% CI: 34.0–46.2%). La supervivencia de los nidos, la depredación y las tasa de inundación no variaron entre las especies, y la depredación fue la principal causa del fracaso de los nidos para ambas especies. La supervivencia aparente de los adultos y la supervivencia de nidos no variaron entre marismas de agua salada con y sin diques para ambas especies, indicando que la creación histórica de los diques en las marismas de agua salada parece no afectar la calidad del hábitat para reproducción de estas especies. Debido a que la depredación fue la principal causa del fracaso de los nidos para ambas especies en New Jersey, sugerimos que futuros estudios se deberían enfocar en identificar las comunidades de depredadores en marismas de agua salada y el potencial para implementar programas de control de depredadores para restringir la disminución poblacional.

Key words: adult survival, *Ammodramus caudacutus*, *Ammodramus maritimus*, ditching, nest survival, predator control, salt marsh

Understanding demographic processes is fundamental to managing wildlife populations because robust vital rates are critical for

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accurately estimating population trajectories. Vital rate estimates are essential for setting harvest rates (Messier 1991, Gaillard et al. 1998, Sandercock et al. 2008) and for identifying factors limiting population growth (Sæther and Bakke 2000, Taylor et al. 2012). A detailed understanding of demographic parameters is especially important for population viability models used to evaluate the long-term persistence of declining wildlife populations (Akçakaya 2000, Reed et al. 2002). Long-term demographic studies are logistically challenging, but are especially important for the conservation of threatened populations. For species vulnerable to climate change, estimating vital rates will permit better modeling of the factors that may aid in maintaining sensitive species through this climatic shift.

Salt marshes are considered highly threatened by global climate change, and thus the wildlife that depend on salt marshes are conservation priorities (Rosenberg et al. 2016). Salt marshes are limited to ~45,000 km² globally, and one-third of salt marshes worldwide are found along the Atlantic and Gulf coasts of North America (Greenberg et al. 2006a). Salt marshes have been degraded and fragmented by urban, residential, agricultural, and commercial development, livestock grazing, invasive species encroachment, pollution, sea-level rise, and grid-ditching for mosquito control (Craft et al. 2009, Gedan et al. 2009, Altieri et al. 2012, Deegan et al. 2012, Coverdale et al. 2013). Accelerated rates of sea-level rise, due to anthropogenic climate change, will continue through the 21st century at a more rapid pace than has occurred over the past 2700 yrs (Kopp et al. 2016). As sea levels and the frequency of storms increase (Knutson et al. 1998, McCabe et al. 2001, Elsner et al. 2008, Bender et al. 2010), salt marshes will continue to be degraded, altered, or lost (Goodbred and Hine 1995, Michener et al. 1997, Scavia et al. 2002, Cahoon 2006).

Seaside (*Ammodramus maritimus*) and Saltmarsh (*A. caudacutus*) sparrows are almost entirely restricted to salt marshes throughout their ranges (Greenlaw and Rising 1994, Post and Greenlaw 1994), making them among the most vulnerable species to changes in habitat caused by changing climates. Seaside Sparrows breed from Texas to southern

Maine (Post and Greenlaw 1994), and are listed globally as a species of least concern (BirdLife International 2015) and as a species of moderate priority in Bird Conservation Region 30 (BCR 30, defined as the Mid-Atlantic and New England Coast; Rosenberg et al. 2016). In the northeastern United States, the Seaside Sparrow population is estimated to consist of 230,000 (174,000–286,000) individuals (Wiest et al. 2016), with a stable population trend in recent decades (Correll et al. 2017). The breeding range of Saltmarsh Sparrows extends from Virginia to southern Maine (Greenlaw and Rising 1994), with an estimated global population of 53,000 (37,000–69,000) individuals (Wiest et al. 2016). Saltmarsh Sparrows are listed as globally vulnerable (BirdLife International 2012), are a species of highest priority in BCR 30 (Rosenberg et al. 2016), and recent population-trend estimates indicate an annual decline of 9% (Correll et al. 2017).

Seaside and Saltmarsh sparrows differ in their life-history traits in ways that may influence their responses to different threats. Therefore, comparison of the vital rates where they co-occur may be critical to determining the best management actions to maintain breeding populations through this period of rapid climate change. Seaside Sparrows typically place nests between 14–28 cm above ground in marsh areas dominated by *Spartina alterniflora* (Post and Greenlaw 1994). In contrast, Saltmarsh Sparrows place nests 2–10 cm above ground in marsh areas dominated by *Spartina patens* (Greenlaw and Rising 1994, Greenberg et al. 2006b). Although the relatively high placement of Seaside Sparrow nests reduces flooding events (Gjerdrum et al. 2005), their nesting success is still affected by flooding (Greenberg et al. 2006b). Differences in nest heights do not indicate relative flooding risks because *S. alterniflora* grows at lower elevations than *S. patens* (Bertness 1999). Saltmarsh Sparrow nest success is strongly influenced by short-term flooding events driven by the timing of nest initiation in relation to lunar tide cycles (Gjerdrum et al. 2005, Shriver et al. 2007) and nest structure (Humphreys et al. 2007).

Here, we present estimates of apparent annual adult survival, nest survival rates, and relative rates of nest failure for Seaside and Saltmarsh sparrows in an unditched salt

marsh and ditched marshes based on 5 yrs (2011–2015) of mark-recapture and nest-monitoring data. Our first objective was to directly compare the apparent annual adult survival and nest survival rates of Seaside and Saltmarsh sparrows. Our second objective was to determine if Seaside and Saltmarsh sparrow vital rates differed between the unditched and ditched marshes. Grid-ditching of salt marshes for mosquito control was ubiquitous during the 1930s and persists as the dominant structural alteration to salt marshes, especially along the Atlantic Coast of the United States where > 90% of salt marshes are grid-ditched (Bourn and Cottam 1950). Grid-ditching affects saltmarsh hydrology and elevation, thus altering natural processes in marsh systems (Wolfe 1996, Tonjes 2013) by reducing water on the marsh surface, draining ponds, and lowering the water table (Daiber 1986, Dale and Hulsman 1990, Wolfe 1996, Adamowicz and Roman 2005, Tonjes 2013). Decreasing the presence of water on the marsh surface may potentially lead to reduced nest flooding for both Seaside and Saltmarsh sparrows. Ditching also increases marsh surface elevation through sediment deposition from within ditches during flooding events (Wolfe 1996). In New Jersey, increased marsh surface elevation can lead to a shift in the dominant vegetation from *S. alterniflora* to *S. patens* (Bertness 1991), favoring breeding Saltmarsh Sparrows by increasing the availability of optimal nesting habitat. Despite their prevalence, the ecosystem-wide effects of ditches are still unclear, and their impact on specific taxa and individual species is largely unknown (Gedan et al. 2009). Our final objective was to identify the factors influencing apparent adult and nest survival rates of Seaside and Saltmarsh sparrows.

METHODS

Study site. We conducted this research at Edwin B. Forsythe National Wildlife Refuge (hereafter, Forsythe NWR) in coastal New Jersey (39.7531757°N –74.1376367°W). Wiest et al. (2016) estimated that coastal New Jersey hosts 23% of the northeastern population of breeding Seaside Sparrows and 38% of the global population of breeding Saltmarsh Sparrows. With 15,000 ha of salt marsh (U. S. Fish and Wildlife Service 2004), Forsythe NWR is

an important breeding area for both sparrows (Wiest et al. 2016). Saltmarsh vegetation at Forsythe NWR is dominated by saltmeadow cordgrass (*S. patens*), smooth cordgrass (*S. alterniflora*), inland saltgrass (*Distichlis spicata*), and Jesuit's bark (*Iva frutescens*). In 2011, we established three study sites (AT&T, Oyster Creek, and Mullica Wilderness) and sampled them annually through 2015 (Fig. 1). These sites experienced different levels of degradation from human activity. AT&T (14 ha; 39.697191°N –74.214032°W) and Oyster Creek (18 ha; 39.504815°N –74.426283°W) were grid-ditched and both sites were partially bordered by forest and a road. These sites were also further modified by open-marsh water management (OMWM) for mosquito control during the past several decades. Mullica Wilderness (17 ha; 39.536166°N –74.438021°W) was not managed with either grid-ditching or OMWM and was bordered by salt marsh and open water. All three sites had similar densities of breeding Seaside and Saltmarsh sparrows (Kern 2015).

Estimating annual apparent adult survival: data collection. We used mark-recapture to estimate annual apparent adult survival of Seaside and Saltmarsh sparrows. To control for sampling effort, we systematically captured and marked sparrows at each site 12 times from mid-May through mid-August 2011–2015 (Ruskin et al. 2016). We initiated sessions at sunrise and operated 12 mist-nets (12 × 2.6 m, 30-mm mesh) for 3 h. We banded every sparrow captured with one U.S.G.S. aluminum band and one colored Darvic band. For each individual, we determined age by plumage characteristics and sex by breeding-condition traits (presence of cloacal protuberance for males or brood patch for females). Birds not in breeding condition were recorded as unknown sex. We opportunistically banded birds at locations with high levels of bird activity, which included known nest locations to increase the number of females captured. We also banded nestlings when they were 5–7 d old. We used all capture data for survival analyses.

Estimating annual apparent adult survival: statistical analyses. We used an open population Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) in 'RMark' (Laake et al. 2013) in program R (version 3.1.3; R Core Team 2014) to compare

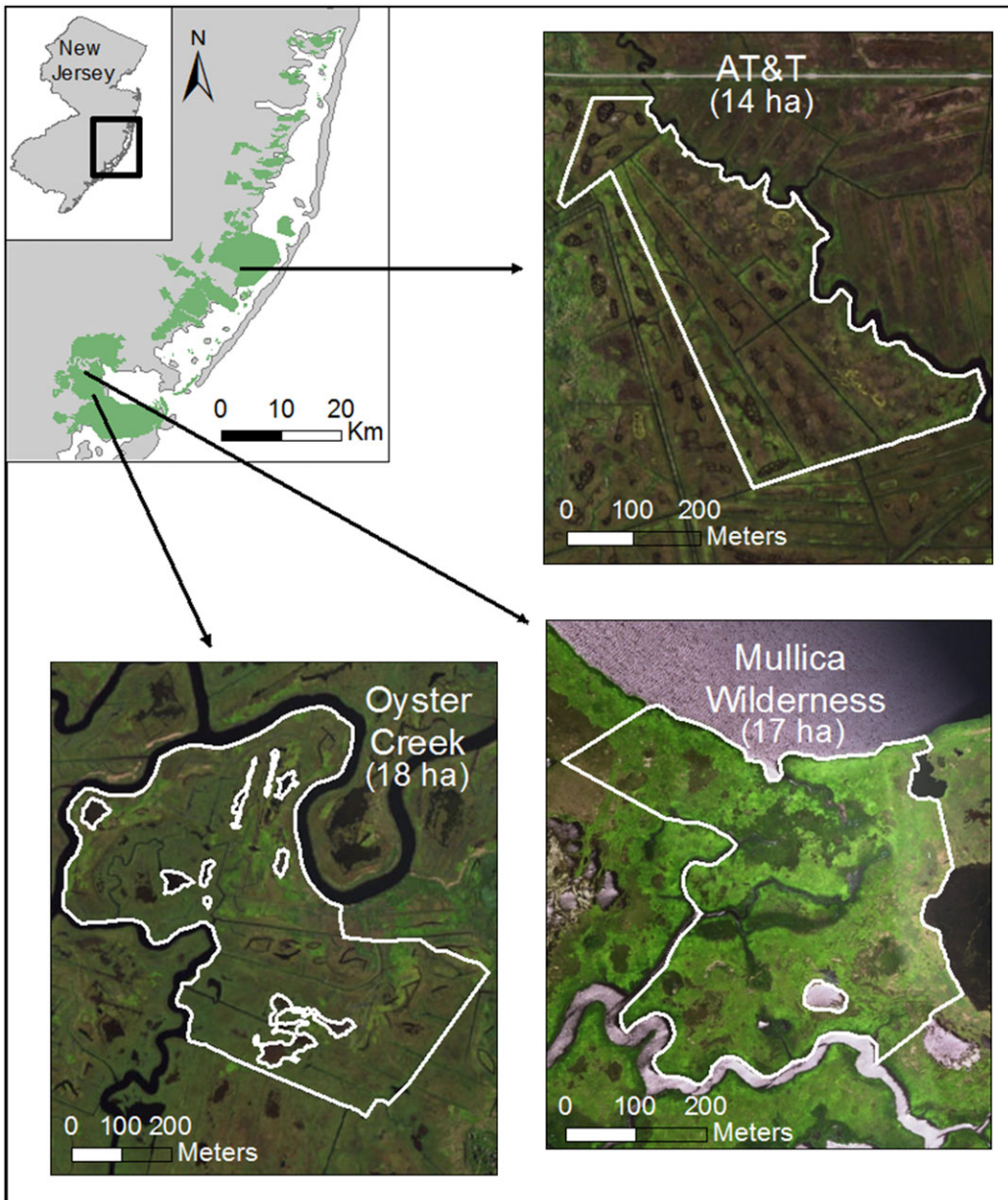


Fig. 1. Study sites used from 2011 to 2015 at the Edwin B. Forsythe National Wildlife Refuge, New Jersey (the green areas in the inset map indicate the extent of the refuge). [Color figure can be viewed at wileyonlinelibrary.com]

apparent adult survival between species, sexes, and site type (unditched or ditched). These estimates are considered apparent survival, not true survival, because we could not distinguish between mortality and emigration from the study sites (Lebreton *et al.* 1992). We used goodness-of-fit tests in program

RELEASE (Burnham *et al.* 1987) to confirm equal recapture probability and, during a given sampling period, equal probability of survival until the next sampling period among marked individuals (Amstrup *et al.* 2005). We first sought to determine if apparent adult survival differed between species. For this

analysis, we modeled survival as constant and assigned species, site type, and sex as individual and additive covariates to compare apparent adult survival between species. We modeled capture probability as constant, as well as species, year, site type, and sex as individual and additive covariates. We ran every combination of these survival and capture probability models, resulting in 65 survival models. Second, we wanted to determine what factors affected apparent adult survival for each species. For this analysis, we modeled survival as constant, with site type and sex as individual and additive covariates. We modeled capture probability as constant and assigned year, site type, and sex as individual and additive covariates. We ran every combination of these survival and capture probability models, resulting in 32 survival models for each species. Sparrows of unknown sex were excluded from the analysis (Seaside Sparrow $N = 53$, 6.8%; Saltmarsh Sparrow $N = 9$, 0.9%). For both analyses, we ranked models using Akaike's Information Criterion (AIC_c) and selected the top models where ΔAIC_c values < 2 (Akaike 1974, Burnham and Anderson 2002). When there was no single top model, we used the model averaging function in package 'RMark' to generate model-averaged estimates.

Nesting success and failure probabilities: data collection. We located and monitored nests of Seaside and Saltmarsh sparrows at each of the three study sites from mid-May through mid-August 2011–2015. We conducted systematic nest searches 6 d per week, visiting each site every 2–4 d such that every nest was checked within 4 d of the previous visit. On all visits, we recorded nest contents and assigned fates based on evidence at nest sites as fledged, failed due to flooding, failed due to predation, failed due to unknown cause, or unknown if fledged or failed. We considered a nest to have fledged young if it survived all previous visits, and was empty and well-worn when chicks were 10 + d old, the age at which they are able to leave nests (Greenlaw and Rising 1994). We assigned a nest the fate of 'flooded' when a nest was observed underwater and found empty during the subsequent check, when intact eggs or uninjured dead chicks were found inside or outside of a nest following a high tide or heavy precipitation, or when a

nest was found empty and wet immediately following a high tide or heavy precipitation. We assigned nests the fate of 'predated' when found empty and their structure or position in the nest substrate was disturbed, when obvious signs of predation remained at the nest site (e.g., injured dead nestlings, nestling body parts, or eggshells), or when a nest was found empty on a day when flooding could not have accounted for failure (no recent high tide or precipitation). When the cause of failure was unclear (e.g., abandonment, eggs were intact, and no evidence of flooding) or in cases of conflicting evidence between nest flooding and predation, we assigned the fate of 'failed due to unknown cause.' Finally, we assigned the nest fate of 'unknown if failed or fledged' when a nest was found empty with no evidence of failure when chicks would have been 9 d old, an age at which they may have fledged. Fully detailed criteria and protocols for nest-fate assignment are provided in Ruskin et al. (2016).

We measured five vegetation characteristics (vegetation height, percent cover high-marsh vegetation, percent cover low-marsh vegetation, nest visibility, and nest height) within a 1-m²-square quadrat centered at nests (Supplemental Methods S1). Vegetation height and percent cover of high-marsh (*S. patens* and *Distichlis spicata*) and low-marsh (*S. alterniflora*) vegetation were recorded within one week of nest completion to limit disturbance of nesting females. We estimated vegetation height by measuring the maximum vegetation height along each side of the quadrat and directly next to each nest, and averaging these five measurements for each nest. We visually estimated percent cover of high-marsh and low-marsh vegetation within the 1-m² frame. Percent cover of high-marsh and low-marsh vegetation was negatively correlated for Saltmarsh Sparrow nest sites (Kern 2015). Therefore, we used high-marsh as a covariate for Saltmarsh Sparrows and low-marsh as a covariate for Seaside Sparrows. Nest visibility and nest height were recorded upon discovery of active nests (with eggs and/or chicks) because these measurements could change as a nest aged due to disturbances or normal chick growth. Seaside and Saltmarsh sparrows weave canopies out of surrounding marsh grasses that cover their nests. We assessed nest visibility by visually estimating the percent obstruction of a paper disc

(6.5-cm diameter) placed in the nest cup from directly above. Nest height was measured as the distance (cm) from the bottom of the nest bowl to the ground.

At each nest, we also recorded covariate measurements for each nest based on remotely collected data. Habitat edges can influence predator populations and avian nesting success rates are influenced by various habitat edge characteristics (Gates and Gysel 1978, Wilcove 1985, Donovan et al. 1997, Batáry and Báldi 2004, Etterson et al. 2014). To estimate an edge effect, we created three edge covariates: distance to road, distance to forest, and distance to water. We digitized all roads, forests, and water features within and surrounding the three study sites, including every ditch, stream, OMWM pond, and bordering canal using base maps in ArcGIS version 10.1 (ESRI, Redlands, CA). We then used the 'Near' tool to separately calculate the distance of each nest to the nearest road, forest edge, and water feature. To incorporate tidal flooding into the nesting success models, we calculated the number of days between the previous new moon and nest initiation, following the procedures of Kern (2015). We assigned precipitation values to each nest based on the total precipitation that occurred during the days between the final two visits to each nest. We acquired precipitation data for the Atlantic City Marina weather station (www.njweather.org), the closest weather station to our study sites.

Nesting success and failure probabilities: statistical analyses. We used program MCestimate (Etterson et al. 2007a,b) to analyze nest success and failure probabilities due to predation and flooding. MCestimate uses a Markov likelihood framework that estimates daily survival, as well as daily failure probabilities due to competing risks (Etterson et al. 2007a,b). To minimize bias, we censored our observations (visits and fate assignments) according to guidelines set by Stanley (2004), Etterson et al. (2007a), and Ruskin et al. (2016). After censoring the nest-monitoring data, we used 511 Seaside Sparrow nests (115 at the unditched site and 396 at ditched sites) and 314 Saltmarsh Sparrow nests (154 at the unditched site and 160 at ditched sites) for subsequent analyses.

For the nest-survival analysis, we had two primary objectives. First, we sought to

determine the factors influencing survival and failure rates of Seaside and Saltmarsh sparrow nests by estimating predation and flooding probabilities independently using a different set of covariates and models for each cause of failure. Second, to determine if predation and flooding probabilities differed between species, we combined the Seaside and Saltmarsh sparrow datasets and included species as a covariate. If the species model did not have a ΔAIC_c value < 2 , we concluded there was no evidence for a difference between species in nest survival or failure rates.

We used nine covariates (site type, nest height, mean vegetation height, nest visibility, distance to forest, distance to road, distance to water, year, and ordinal date) to estimate the factors that most influenced predation rates (Table 1). With no information about the true predator community at our sites, we could not predict the effect of site type on predation. We predicted that (i) nest height would be positively associated with predation rates because higher nests often have reduced cover and are more visible to predators (Pietz and Granfors 2000, Greenberg et al. 2006b), (ii) vegetation height and nest visibility would have a negative relationship with predation rates (Colombelli-Négrel and Kleindorfer 2008), and (iii) the distance of nests to forest, road, and water features would be negatively related to predation rates (Gates and Gysel 1978, Etterson et al. 2014). Finally, year and date were included because predation rates may have varied over time.

We included seven covariates (site type, nest height, percent coverage of low-marsh/high-marsh vegetation, days since new moon, precipitation, year, and date) that we predicted to have the greatest influence on flooding probability (Table 1). We predicted that (i) the unditched site would have a higher nest-flooding rate because ditched marshes drain more readily after flooding (Tonjes 2013), (ii) flooding would be negatively related to date because sparrow nest initiation becomes more synchronized with tide cycles as the breeding season progresses (Shriver et al. 2007), (iii) nest height would have a negative relationship with nest-flooding rates (Bayard and Elphick 2011), (iv) percent cover of high-marsh is negatively related to flooding because this elevation zone in the marsh only floods during monthly high tides (Bertness 1999, Mitsch and Gosselink

Table 1. Covariates used to model predation and flooding probabilities for nests of Seaside (SESP) and Saltmarsh (SALS) sparrows (abbreviations are provided in parentheses) from 2011 to 2015 at the Edwin B. Forsythe National Wildlife Refuge, New Jersey.

Covariate	Fate used for	Description	SESP mean values	SALS mean values
Site type	Predation and flooding	Unditched or grid-ditched study site	–	–
Year	Predation and flooding	Year the nest was monitored	–	–
Date	Predation and flooding	Day of the year (ordinal date) the nest was last visited	–	–
Mean vegetation height (Mean veg. height)	Predation	Mean height of vegetation within 1 m ² of nest	45.3 cm	34.3 cm
Nest visibility	Predation	Percent of the nest contents visible from above	31.6%	20.3%
Distance to forest	Predation	Distance of the nest to the closest forest	648.5 m	985.6 m
Distance to road	Predation	Distance of the nest to the closest road	820.0 m	1106.5 m
Distance to water	Predation	Distance of the nest to the closest water feature	10.3 m	19.6 m
Nest height	Predation and flooding	Distance of the bottom of the nest to the ground	13.3 cm	7.4 cm
Low-marsh cover (Low-marsh)	Flooding (Seaside Sparrow only)	Percent coverage of low-marsh vegetation within 1 m ² of the nest	64.8%	–
High-marsh cover (High-marsh)	Flooding (Saltmarsh Sparrow only)	Percent coverage of high-marsh vegetation within 1 m ² of the nest	–	73.2%
Days since new moon	Flooding	Days since the most recent new moon that the nest was initiated	13.7 d	14.7 d
Precipitation (Precip)	Flooding	Total precipitation 3 d prior to the final visit to the nest	1.28 cm	1.10 cm

2007), (v) low-marsh cover is positively related to flooding because areas containing this vegetation are flooded on a daily basis (Bertness 1999, Mitsch and Gosselink 2007), (vi) because tide height was greatest during the new moon, flooding rates would be lower the sooner a nest was initiated after a new moon because this maximizes the nesting window before the next peak tide (Gjerdrum et al. 2005, Shriver et al. 2007), and (vii) precipitation would be positively related to nest-flooding rates (Shriver et al. 2016). Finally, we included year as a random covariate because the magnitude and frequency of marsh surface flooding varies annually.

The model list for each cause of failure included a subset of models that we

hypothesized to be the most biologically relevant (Table 2). For most variables, we included a univariate model to evaluate the effect of a single variable on nest-failure probabilities. We also included additive models to specifically evaluate the additive effect of multiple covariates on these probabilities. The additive model ‘Distance to forest + distance to road + Distance to water’ was used to test for an effect of landscape features on nest-predation probabilities. We included the model ‘Nest visibility + Mean veg height’ because the visibility of a nest to predators could be linked to both of these covariates. To evaluate the combined effect of annual and within-season variation in predation and flooding, we included the model ‘Year + Date’ for each

Table 2. Nest predation and flooding models used to analyze Seaside and Saltmarsh sparrow nest monitoring data collected from 2011 to 2015 at the Edwin B. Forsythe National Wildlife Refuge, New Jersey (the global model is an additive model of all covariates).

Predation	
Global	
Null	
Site type	
Distance to forest	
Distance to forest + Distance to road	
+ Distance to water	
Distance to road	
Distance to water	
Nest height	
Nest visibility + Mean veg height	
Date	
Year	
Year + Date	
Species ¹	
Flooding	
Global	
Null	
Site type	
Days since new moon	
Days since new moon + Date	
Nest height	
Nest height + High-marsh (Saltmarsh Sparrow)	
or Low-marsh (Seaside Sparrow)	
Precip	
Precip + Days since new moon	
Date	
Date + Precip	
Year	
Year + Date	
Site type * Nest height	
Species ¹	

¹Only used for the species comparison analysis.

cause of failure. For flooding models, we also included the model 'Nest height + High-marsh or Low-marsh' because the relative amount of these vegetation communities may influence flooding probabilities. We used the additive model 'Days since new moon + Date' to test for an effect of the tide cycle and time in season on flooding probability and the additive model 'Days since new moon + Precip' to test for a combined effect of the tide cycle and precipitation on flooding probability. We included the additive model 'Date + Precip' to determine if there was a within-season pattern of increased flooding probability and precipitation. Lastly, we

included an interaction term of 'Site type * Nest height' to determine if the relationship between nest height and flooding depended on whether a site had grid-ditching, given that grid-ditching influences marsh flooding regimes. We also included a null and a global model for each model set. Models were ranked using AIC_c values and models with a Δ AIC_c value < 2 were considered equivalent (Akaike 1974, Burnham and Anderson 2002). To evaluate variation within each covariate, we calculated the daily success and failure probabilities for each category in the categorical covariates (i.e., each year) and the extremes (minimum and maximum) for each continuous variable in the top models for flooding and predation for each species.

RESULTS

Apparent adult survival. We banded 173 adult Seaside Sparrows at the unditched site and 547 at the ditched sites (720 total from 2011 to 2015, with 452 males and 268 females). We banded 467 adult Saltmarsh Sparrows at the unditched site and 562 adults at the two ditched sites (1029 total from 2011 to 2015, with 673 males and 356 females). Prior to conducting each survival analysis, we performed goodness-of-fit tests using program RELEASE (defined as Test 2 and Test 3 in the software; Burnham et al. 1987) to confirm that the data met the assumptions that every marked bird in the population had the same recapture probability (Test 2) and that every marked bird in the population during a given sampling period had the same survival probability until the next sampling period (Test 3; Amstrup et al. 2005). These goodness-of-fit tests did not indicate a lack of fit of the full CJS models to the data in the species-comparison analysis (Test 2: $\chi^2_{0.05, 16} = 7.3$, $P = 0.97$, Test 3: $\chi^2_{0.05, 32} = 19.1$, $P = 0.97$). Similarly, no violation of model assumptions was found for the within-species analysis for either Seaside Sparrows (Test 2: $\chi^2_{0.05, 8} = 2.9$, $P = 0.94$, Test 3: $\chi^2_{0.05, 16} = 3.8$, $P = 1.00$) or Saltmarsh Sparrows (Test 2: $\chi^2_{0.05, 8} = 4.4$, $P = 0.82$, Test 3: $\chi^2_{0.05, 16} = 15.2$, $P = 0.51$).

Annual apparent adult survival of Seaside Sparrows (61.6%, 95% CI: 52.5–70.0%) averaged 21.7% greater than that of Saltmarsh Sparrows (39.9%, 95% CI: 34.0–46.2%)

Table 3. Top five adult survival models (of 65) from the species survival comparison analysis based on mark-recapture sampling from 2011 to 2015 at the Edwin B. Forsythe NWR, New Jersey.

Model	ΔAIC_c	Weight	Deviance	K
Phi(~Species)p(~Year + Site type + Species)	0.00	0.46	182.79	8
Phi(~Species)p(~Year + Site type + Sex + Species)	1.31	0.24	182.07	9
Phi(~Species)p(~Year + Sex + Species)	2.42	0.14	185.21	8
Phi(~Species)p(~Year + Site type)	4.19	0.06	189.00	7
Phi(~Species)p(~Year + Site type + Sex)	4.83	0.04	187.61	8

based on model-averaged estimates (Table 3). For both species, the null model was among those with $\Delta AIC_c < 2$, indicating that sex and site type were weak predictors of apparent adult survival.

Nesting success and failure probabilities.

We located and monitored 511 Seaside Sparrow nests (39% fledged young, 37% predated, 10% flooded, and 14% failed due to an unknown cause), providing an effective sample size of 4525 exposure days. We located and monitored 314 Saltmarsh Sparrow nests (39% fledged young, 29% predated, 16% flooded, and 16% failed due to an unknown cause), providing an effective sample size of 2794 exposure days. Nest predation and flooding probabilities for nests of Seaside Sparrows were best predicted by year and date (Table 4). The probability of daily nest predation increased across the years of our study for Seaside

Sparrows, and was approximately four times greater in 2015 than in 2011. The probability of nest predation for Seaside Sparrows declined throughout the breeding season (Table 5). The probability of flooding also declined throughout the breeding season (Table 5) and varied among years. The probability of nest predation for Saltmarsh Sparrows was best predicted by date (Table 6) and decreased throughout the breeding season (Table 7), whereas the probability of nest flooding was best predicted by year and date (Table 6). Flooding probability varied among years and decreased throughout the breeding season (Table 7). Finally, in the species-comparison analysis, the univariate species model was not among the top models, indicating no differences between Seaside and Saltmarsh sparrows in either daily nest survival or predation and flooding probabilities.

Table 4. The top five MCEstimate models for predation and flooding probabilities for nests of Seaside Sparrows from 2011 to 2015 at the Edwin B. Forsythe NWR, New Jersey.

Cause of failure	Model	ΔAIC_c	Weight	K
Predation	Predated(Year + Date)Flooded(.)	0.00	0.71	7
	Predated(Site type + Year + Distance to forest + Distance to road + Distance to water + Date + Nest height + Percent visible + Mean veg. height) Flooded(.)	1.84	0.28	14
	Predated(Year)Flooded(.)	14.00	0.00	6
	Predated(Date)Flooded(.)	26.32	0.00	3
	Predated(Distance to road+ Distance to forest + Distance to water)Flooded(.)	33.79	0.00	5
Flooding	Predated(.)Flooded(Year + Date)	0.00	0.81	7
	Predated(.)Flooded(Year)	3.24	0.16	6
	Predated(.)Flooded(Site type + Year + Days since new moon + Precip + Date + Nest height + Low-marsh)	6.73	0.03	12
	Predated(.)Flooded(Date + Precip)	12.09	0.00	4
	Predated(.)Flooded(Date)	13.09	0.00	3

Table 5. Predicted daily and nest period (25 d) success and cause-specific failure probabilities for Seaside Sparrows based on covariates from the top MCestimate models for each year (while holding date constant at the mean value) and the first and last day of the breeding season (while holding year constant at the intercept) from 2011 to 2015 at the Edwin B. Forsythe National Wildlife Refuge, New Jersey.

Fate	Covariate	Parameter	Beta	SE	Daily success	SE	Daily failure	SE	Nest period success	SE	Nest period failure	SE	
Predation	Year	Intercept (Year: 2011)	-1.035	0.810	0.969	0.005	0.016	0.005	0.460	0.065	0.283	0.080	
		Year: 2012	0.420	0.457	0.961	0.007	0.024	0.007	0.374	0.071	0.393	0.090	
		Year: 2013	0.894	0.427	0.948	0.010	0.038	0.010	0.259	0.066	0.540	0.087	
		Year: 2014	1.192	0.361	0.935	0.006	0.051	0.006	0.186	0.031	0.638	0.042	
		Year: 2015	1.408	0.352	0.924	0.006	0.063	0.006	0.138	0.021	0.706	0.032	
Flooding	Year	Intercept	-1.035	0.810	-	-	-	-	-	-	-	-	
		Date	-0.017	0.004	-	-	-	-	-	-	-	-	-
		First day of season (147)	-	-	0.884	0.014	0.103	0.014	0.045	0.018	0.846	0.033	
		Last day of season (219)	-	-	0.953	0.007	0.007	0.007	0.303	0.054	0.484	0.070	
		Intercept (Year: 2011)	-1.373	1.530	0.944	0.005	0.008	0.004	0.237	0.029	0.103	0.047	
Date	Date	Year: 2012	0.345	0.687	0.941	0.006	0.011	0.005	0.219	0.033	0.141	0.061	
		Year: 2013	-0.111	0.843	0.945	0.005	0.007	0.005	0.241	0.034	0.093	0.059	
		Year: 2014	-0.332	0.618	0.946	0.004	0.005	0.002	0.250	0.024	0.076	0.027	
		Year: 2015	1.133	0.513	0.929	0.004	0.023	0.004	0.159	0.019	0.275	0.037	
		Intercept	-1.373	1.530	-	-	-	-	-	-	-	-	-
Fate	Date	Date	-0.019	0.009	-	-	-	-	-	-	-	-	
		First day of season (147)	-	-	0.911	0.011	0.042	0.012	0.098	0.030	0.427	0.080	
		Last day of season (219)	-	-	0.941	0.005	0.004	0.002	0.262	0.026	0.050	0.032	

Table 6. The top five MCEstimate models for predation and flooding probabilities for nests of Saltmarsh Sparrows from 2011 to 2015 at the Edwin B. Forsythe NWR, New Jersey.

Cause of failure	Model	Δ AICc	Weight	K
Predation	Predated(Date)Flooded(.)	0.00	0.54	3
	Predated(.)Flooded(.)	3.04	0.12	2
	Predated(Distance to forest)Flooded(.)	4.02	0.07	3
	Predated(Site type)Flooded(.)	4.07	0.07	3
	Predated(Distance to road)Flooded(.)	4.14	0.07	3
Flooding	Predated(.)Flooded(Year + Date)	0.00	0.74	7
	Predated(.)Flooded(Site type + Year + Days since new moon + Precip + Date + Nest height + High-marsh)	3.19	0.15	12
	Predated(.)Flooded(Days since new moon + Date)	4.66	0.07	4
	Predated(.)Flooded(Year)	6.62	0.03	6
	Predated(.)Flooded(Date)	9.03	0.01	3

DISCUSSION

With extensive ditching present throughout ~90% of the salt marshes along the Atlantic Coast of the United States (Bourn and Cottam 1950, Correll et al. 2017), evaluating possible differences in wildlife vital rates between unditched and ditched marshes is critical. We found no differences between an unditched site and ditched sites in either apparent adult survival or daily nest survival for either Seaside or Saltmarsh sparrows. Although mixed conclusions have been reported about the suitability of ditched marshes as Seaside Sparrow nesting habitat (Post and Greenlaw 1975, Marshall and Reinert 1990), Post (1974) also found no difference in nesting success of Seaside Sparrows in unditched and ditched salt marshes. Similarly, Pepper and Shriver (2010) found no difference between the nest success rates of Seaside Sparrows on sites with extensive OMWM and sites with limited OMWM. Our results thus join a growing body of evidence that ditched salt marshes are not lower-quality breeding sites for Seaside and Saltmarsh sparrows than unditched sites. Ditch plugging has increased in recent decades in an attempt to either restore historic saltmarsh hydrology or create open water habitat for fish or waterbirds in ditched marshes (Vincent et al. 2013). However, with no difference in nest survival between unditched and ditched sites, habitat management for Seaside and Saltmarsh sparrows apparently does not require ditch plugging. In fact, ditch plugging might actually reduce

habitat quality for these species by increasing marsh surface flooding and contributing to an overall loss of nesting habitat (Goodman et al. 2007, Vincent et al. 2013).

Our estimated annual apparent adult survival rates suggest that the annual apparent adult survival of Seaside Sparrows was > 1.5 times greater than that of Saltmarsh Sparrows. The magnitude of this difference is apparent when considered over the expected lifespan of these species (Greenlaw and Rising 1994, Post and Greenlaw 1994). With an annual apparent survival rate of 61.6%, Seaside Sparrows that survive year one have a 23.4% chance of surviving to year four, whereas Saltmarsh Sparrows, with an annual apparent survival rate of 39.9%, have only a 6.4% chance of reaching year four. This difference may partially explain recent regional population trend estimates that indicate stable Seaside Sparrow populations, but populations of Saltmarsh Sparrows declining at an average rate of 9% per year (Correll et al. 2017). There is little evidence of adult mortality on the breeding grounds for either species, suggesting that differences in mortality occur away from the breeding grounds (Borowske 2015). Identifying the factors that explain why apparent adult survival rates vary by this magnitude should be a research priority. One possibility is that our methods did not permit estimation of 'true' survival, and the lower apparent survival of Saltmarsh Sparrows may have been due to higher rates of emigration from our study sites compared to Seaside Sparrows. However, we do not know of any reason why emigration rates would differ between species.

Recent estimates of adult survival rates of Seaside and Saltmarsh sparrows have been reported for breeding (DiQuinzio et al. 2001, Borowske 2015, Field 2016) and wintering (Winder et al. 2012, Borowske 2015) populations. Winder et al. (2012) estimated wintering survival for both species in North Carolina and found no significant difference between species, with an estimate of 48% (± 0.07 SE) for Seaside Sparrows and 52% (± 0.12 SE) for Saltmarsh Sparrows. Borowske (2015) also found no evidence of a difference in within-season apparent adult survival of Seaside and Saltmarsh sparrows in either breeding (Connecticut) or wintering (South Carolina) areas. In contrast, our survival estimates indicate a significant difference in apparent annual survival of Seaside and Saltmarsh sparrows. Our estimate of Saltmarsh Sparrow apparent survival (39.9%, 95% CI: 34.0–46.2%) is similar to those reported by Field (2016), with range-wide mean survival rates for Saltmarsh Sparrows of 0.44 for females (95% credible interval = 0.37–0.52) and 0.49 (0.42–0.56) for males.

Despite differences between species in apparent adult survival rates, our results suggest that use of similar management strategies for breeding Seaside and Saltmarsh sparrows may be beneficial. Three lines of evidence support this conclusion. First, we found that mean daily nest survival and predation and flooding rates of Seaside and Saltmarsh sparrows did not differ. Second, for both species, the best predictors of nest predation and flooding rates were temporal covariates. The additive model of year and date was the top model for predation and flooding probabilities for Seaside Sparrows, and flooding probabilities for Saltmarsh Sparrows. Annual variation in flooding probabilities is largely explained by the annual variation in the timing of new moon tides in relation to the start of the breeding season and annual differences in precipitation (Kern et al. 2012, Shriver et al. 2016). The only difference between the two species in the top models was that date was the sole predictor of predation probability for Saltmarsh Sparrows. Both species also exhibited the same decreasing trend in predation and flooding rates during the breeding season. Nest predation rates in relation to date have not previously been reported for saltmarsh breeding birds, but predation rates

have been found to both increase (Grant et al. 2005) and decrease (Burhans et al. 2002) throughout the breeding season in grasslands. A decline in predation rates during the breeding season may indicate either a temporal change in predator population dynamics or some adjustment in the nesting behavior of individual birds throughout the season (Thompson 2007).

The decline in probability of flooding during the breeding season was expected because tide height generally decreased during the breeding season (NOAA/National Ocean Service 2016) and tidal marsh sparrows synchronize nest initiation with spring tides after nest failures early in the season (Shriver et al. 2007). The absence of any effect of the timing of nest initiation in relation to the lunar cycle on flooding probabilities for Saltmarsh Sparrows was surprising given the importance of this variable for this species in New England (Gjerdrum et al. 2005, Shriver et al. 2007).

Finally, for both species, we detected a greater probability of nest failure due to predation than to flooding, indicating that nest predation may be limiting population growth. In the northern hemisphere, where tidal ranges are correlated with latitude, these results support the latitudinal relationship between competing causes of nest failure, with flooding greatest at higher latitudes and predation increasing in the south (Reinert 2006, Greenberg et al. 2006b, Ruskin 2015). At the northern extent of the ranges of both species in New England, most nest failures are due to flooding (Marshall and Reinert 1990, DiQuinzio et al. 2002, Shriver et al. 2007, Bayard and Elphick 2011, Ruskin 2015). Farther south on Long Island, New York, Post and Greenlaw (1982) reported similar rates of nest failure due to predation and flooding. In Florida, Post et al. (1983) found that predation accounted for 89% of nest failures for a non-migratory subspecies of Seaside Sparrows.

Field (2016) examined vital rates across the northeastern United States and found that population trends for Seaside and Saltmarsh sparrows may be driven by fecundity. Despite regional differences in the prominent cause of nest failure, flooding and predation are threats to sparrow fecundity across the range of both species. In addition to habitat loss, sea-level rise threatens coastal wetland ecosystem function, including sparrow nest flooding regimes,

by altering the magnitude and frequency of marsh surface inundation (Morris et al. 2002, Craft et al. 2009). To combat these threats, marsh elevation can be maintained through thin-layer sediment deposition (Ford et al. 1999, Schrifft et al. 2008) and shoreline erosion and loss can be ameliorated through implementation of living shorelines (Scyphers et al. 2011, Toh et al. 2017). Given that predation is the primary cause of nest failure in this critical breeding location, studies are needed to help develop management actions to mitigate the effect of predators on sparrow populations. We found variation in predation rates within and between breeding seasons, but the identity of dominant nest predators and the relative abundance of different nest predators remain to be determined. Video surveillance of nests would help identify predator species and their relative importance to sparrows (Stake et al. 2004, Bolton et al. 2007, Thompson 2007) and reduce uncertainty concerning reasons for nest failure (Etterson and Stanley 2008).

If nest predators can be identified, land managers could target predator populations in salt marshes and potentially increase sparrow reproductive output. Previously, possible methods for reducing rates of nest predation in Seaside Sparrow populations have been tested in only two studies involving the use of nest enclosures (Post and Greenlaw 1989, Boulton and Lockwood 2010), and no predator-control research has specifically been conducted for Saltmarsh Sparrow populations. Given the threat to salt-marsh breeding birds posed by rising sea levels, potential solutions to more plausibly managed threats, such as nest predation, should be considered. Predator-control programs have been used for bird conservation in a number of taxa (Lavers et al. 2010, Smith et al. 2010, 2011, Hartway and Mills 2012) with notable success in some systems, like island-breeding birds (Vanderwerf and Smith 2002, Innes et al. 2010, Armstrong et al. 2014). Given the results of our study, these methods deserve further consideration as an option for conserving saltmarsh birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Data S1. Nest vegetation measurements SOP.