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THE CENTER FOR CONSERVATION BIOLOGY
WILLIAM & MARY

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Project Partners:

United States Fish and Wildlife Service
The Center for Conservation Biology
William & Mary

Front Cover: A Saltmarsh Sparrow captured at Bull Marsh during January 2021. Photograph by Laura Duval.

The Center for Conservation Biology is an organization dedicated to discovering innovative solutions to environmental problems that are both scientifically sound and practical within today's social context. Our philosophy has been to use a general systems approach to locate critical information needs and to plot a deliberate course of action to reach what we believe are essential information endpoints.

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EXECUTIVE SUMMARY

The tidal saltmarsh habitat in the Chesapeake Bay region supports a diverse marsh sparrow suite during winter, which is among the most poorly understood intervals of a songbirds' life. Research on the status and distribution of these species has primarily focused on the breeding season despite the fact that winter accounts for a significant portion of songbird mortality. A lack of information about these periods hampers our ability to conserve habitats that support birds. To better understand the factors that influence marsh sparrow winter ecology, we used capture-recapture sampling and double-pass rope drag transect surveys to explore parameters that affect winter mortality and density on the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR) and Fisherman Island National Wildlife Refuge (FINWR).

During the winter of 2020-2023, we captured 124 Nelsons sparrows, 74 saltmarsh sparrows, and 24 seaside sparrows. Our top Cormack-Jolly-Seber model included a time-varying predictor that accounted for differential survival between the early and late portions of the winter, species, marsh, and an interaction between marsh and species within the survival function of the model with zero predictors in the recapture function. Recapture probability was estimated at 0.34 ± 0.07 SE. and daily survival ranged from 0.97-1.00, depending on species, study site, and winter period (early/late). Survival was higher during the early portion of winter for all species, possibly because seed availability declines throughout the winter. Survival was similar among all study sites for saltmarsh sparrows, highest for Nelsons sparrows at the ESVNWR Boat Ramp Marsh and highest for seaside sparrows at FINWR.

We also observed 226 sharp-tailed sparrows and 12 seaside sparrows on double-pass rope drag transects. We were unable to incorporate seaside sparrows into N-mixture models due to data deficiency. For saltmarsh and Nelson's sparrows, survey site, survey season and an interaction between the two terms were included within the abundance function of our top model. Transect identity was included within the availability function of our top model and no predictors were included in the detection function. Detection was estimated at 0.86 ± 0.03 SE. Saltmarsh sparrow densities were between 0.6 – 1.3 birds per ha and were highest at a transect in at ESVNWR Bull Marsh while Nelson's sparrow densities were between 0.6 – 3.2 birds per ha and were highest at the ESVNWR Boat Ramp Marsh.

Saltmarsh and seaside sparrows were both associated with marshes with more cover and seed availability though saltmarsh sparrow densities were greatest in portions of the marsh further from the upland-marsh transition zone while seaside sparrows observations and survival were positively associated with marshes with taller vegetation like that found near the margins of tidal waterways. Nelson's sparrows were associated with marsh that lacked attributes favored by saltmarsh and seaside sparrows, possibly to avoid interspecific competition. Some evidence of intra-specific habitat segregation also exists for Nelsons sparrow as sex ratios skewed female at ESVNWR Boat Ramp and male at other field sites. The other two species of marsh sparrows had relatively even sex ratios at all sites.

BACKGROUND

The suite of species utilizing tidal saltmarsh habitat in the Chesapeake Bay region during winter is of high conservation concern. Included in this suite are the Saltmarsh Sparrow (*Ammospiza caudacuta*), Nelson's Sparrow (*A. nelsoni*), and Seaside Sparrow (*A. maritima*). All of these species fall into several high priority bird conservation lists, including the Atlantic Coast Joint Venture Salt Marsh Bird Conservation Plan (ACJV 2019), Virginia Wildlife Action Plan (VDGIF 2015), and the Mid-Atlantic Partners in Flight Coastal Plain Bird Conservation Plan (Watts 1999). In addition, the Saltmarsh Sparrow is one of three species under the Atlantic Coast Joint Venture's Flagship Species Initiative with an estimated 80% population decline in just the last 15 years (ACJV 2019) and is currently being considered for protection under the Endangered Species Act.

Research on the status and distribution of these species has primarily focused on the breeding season. However, few studies have examined the migratory and wintering portions of their life cycle despite the fact that marsh sparrows may spend up to six months on winter areas during a period that may be most critical for adult survival. Several forms of marsh sparrow species that emanate from different breeding locations can be found wintering in the Chesapeake Bay Region, including all three subspecies of Nelson's Sparrows *(A. n. alterus*, *A.n. nelsoni,* and *A. n. subvirgata)*, both subspecies of Saltmarsh Sparrows (*A. c. caudacuta* and *A. c. diversus*), and the nominate Seaside Sparrow subspecies (*A. m. maritima*). A 2014 study conducted by The Center for Conservation Biology revealed that Virginia appears to be an important wintering area for these marsh sparrows (Watts and Smith 2015). Several of these marsh sparrow taxa appear vulnerable to threats that include sea-level rise, extreme flooding events, tidal ditching, and development. Saltmarsh Sparrows are particularly sensitive to these threats and some biologists have predicted a global population collapse within the next 50 years (Correll et al. 2017).

The goal of this project is to estimate survival and abundance for marsh sparrows at an important wintering location, the southern tip of the Delmarva Peninsula, and compare these metrics among multiple study years. The results of this study provide a multiyear comparison that may allow us to determine what factors may influence habitat use and overwinter survival.

OBJECTIVES

The overarching goals of this project are to:

1) Quantify and compare overwinter survival between marshes between multiple years.

2) Quantify and compare wintering marsh sparrow densities between multiple years.

3) Determine whether vegetation characteristics are associated with marsh sparrow survival and density.

METHODS

Study Area

Field work occurred in two marshes (Bull Marsh and Boat Ramp Marsh) at the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR, Figures 1 and 2) and at Fisherman Island National Wildlife Refuge (FINWR, Figure 3). Sampling locations chosen within the study area were the same that were used during the 2013-2014 winter (Smith et al. 2014). All sampling areas were low marsh habitat dominated by *Spartina alterniflora* bordered by high marsh habitat dominated by *Spartina patens*, *Iva frutescens*, *Morella spp.,* and *Baccharis halimifolia*.

Figure 1. Transects and trapping locations adjacent to the boat ramp at the Eastern Shore of Virginia NWR.

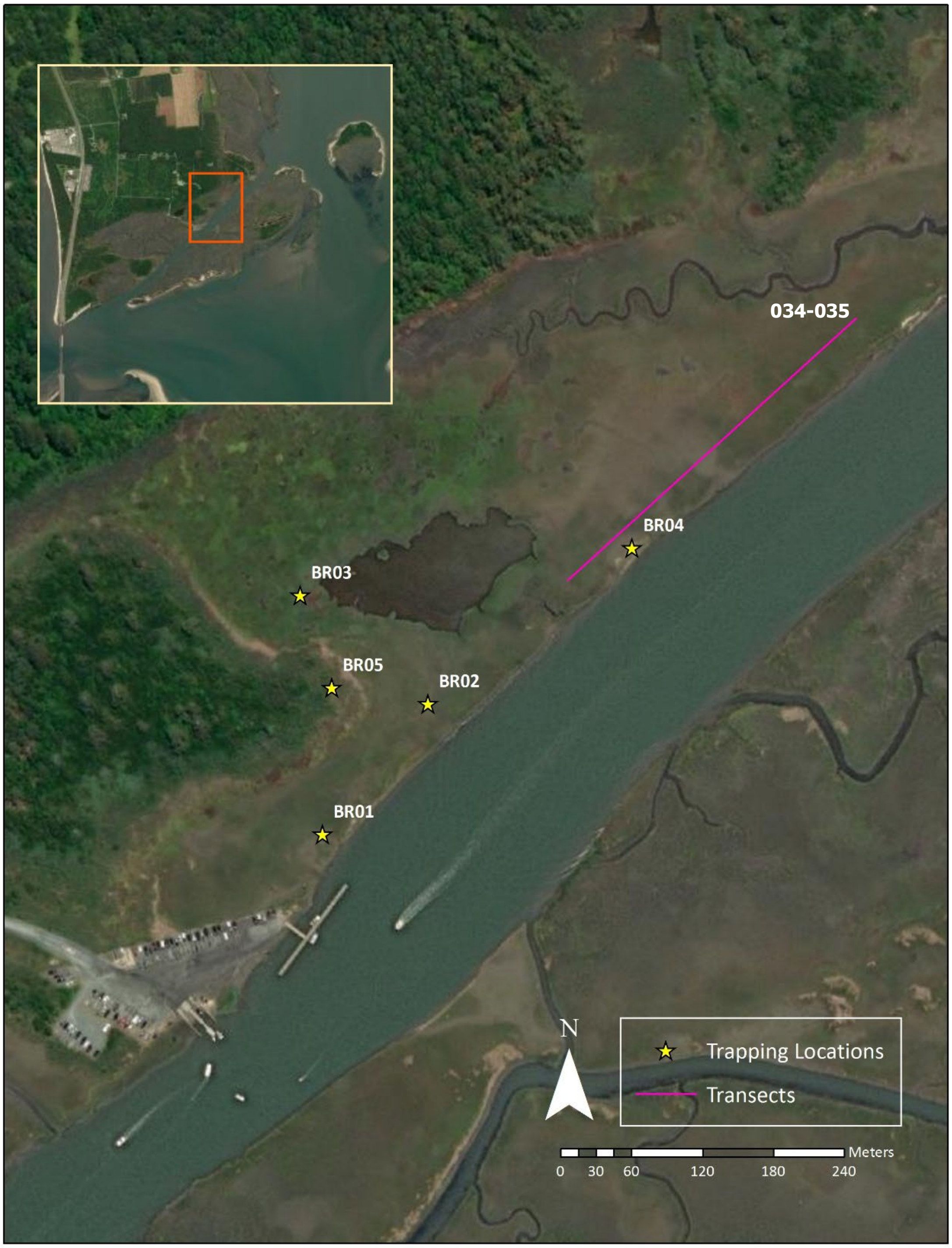


Figure 2. Transects and trapping locations at Bull Marsh at the Eastern Shore of Virginia NWR

Figure 3. Transects and trapping locations at Fisherman Island NWR.

Sparrow Capture

Sparrows were captured at each site once per sampling period: Capture attempts were made once in each of the sampling periods: 26 November – 10 December, 13 January – 02 February, and 18 February – 01 March, for a total of 3 capture attempts at each site. We used portable mist nets that were erected where sparrows concentrated at tidal highs near transect sampling locations. These areas (i.e., roosts) included high marsh points, relatively tall patches of *S. alterniflora*, and isolated patches of wrack (Figures 1 – 3). After nets were erected, we dragged a rope through the marsh near the nets to flush birds to the roosts and then flushed birds from the roosts into the nets. Once captured, we banded sparrows with a standard USGS tarsal band. Morphometric measurements taken included: wing chord (mm), tail length (mm), culmen length (0.1 mm), tarsus length (0.1 mm), and mass (0.1 g). Age was determined using a combination of feather wear and structure and skull pneumatization when possible. We also took 3 – 5 body feathers to analyze for sex determination during the 2022-2023 winter(Avian Biotech).

Sparrow Density Surveys

We used a standardized double-pass rope drag transect (Peterson and Best 1985) to sample marsh sparrow density. Transects were 60 m wide (rope distance) and 250 m long (Figures 1 – 3). We surveyed the same transects as in the baseline 2013-2014 survey that covered the greater Chesapeake Bay area. Each transect was surveyed once in each of the sampling periods: 26 November – 09 December, 13 January – 02 February, and 18 February – 01 March, for a total of three surveys per year at each site. Surveys were conducted between mid-falling and mid-rising tide to avoid any biases produced by high tide inundation that potentially moves birds out of lower marshes and into high marsh roosting habitats (Paxton 2007).

Rope drags are designed to increase the detection probability by flushing birds hidden within dense vegetation. We implemented a double-pass technique that would help determine detection probability by comparing the detection decay rate between the first and second pass (Watts et al 2023). A transect was walked by three people, with two stationed on either end of the rope and one walking down the middle. On the initial pass all detected birds were registered and tracked to determine if they flushed off the transect. A reverse pass was made immediately after to detect any additional birds missed by the first pass. Detections of Nelson’s and saltmarsh sparrows were combined simply as “sharp-tailed sparrow” because of difficulty in discerning these two species visually on flush surveys. Additionally, we marked every initial location from where birds flushed and placed a pin flag at the location for follow-up vegetation measurements.

Vegetation Characteristics

At every location where sparrows were flushed during the density surveys, and at 10 randomly selected control points, we measured *S. alterniflora* density (stem count and ocular estimation), height of the tallest *S. alterniflora* stem, and determined seed availability by counting the number of *S. alterniflora* inflorescences (i.e., seed heads) that retained spikes with spikelets (i.e., seeds) within a circular plot measuring $0.65m^2$. Vegetation surveys at bird detection locations were conducted immediately following transect surveys. Controls were conducted during the second period of surveys in late January and early February during 2020-2021 and 2021-2022. During the 2022-2023 winter, controls were surveyed during all three sampling periods.

Statistical Analyses

All statistical analyses were performed in program R (2022). We used an exact binomial test to determine if sex ratios were different from 50:50 and a test of equal proportions to determine if males or females were more likely to be recaptured. We calculated apparent survival and capture probability using the package ‘marked’ (Laake et al. 2013) in program R (R Core Team 2020). We constructed a set of Cormack-Jolly-Seber survival models that included marsh location (Bull Marsh, Boat Ramp Marsh, FINWR), sparrow species, an interaction between the marsh and sparrow species to account for species specific differences in survival at each marsh and time of season within the survival function. We included marsh identity, sparrow species, and the height of the high tide during the trapping session within the capture probability function. We also included models with only intercepts in the survival and capture probability functions. We used the most parsimonious model according to AIC score to predict survival and capture probabilities with a cutoff of ΔAIC <2.00 to determine the top model.

We calculated density with the package ‘unmarked’ (Fiske and Chandler 2011) using generalized multinomial N-mixture models (Royle et al. 2004). We treated our rope drags as removal experiments where birds flushed from transects on the initial drag were “removed” and birds we encountered on the return drags were newly encountered birds. We used a multi-step process to select the most parsimonious model according to AIC scores and considered models with ΔAIC <2 to be more parsimonious. We first evaluated whether including wind, temperature or day of year improved model fit over the null model (i.e., zero predictors). We acquired wind and temperature data from NOAA’s National Climatic Data Center, via the R package, ‘rnoaa’. Then, because our goal was to compare abundance of birds among the areas we surveyed, we compared models with site (Bull, Boat Ramp or Fisherman Island) within the abundance function and transect identity in the availability function. Finally, we evaluated whether the inclusion of survey season as well as an interaction between survey season and site improved fit. We used the most parsimonious model according to AIC score to predict abundance, availabilty and detection probabilities with a cutoff of ΔAIC <2.00 to determine the top model. We report the output of the model as well as species-specific density for Nelson’s and saltmarsh sparrow in each marsh calculated as (mean abundance * mean availability * mean annual percentage of saltmarsh and Nelson’s sparrows captured at each site (excluding 2014 because not all sites were captured during this year))/area surveyed (60 X 250 m transect).

We used Kendal rank correlation test to determine if stem counts and ocular estimates were correlated. To determine what factors influenced stem height, cover, and seed availability, we used results of vegetation surveys in all years and at all sites to construct generalized linear models (GLMs) that included type (Control/bird observation point), sampling season, marsh location, and day of season as predictors. We used normal distributions for GLMs with cover and stem height as response variables and a Poisson distribution for the GLM with seed availability as a response variable.

RESULTS

Bird Capture and Survival

Captures – We recorded 334 captured birds from 222 individual sparrows (Appendix I) including 124 Nelsons sparrows, 74 saltmarsh sparrows, and 24 seaside sparrows. The number of individuals captured was greater during the 2020-2021 winter (113) than the 2021-2022 (77) and 2022-2023 winters (79). We also caught more individuals during period 1 (130) than period 2 (105) and three (69) though this was not consistent for all years (Table 1).

We captured more individual birds at Bull Marsh (101) than FINWR (64) or at Boat Ramp Marsh (58). Nelsons sparrows accounted for 82.8% of individuals captured at Boat Ramp Marsh, 43.6% at Bull Marsh, and 51.6% of birds at FINWR. Saltmarsh sparrows accounted for 15.5%, 43.63%, and 32.8% of individual birds captured at Boat Ramp Marsh, Bull Marsh, and FINWR. Seaside sparrows accounted for 1.7%, 12.9%, and 15.6% of individual birds captured at the Boat Ramp Marsh, Bulls Marsh, and FINWR.

The total number of captures we accumulated was 334 and we captured each individual Nelsons and saltmarsh sparrow 1.5 ± 0.08 SE times compared to 1.755 ± 0.26 for seaside sparrows. The most captures for any individual bird was five for both Nelsons and seaside sparrows, while the most captures of any saltmarsh sparrow was three. Five Nelsons (2.4%) and two seaside sparrows (8.3%) were captured at least once during all three seasons while one saltmarsh sparrow (1.3%) was captured all three seasons. Twenty-nine Nelsons sparrows (23.4%) were captured during two of the three seasons compared to 15 saltmarsh sparrows (20.3%) and five seaside sparrows (20.8%). All birds that we recaptured were recaptured at their original banding location except for one foreign recapture that was initially banded in New Hampshire.

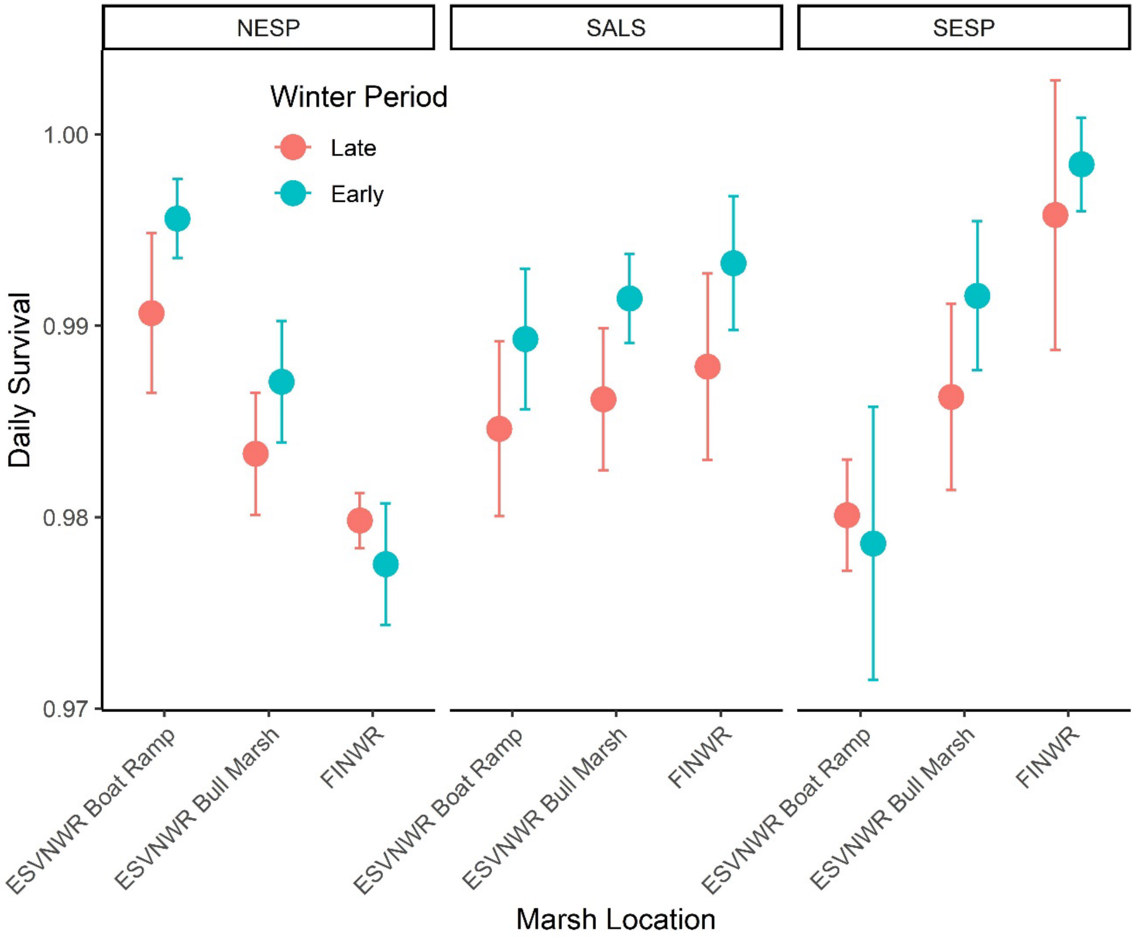
Sex – We genetically determined sex for 84 birds and sex ratios were not different from 1:1 for Nelsons sparrows (56.4% female, n = 39, p = 0.419), saltmarsh sparrows (45.4% female, n = 33, p = 0.059), and seaside sparrows (41.7% female, n = 12, p = 0.263). Male wing chord was greater than female for Nelson's sparrows (T = -2.80, df = 35.55, p=0.008), saltmarsh sparrows (T = -5.22, df = 28.55, p<0.001), and seaside sparrows (T = -3.87, df = 9.53, p=0.003). Sex ratios for saltmarsh sparrows and seaside sparrows were not different among sites (χ^2=4.694,p=0.095 and χ^2=1.577,p=0.454, respectively), but Nelson's sparrow ratios were different among sites (χ^2=7.672,p=0.022). A higher percentage of Nelson's sparrows were female at the boat ramp (78.9%, n = 19) than at Bull marsh (33.3%, n = 9) and Fisherman's Island (36.4%, n = 11).

Table 1. Locations and total number of birds captured during the 2020-2022 winters.

Species	Unit	Period 1	Period 2	Period 3	Total
SALS	ESVNWR Boat Ramp	6	6	2	**14**
	ESVNWR Bull Marsh	24	29	10	**63**
	FINWR	14	13	6	**33**
NESP	ESVNWR Boat Ramp	35	27	22	**84**
	ESVNWR Bull Marsh	24	16	17	**57**
	FINWR	22	9	10	**41**
SESP	ESVNWR Boat Ramp	1	1	0	**2**
	ESVNWR Bull Marsh	9	8	1	**18**
	FINWR	9	7	6	**22**
Total		**144**	**116**	**74**	**334**

Survival – Our top CJM model included a time-varying predictor that accounted for differential survival between the early and late portions of the winter, species, marsh, and an interaction between marsh and species within the survival function of the model with zero predictors in the recapture function (Appendix II). Two models were within 2AIC points of the top model, but both were identical to the top model except for an additional uninformative parameter (similar log-likelihood to top model with insignificant effect size for additional predictor (Appendix 2). Recapture probability was estimated at 0.34 ± 0.07 SE. Daily survival varied by marsh and species but was greater between the first two trapping periods (β = 1.43±0.79 SE) for all species (Figure 4). Survival rates were highest at FINWR, followed by Bull Marsh, and Boat Ramp Marsh for saltmarsh and seaside sparrows while Nelson's sparrow survival was highest at Boat Ramp Marsh followed by Bull Marsh and FINWR (Figure 4). Recapture probability was estimated at 0.34±0.07 SE.

Figure 4. Daily survival for Nelson's Sparrow (NESP), saltmarsh sparrow (SALS), and seaside sparrows (SESP) captured on the Eastern Shore of Virginia during the 2020-2022 early (blue) and late (red) portions of winter. Error bars represent standard error.



Sparrow Density Surveys

Survey Results – During the winters of 2020-2021, 2021-2022, and 2022-2023, we observed a total of 163 Sharp-tailed Sparrows, 7 Seaside Sparrows, and 6 Marsh Wrens during rope-drag transect surveys. We detected almost twice as many birds in the 2020-2021 winter (83) as we did in 2021-2022 (46) and 2022-2023 winters (47). These numbers are comparable to the 2013-2014 winter when we observed a total of 70 birds including 63 sharp-tailed sparrows, 5 seaside sparrows, and 2 marsh wrens.

Overall, total birds observed on transects was relatively steady throughout the winter with 83 in period 1, 76 in Period 2, and 79 in Period 3 (Table 2). During the winters of 2020-2021, 2021-2022, and 2022-2023, 154 birds were detected on the initial pass (87.5%) and 22 were detected on the return pass. This compares to 64 detected during the initial pass (91.4%) and six detected during the return pass in 2013-2014.

The greatest number of sharp-tailed sparrow observations occurred at transect 034-035 in Boat Ramp Marsh (n = 64) followed by 038-039 near the end of the dike at Bull Marsh (63). The two transects at FINWR, 046-047 and 048-049, accounted for 25 and 22 observations respectively, while the fewest detections occurred at Bull Marsh transects 036-037 (25) and 040-041 (27) in Bull Marsh. The greatest number of seaside sparrows occurred at 046-047 at FINWR (8). Seaside sparrow detections during rope drag transects also occurred at 036-037 in Bull Marsh (1) and 034-035 at the Boat Ramp Marsh (1), and 048-049 at FINWR (2).

Table 2. Birds observed on transects during the 2014 and 2020-2022 winters. Results for Bull Marsh are shaded gray to facilitate reading the table.

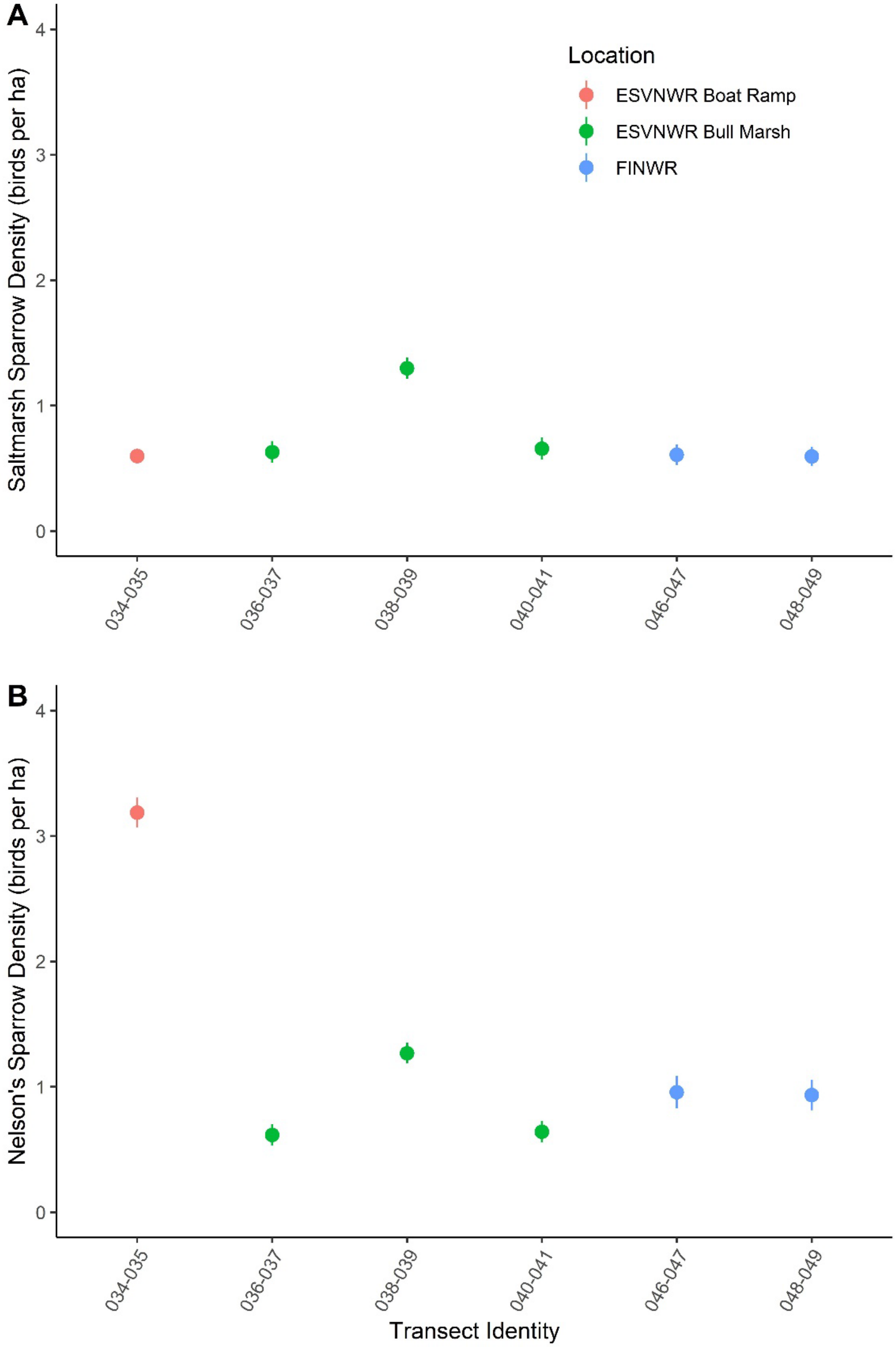
Species	Unit	Transect	P1	P2	P3	Tot
STSP	ESVNWR Boat Ramp	034-035	15	27	22	**64**
	ESVNWR Bull Marsh	036-037	10	9	6	**25**
		038-039	26	17	20	**63**
		040-041	4	7	16	**27**
	FINWR	046-047	12	8	5	**25**
		048-049	10	4	8	**22**
SESP	ESVNWR Boat Ramp	034-035	1	0	0	**1**
	ESVNWR Bull Marsh	036-037	1	0	0	**1**
	FINWR	046-047	4	2	2	**8**
		048-049	0	2	0	**2**
Total			83	76	79	**238**

N-mixture model – Survey site, survey season and an interaction between the two terms were included within the abundance function of our top model for sharp-tailed sparrow abundance (Table 3). Mean predicted bird abundance was greatest at the boat ramp marsh (12.1 ± 4.0 birds per transect), followed by Bull marsh (8.4 ± 4.9), and the marshes on Fisherman's Island (6.4 ± 4.3), though this varied by season (Appendix III). Mean predicted abundance was greatest in 2020 (11.8 ± 4.1), followed by 2014 (9.4 ± 3.8), 2021 (6.3 ± 3.7), and 2022 (6.0 ± 3.6). Transect identity was included within the availability function of our model and birds were most available at transect 038-039 in Bull Marsh (0.57 ± 0.06) and 034-035 in the Boat Ramp marsh (0.46 ± 0.06), followed by 046-047 (0.29 ± 0.09) and 048-049 (0.28 ± 0.08) at FINWR and 040-041 (0.27 ± 0.06) and 036-037 (0.26 ± 0.06) at Bull Marsh (Appendix IV). No predictors were included in the detection function and detection was estimated at 0.86 ± 0.03 SE. Species-specific densities varied by transect and were greatest at 038-039 (1.3 birds per ha) in Bull marsh for saltmarsh sparrows and at 034-035 (3.2 birds per ha) at the ESVNWR boat ramp for Nelson's sparrow (Figure 5).

Table 3. Candidate model list for N-mixture model including parmaters within the abundance (λ), availability (Φ), and detection (ρ) functions, number of parmaters (k), log-likelihood (logLik), AIC score, ΔAIC, and model weight used to predict abundance and densities for sharp-tailed sparrows on the eastern shore of Virginia.

Model Parameters	k	logLik	AIC	ΔAIC	weight
λ~Season+Marsh+Marsh*Season, Φ~Transect, ρ~1	19	-17.67	73.33	0.00	0.63
λ~Season+ Marsh, Φ~Transect, ρ~1	13	-24.90	75.80	2.47	0.18
λ~ Marsh, Φ~Transect +Season ρ~1	13	-25.60	77.21	3.88	0.09
λ~, Φ~Site, ρ~1	8	-31.53	79.05	5.72	0.04
λ~ Marsh, Φ~ Transect, ρ~1	10	-30.12	80.25	6.92	0.02
λ~Season+Marsh, Φ~ Transect +Season ρ~1	16	-24.36	80.73	7.40	0.02
λ~Site, Φ~Marsh, ρ~1	10	-33.40	86.79	13.46	0.00
λ~ Marsh, Φ~1, ρ~1	5	-38.91	87.82	14.49	0.00
λ~ Marsh+Transect, Φ~ Transect + Marsh, ρ~1	17	-29.55	93.10	19.77	0.00
λ~1, Φ~1, ρ~Day	4	-44.52	97.04	23.71	0.00
λ~1, Φ~1, ρ~Wind	4	-44.79	97.59	24.26	0.00
λ~1, Φ~1, ρ~1	3	-45.82	97.64	24.31	0.00
λ~1, Φ~1, ρ~Temp	4	-45.50	99.00	25.67	0.00
λ~1, Φ~1, ρ~Wind+Temp	5	-44.65	99.31	25.98	0.00

Figure 5. Density for A.) saltmarsh sparrow and B.) Nelson's sparrow at all transects surveyed during the 2014 and 2020-2022 winters on the eastern shore of Virginia. Error bars represent standard error.



Vegetation Characteristics

Spartina alterniflora was present at all 476 vegetation surveys. *Salicornia depressa* was present at 45 surveys, *Spartina patens* was present at six locations and *Distichlis spicata* was present at three locations. Wrack was present at 9 locations. Mean spartina cover was 67% and the mean number of S. alterniflora stems was 71 per plot. We found that the ocular estimates and stem counts were correlated ($\tau = 0.547$, $Z = 17.006$, $p < .001$) and exclusively used ocular estimates for all further vegetation cover analyses.

Among all vegetation surveys in all years, cover was significantly greater at bird location points ($\beta = 3.68 \pm 1.83$, $p=0.045$), at Bull Marsh ($\beta=9.44 \pm 2.14$, $p < 0.001$) and FINWR ($\beta = 6.84 \pm 2.28$, $p < 0.001$) relative to Boat Ramp Marsh (Figure 6), and not different among years relative to the 2020-2021 winter ($\beta_{2021\text{-}2022} = 2.65 \pm 2.35$, $p = 0.179$, $\beta_{2022\text{-}2023} = 0.86 \pm 2.02$, $p = 0.669$) or day of year ($\beta=0.03 \pm 0.31$, $p = 0.323$).

The height of the tallest stem was not different between control and bird location points ($\beta_{Control} = -2.95 \pm 1.70$, $p=0.0824$) or by day of year ($\beta=-0.046 \pm 0.03$, $p = 0.093$). The tallest stems were shorter at Bull Marsh ($\beta=-15.68 \pm 2.00$, $p < 0.001$) and taller at FINWR ($\beta = 14.24 \pm 2.11$, $p < 0.001$) relative to Boat Ramp Marsh. Stems were also shorter during the 2022-2023 ($\beta = -4.66 \pm 1.87$, $p = 0.008$) and 2021-2022 ($\beta = -10.95 \pm 2.18$, $p < 0.001$) seasons relative to the 2020-2021 season (Figure 7).

We counted 1,363 *S. alterniflora* inflorescences that still held seeds during the survey period. Overall, 63.6% of vegetation plots surveyed included stems with seeds including 67.7% (n = 65) during early winter, 65.4% (n = 358) during mid-winter, and 47.2% (n = 53) during late winter. The number of seed heads per plot declined throughout the winter from 5.2 seed heads with seeds per plot during early winter to 2.7 with seeds per plot during mid-winter to 1.3 with seeds per plot during late winter. The number of seed heads with seeds was not different between control and bird location points ($\beta_{Control} = -0.02 \pm 0.07$, $p=0.790$). The number of seed heads was greater in 2021-2022 ($\beta = 0.37 \pm 0.08$, <0.001) and in 2022-2023 ($\beta=0.39 \pm 0.07$ $p < 0.001$) relative to 2020-2021 season. There were more seed heads with seeds at Bull Marsh relative to Boat Ramp Marsh ($\beta=0.35 \pm 0.07$ $p < 0.001$) but the difference was not significant for FINWR ($\beta=0.12 \pm 0.08$ $p = 0.141$). Fewer seed heads also supported seeds with each advancing day of the season ($\beta = -0.02 \pm 0.00$, $p < 0.001$, Figure 8).

Figure 6. Predicted percentage cover by Spartina alterniflora per bird location and control plots at the Boat Ramp Marsh, Bull Marsh, and FINWR at the mean mid-winter sampling date during the 2020-2023 winters on the eastern shore of Virginia. Error bars represent standard error.

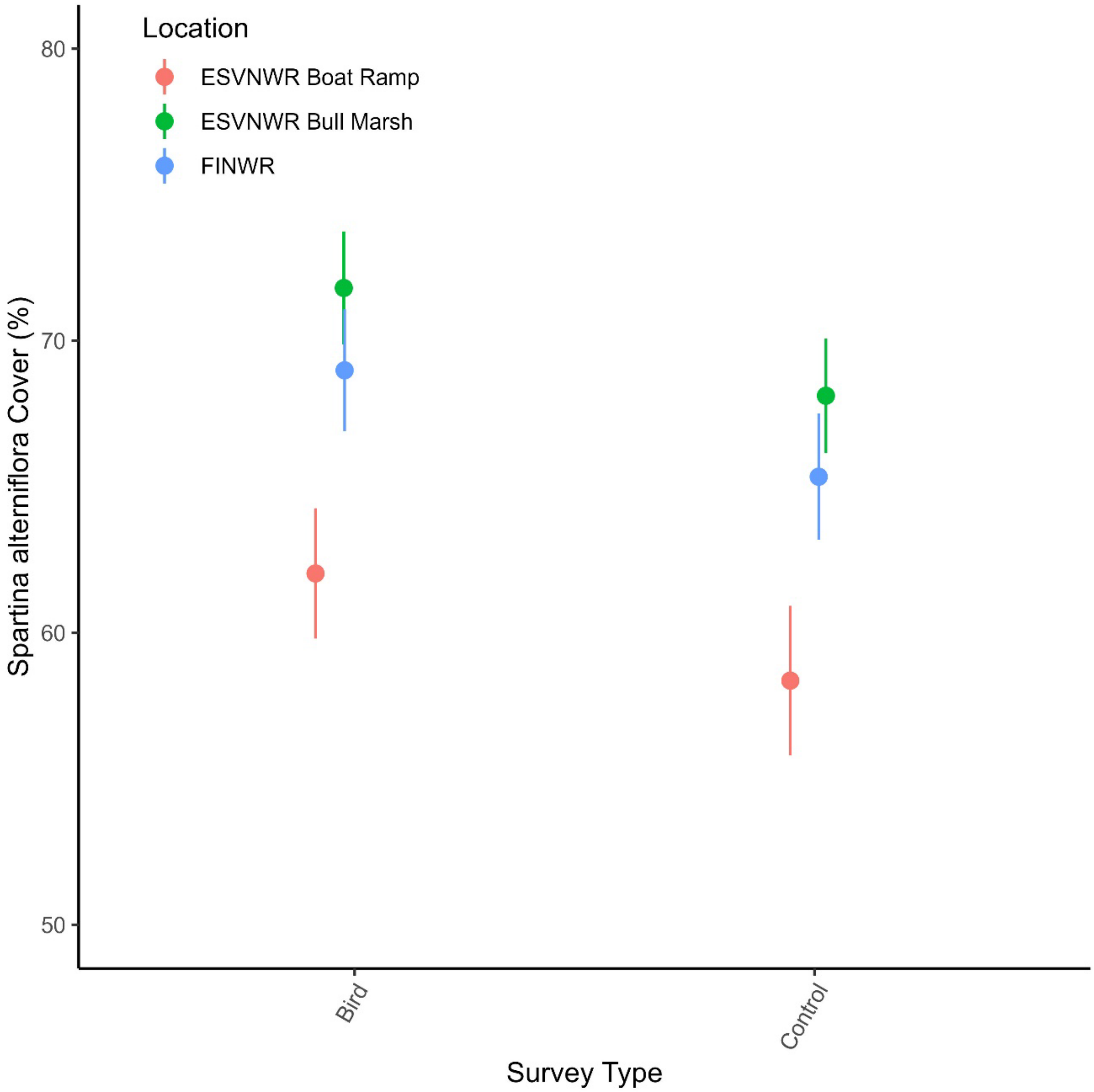


Figure 7. Predicted height of the tallest stem among survey years at the Boat Ramp Marsh, Bull Marsh, and FINWR at the mean mid-winter sampling date, mean sampling date, and mean last sampling date during the 2020-2023 winters on the eastern shore of Virginia. Site type was set to control for these predictions and error bars represent standard error.

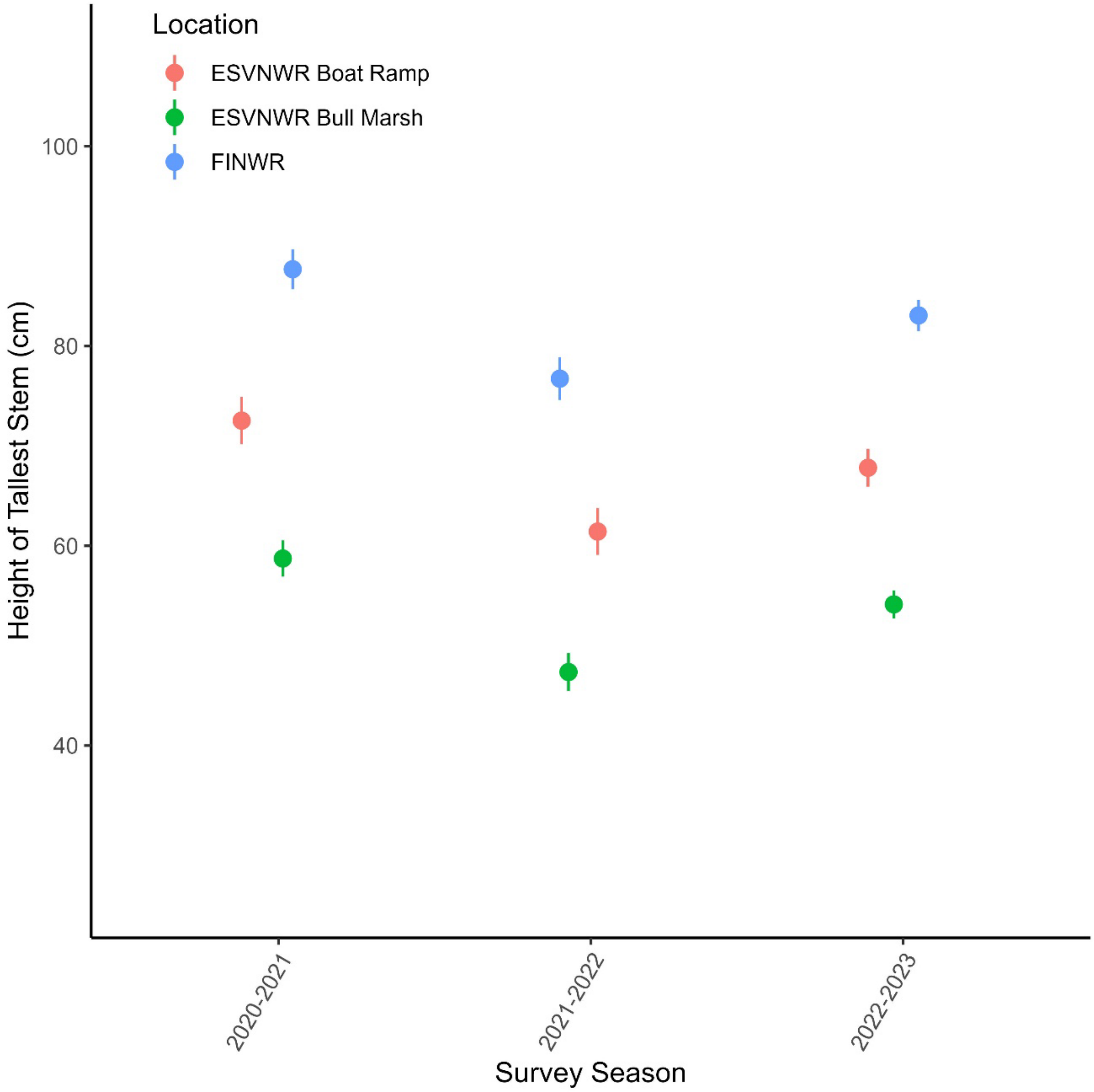
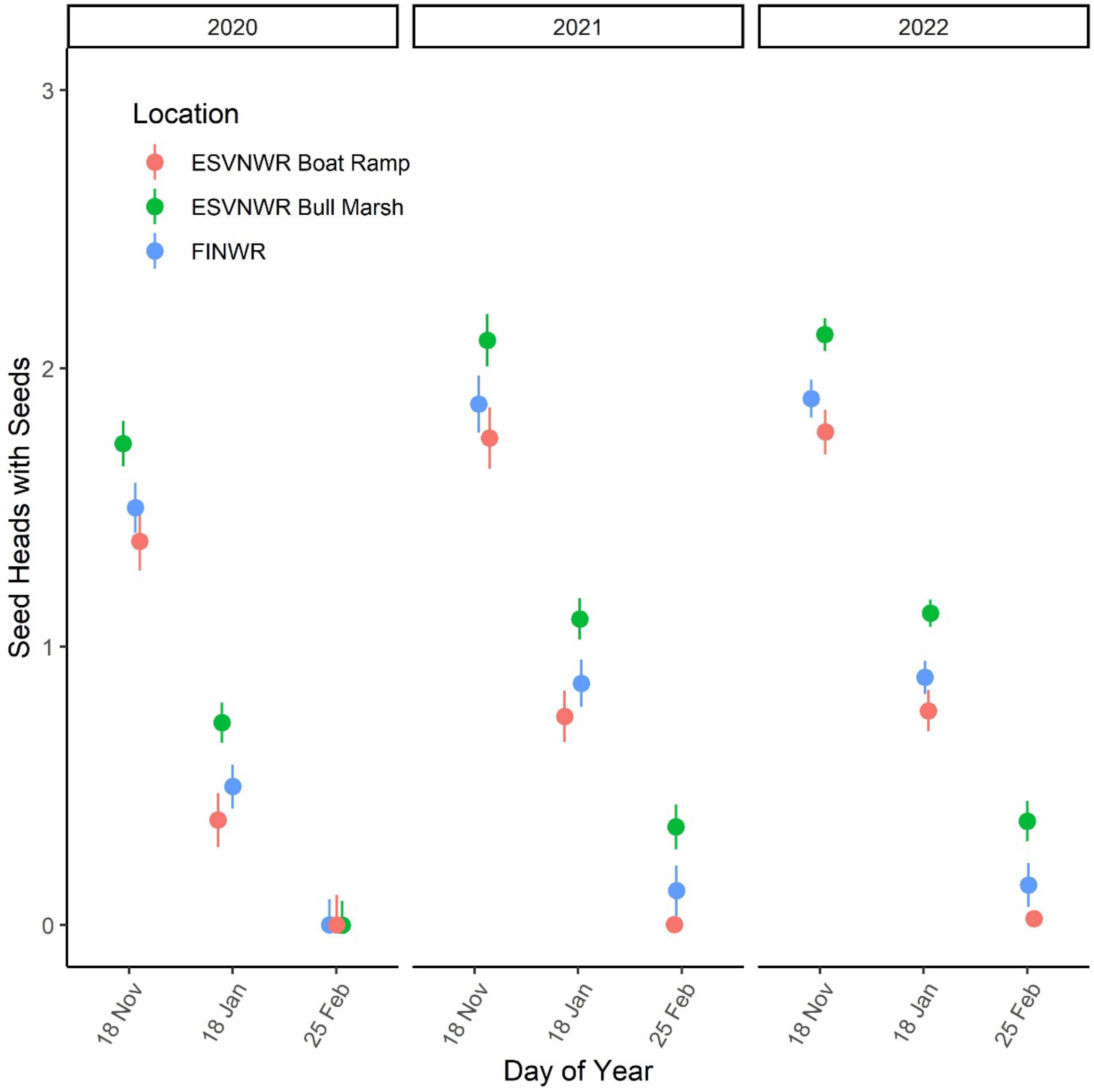


Figure 8. Predicted seed heads per plot at the Boat Ramp Marsh, Bull Marsh, and FINWR at the mean first sampling date, mean sampling date, and mean last sampling date. 2020-2023 winters on the eastern shore of Virginia. Site type was set to control for these predictions and error bars represent standard error.



DISCUSSION

We used capture-recapture sampling and double-pass rope drag transect surveys to explore how heterospecific marsh sparrow populations use marshes on the southern tip of the Delmarva Peninsula. We found that sampling location was among factors that influenced both survival and density estimates. Differences exist both within and among the marshes used as field sites and varied by species.

For saltmarsh sparrow, survival was relatively even among all marshes, but density was approximately twice as great at 038-039 in Bull Marsh as any other transect. This transect is unique because it is the furthest from the marsh-upland transition zone. While a dike with some upland vegetation does extend into the marsh near this transect, the forested upland edge is >900 m away compared to other transects where the edge is 100 - 500 m from the transect. This is consistent with findings from other studies of saltmarsh sparrows at breeding locations (Marshall et al 2020) where marshes with a greater proportion of habitat further away from the mainland edge are more likely to support this species.

Seaside sparrow survival was highest at FINWR, where the most birds were observed on transect, and lowest at Boat Ramp Marsh. Rope-drag survey data was too sparse to incorporate into N-mixture models, but this species was observed ≤2 times at all transects except 046-047 in FINWR. Similar to 038-039, this transect is unique among our survey sites. It is the only one to pass over tidal guts. Seaside sparrows would often flush from near the margins of the tidal guts. It is possible that foraging opportunities or risk of predation differs between saltmarsh near tidal guts and further away. Seed availability and cover were not different between this site and Bull Marsh, but both were greater than that found at the Boat Ramp Marsh and FINWR supported the tallest stems among all field sites.

Similar to saltmarsh sparrow, Nelson's sparrow density was greater at 038-039 relative to the other transects within Bulls Marsh, but this species was most dense at Boat Ramp Marsh where they were more than twice as abundant as on any other transect. Nelson's sparrow survival was also highest at Boat Ramp Marsh followed by Bull Marsh and FINWR. Boat Ramp Marsh provides the least cover and fewest seeds among all of our sites, so it is not clear whether a habitat parameter we failed to measure drives these metrics or another factor unrelated to habitat is at play.

We found that survival was higher during the early portion of the winter (generally between early December and mid-January) compared to the late (generally between mid-January and late February). We do not attribute this to winter weather because weather was colder between the first two sampling sessions than between the second two sessions. The coldest days of the year during all three seasons occurred during December or January and the average temperature was coldest in December during the first and third season and coldest in January during the second season (NOAA 2023). Food limitation is another potential source of mortality that could explain the difference in survival between the early and late winter periods. Foraging marsh sparrows typically probe and glean invertebrates and plant seeds from mud (Post and Greenslaw 2006). Invertebrates are less abundant during winter when marsh sparrow diets consist almost exclusively of *S. alterniflora* seeds (Michaelis 2009). Though the percentage of plots that supported seeds declined between the first and second sampling period, seed heads were still available at most plots during mid-winter. However, seed availability declined by approximately 75% by the third sampling period and predicted seed availability was at zero for some sites (Figure 8).

Food limitation may explain why Nelson's sparrows are so abundant at Boat Ramp Marsh because food limitation can lead to dominance-mediated inter- and intra-specific habitat segregation where larger (i.e., more dominant) birds occupy habitats with more food or cover from predators (Cox 1968, Marra and Holmes 2001). Among our study species, seaside sparrows are largest, followed by saltmarsh and Nelson's sparrows. Additionally, females are smaller than males for all of these species. Nelson's sparrows captured at the boat ramp were primarily female (78.9%), while the majority of Nelson's sparrows at the other two locations were male (60.0%). The smaller Nelson's sparrows, and especially female Nelson's sparrows, may be using Boat Ramp Marsh to avoid competition with the larger sparrows at Bull Marsh and FINWR where seeds and cover are both more abundant.

Contrary to our survival modeling, seasonality was not included in our top models for predicting. You would expect density to decline through the winter if birds are subject to mortality and these populations are relatively closed. Birds immigrating to our study sites and replacing deceased birds could explain this discrepancy. We did not observe any between study site movements between or within study seasons but condition may be worse in other marshes and force birds to relocate. One possible source for immigrating birds are marshes within the seaside lagoon system of the Delmarva Peninsula. These marshes are on islands that serve as a buffer for the mainland and mute tidal amplitude during storms but are more prone to being washed over by high tides and also experience greater wind speeds (Roelvink et al. 2009). Greater tidal flooding combined with higher winds likely means that seeds are more quickly stripped during winter. This effect is most pronounced during storms when flooding and winds are most severe and a higher proportion of available seeds may be dispersed into the water and possibly away from the local habitat (i.e., lost to the ocean). If seeds become more scarce quicker on the islands, birds that use them during the beginning of winter may suffer from food shortages and migrate to mainland marshes where food is more available. If true, the value of mainland marshes relative to wintering marsh sparrows is much higher than marshes within the seaside lagoon system. Further investigation of this aspect is warranted to validate our survival and density metrics.

Conclusion

We found that the values of our study sites are different relative to each species of marsh sparrow. Saltmarsh sparrow is the species of most conservation concern and are currently being considered for listing under the Endangered Species Act. For this species, survival was relatively even among marshes, but the greatest density was found furthest away from the mainland edge so protecting this portion of the marsh in more extensive marshes should be prioritized. The study area supports far fewer seaside sparrows, but this species had higher survival and was most often observed in areas with taller and denser vegetation like that found near tidal creeks. Nelson's sparrows were most dense and survived at the greatest rate at the study site lacking components associated with saltmarsh and seaside sparrows (marsh further from marsh-upland transition zone and tidal creeks), so marshes that fail to provide these components may be the most important to this species.

Further study of winter marsh sparrow movement within and between marshes, particularly nearby marsh islands that are subjected to harsher winter weather and tidal flooding, is warranted to validate our modeling results and to better set into context the value of the ESVNWR and FINWR marshes.

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APPENDICES

Appendix I. Birds captured during winter between 2020-2023 at the Eastern Shore of Virginia NWR and Fisherman Island NWR

Band Number	Species	Capture Date	Capture Location	Band Number	Species	Capture Date	Capture Location
80070705	NESP	12/2/2020	BR02	174189408	NESP	12/5/2021	BM03
80070705	NESP	1/13/2021	BR01	174189409	NESP	12/5/2021	BM03
80070705	NESP	12/4/2021	BR01	174189409	NESP	2/18/2023	BM03
80070705	NESP	3/1/2022	BR01	174189410	NESP	12/5/2021	BM03
80070705	NESP	12/9/2022	BR01	174189411	SALS	12/5/2021	BM04
80070706	NESP	12/2/2020	BR02	174189412	NESP	12/5/2021	BM04
80070706	NESP	1/13/2021	BR01	174189413	NESP	12/5/2021	BM04
80070706	NESP	12/4/2021	BR01	174189414	SALS	12/6/2021	FI01
80070707	NESP	12/2/2020	BR02	174189415	SALS	12/6/2021	FI01
80070707	NESP	1/13/2021	BR05	174189415	SALS	1/21/2023	FI05
80070707	NESP	2/25/2021	BR01	174189416	NESP	12/6/2021	F104
80070707	NESP	3/1/2022	BR01	174189417	NESP	12/6/2021	F104
80070708	NESP	12/2/2020	BR02	174189417	NESP	12/10/2022	FI01
80070708	NESP	2/25/2021	BR01	174189418	NESP	12/6/2021	F104
80070709	NESP	12/2/2020	BR02	174189419	SWSP	12/6/2021	F104
80070709	NESP	2/25/2021	BR01	174189420	SWSP	12/6/2021	F104
80070709	NESP	12/4/2021	BR01	174189421	SALS	12/6/2021	F103
80070709	NESP	3/1/2022	BR01	174189422	SALS	12/6/2021	F103
80070710	SALS	12/2/2020	BR03	174189423	SALS	12/6/2021	F103
80070710	SALS	1/13/2021	BR05	174189424	SALS	12/6/2021	F103
80070711	NESP	12/2/2020	BR04	174189425	SWSP	12/6/2021	F103
80070711	NESP	12/9/2022	BR01	174189426	SALS	12/6/2021	F103
80070711	NESP	1/23/2023	BR01	174189427	SALS	1/31/2022	BM03
80070712	NESP	12/2/2020	BR04	174189428	NESP	1/31/2022	BM03
80070712	NESP	2/25/2021	BR01	174189429	NESP	1/31/2022	BM03
80070713	NESP	12/2/2020	BR04	174189429	NESP	2/27/2022	BM03
80070714	NESP	12/2/2020	BR04	174189430	SALS	1/31/2022	BM03
80070714	NESP	1/13/2021	BR04	174189431	SALS	1/31/2022	BM04
80070715	NESP	12/2/2020	BR04	174189432	NESP	1/31/2022	BM04
80070715	NESP	1/13/2021	BR04	174189433	NESP	1/31/2022	BM04
80070716	NESP	12/2/2020	BR04	174189434	SALS	1/31/2022	BM04
80070717	NESP	12/2/2020	BR04	174189434	SALS	11/26/2022	BM03
80070717	NESP	1/13/2021	BR04	174189435	NESP	2/1/2022	BR01
80070718	NESP	12/2/2020	BM01	174189436	NESP	2/1/2022	BR01

Band Number	Species	Capture Date	Capture Location	Band Number	Species	Capture Date	Capture Location
80070718	NESP	1/13/2021	BR01	174189436	NESP	3/1/2022	BR01
80070719	SALS	12/3/2020	BM01	174189437	SALS	2/1/2022	BR01
80070720	NESP	12/3/2020	BM01	174189438	NESP	2/2/2022	FI04
80070721	NESP	12/3/2020	BM02	174189438	NESP	2/19/2023	FI04
80070722	NESP	12/3/2020	BM02	174189439	SALS	2/2/2022	FI03
80070722	NESP	1/14/2021	BM04	174189440	SALS	2/2/2022	FI03
80070722	NESP	2/26/2021	BM02	174189440	SALS	1/21/2023	FI03
80070723	NESP	12/3/2020	BM01	174189440	SALS	2/19/2023	FI03
80070723	NESP	1/14/2021	BM03	174189441	NESP	2/27/2022	BM03
80070724	SALS	12/3/2020	BM01	174189442	NESP	2/27/2022	BM03
80070725	SALS	12/3/2020	BM01	174189443	NESP	2/27/2022	BM03
80070725	SALS	12/5/2021	BM03	174189444	SALS	2/27/2022	BM05
80070725	SALS	1/31/2022	BM03	174189445	SALS	2/27/2022	BM05
80070726	NESP	12/3/2020	BM01	174189445	SALS	1/22/2023	BM03
80070726	NESP	1/14/2021	BM03	174189446	SALS	3/1/2022	BR01
80070727	SALS	12/3/2020	BM01	174189447	SALS	3/2/2022	FI03
80070728	NESP	12/3/2020	BM01	174189447	SALS	1/21/2023	FI03
80070729	NESP	12/3/2020	BM01	174189450	NESP	11/26/2022	BM03
80070730	NESP	12/3/2020	BM01	174189451	SALS	11/26/2022	BM03
80070731	SALS	12/3/2020	BM01	174189451	SALS	1/22/2023	BM03
80070731	SALS	1/14/2021	BM03	174189452	SALS	11/26/2022	BM03
80070732	SALS	12/3/2020	BM01	174189453	NESP	11/26/2022	BM03
80070732	SALS	1/31/2022	BM03	174189454	SALS	11/26/2022	BM03
80070732	SALS	11/26/2022	BM03	174189455	NESP	11/26/2022	BM03
80070733	SALS	12/3/2020	BM01	174189456	NESP	11/26/2022	BM03
80070733	SALS	1/14/2021	BM03	174189457	SALS	11/26/2022	BM03
80070733	SALS	11/26/2022	BM03	174189457	SALS	1/22/2023	BM03
80070734	NESP	12/3/2020	BM01	174189458	SALS	11/26/2022	BM04
80070734	NESP	1/14/2021	BM03	174189459	SALS	11/26/2022	BM04
80070735	NESP	12/3/2020	BM01	174189460	SALS	11/26/2022	BM04
80070735	NESP	1/14/2021	BM03	174189461	SWSP	11/26/2022	BM04
80070736	NESP	12/3/2020	BM01	174189462	SWSP	11/26/2022	BM04
80070737	NESP	12/4/2020	FI01	174189463	NESP	12/9/2022	BR01
80070738	NESP	12/4/2020	FI01	174189463	NESP	2/20/2023	BR01
80070739	NESP	12/4/2020	FI01	174189464	NESP	12/9/2022	BR01
80070739	NESP	1/15/2021	FI04	174189465	NESP	12/9/2022	BR01
80070740	NESP	12/4/2020	FI01	174189465	NESP	1/23/2023	BR01
80070741	SALS	12/4/2020	FI01	174189466	NESP	12/9/2022	BR01
80070742	NESP	12/4/2020	FI01	174189467	NESP	12/9/2022	BR01

Band Number	Species	Capture Date	Capture Location	Band Number	Species	Capture Date	Capture Location
80070743	NESP	12/4/2020	FI01	174189467	NESP	2/20/2023	BR01
80070744	NESP	12/4/2020	FI01	174189468	NESP	12/9/2022	BR01
80070745	SALS	12/4/2020	FI01	174189469	SALS	12/9/2022	BR01
80070745	SALS	1/15/2021	FI01	174189470	SALS	12/9/2022	BR01
80070746	SALS	12/4/2020	FI01	174189471	NESP	12/9/2022	BR01
80070746	SALS	1/15/2021	FI04	174189472	SALS	12/10/2022	FI01
80070746	SALS	2/27/2021	FI04	174189473	NESP	12/10/2022	FI05
80070747	NESP	12/4/2020	FI01	174189474	NESP	12/10/2022	FI03
80070748	SWSP	12/4/2020	FI02	174189475	NESP	12/10/2022	FI03
80070749	NESP	12/4/2020	FI02	174189476	SALS	12/10/2022	FI03
80070749	NESP	1/15/2021	FI04	174189476	SALS	1/21/2023	FI03
80070749	NESP	2/27/2021	FI04	174189477	NESP	1/21/2023	FI05
80070749	NESP	12/6/2021	FI04	174189478	NESP	1/21/2023	FI03
80070749	NESP	3/2/2022	FI04	174189479	SALS	1/22/2023	BM03
80070750	NESP	12/4/2020	FI02	174189480	SALS	1/22/2023	BM03
80070751	NESP	12/4/2020	FI02	174189481	SALS	1/22/2023	BM03
80070752	NESP	12/4/2020	FI02	174189482	SALS	1/22/2023	BM03
80070753	NESP	12/4/2020	FI03	174189482	SALS	2/18/2023	BM03
80070754	NESP	1/13/2021	BR01	174189483	SALS	1/22/2023	BM04
80070754	NESP	3/1/2022	BR01	174189484	SALS	1/22/2023	BM04
80070755	NESP	1/13/2021	BR01	174189485	SALS	1/23/2023	BR01
80070756	NESP	1/13/2021	BR01	174189486	NESP	1/23/2023	BR01
80070757	NESP	1/13/2021	BR01	174189487	NESP	2/18/2023	BM03
80070758	NESP	1/13/2021	BR01	174189488	SALS	2/18/2023	BM03
80070759	NESP	1/13/2021	BR05	174189489	SWSP	2/18/2023	BM03
80070759	NESP	2/25/2021	BR01	174189490	SWSP	2/18/2023	BM03
80070759	NESP	12/4/2021	BR01	174189491	NESP	2/19/2023	FI05
80070759	NESP	2/1/2022	BR01	174189492	NESP	2/19/2023	FI05
80070759	NESP	3/1/2022	BR01	174189493	NESP	2/19/2023	FI05
80070760	SALS	1/13/2021	BR05	174189494	NESP	2/20/2023	BR01
80070760	SALS	2/1/2022	BR01	174189495	NESP	2/20/2023	BR01
80070760	SALS	12/9/2022	BR01	174189496	NESP	2/20/2023	BR01
80070761	SWSP	1/13/2021	BR05	174189497	NESP	2/20/2023	BR01
80070762	NESP	1/13/2021	BR04	204010048	NESP	2/26/2021	BM02
80070763	NESP	1/13/2021	BR04	204010049	SALS	2/26/2021	BM02
80070764	NESP	1/13/2021	BR04	204010050	NESP	2/27/2021	FI04
80070765	NESP	1/13/2021	BR04	204010050	NESP	12/10/2022	FI04
80070766	NESP	1/13/2021	BR04	204010051	NESP	2/27/2021	FI04
80070767	NESP	1/13/2021	BR04	204010052	NESP	2/27/2021	FI04

Band Number	Species	Capture Date	Capture Location	Band Number	Species	Capture Date	Capture Location
80070767	NESP	2/25/2021	BR04	204010053	NESP	2/27/2021	FI04
80070768	SALS	1/14/2021	BM06	204010054	SALS	2/27/2021	FI03
80070769	SALS	1/14/2021	BM02	204010055	SALS	2/27/2021	FI03
80070769	SALS	2/26/2021	BM05	240113293	SALS	12/2/2020	BR01
80070770	SALS	1/14/2021	BM02	240113294	NESP	12/2/2020	BR01
80070771	SALS	1/14/2021	BM02	240113295	NESP	12/2/2020	BR01
80070772	NESP	1/14/2021	BM02	240113295	NESP	1/13/2021	BR01
80070773	SALS	1/14/2021	BM02	240113295	NESP	2/25/2021	BR01
80070773	SALS	12/5/2021	BM03	240113296	NESP	12/2/2020	BR01
80070774	NESP	1/14/2021	BM02	240113297	NESP	12/2/2020	BR01
80070774	NESP	12/5/2021	BM03	240113297	NESP	12/4/2021	BR01
80070774	NESP	2/27/2022	BM03	240113297	NESP	3/1/2022	BR01
80070774	NESP	2/18/2023	BM03	240113298	NESP	12/2/2020	BR01
80070775	SALS	1/14/2021	BM02	240113299	NESP	12/2/2020	BR01
80070776	SALS	1/14/2021	BM02	240113300	SALS	12/2/2020	BR02
80070777	NESP	1/14/2021	BM04	240113300	SALS	1/13/2021	BR05
80070778	SALS	1/14/2021	BM04	240113300	SALS	3/1/2022	BR01
80070778	SALS	12/5/2021	BM04	244164230	SESP	12/4/2020	FI03
80070779	NESP	1/14/2021	BM04	244164230	SESP	12/6/2021	FI01
80070779	NESP	1/22/2023	BM04	244164231	SESP	1/15/2021	FI03
80070780	SALS	1/14/2021	BM04	244164231	SESP	12/6/2021	FI03
80070780	SALS	1/31/2022	BM04	244164231	SESP	2/2/2022	FI03
80070781	SALS	1/15/2021	FI01	244164231	SESP	3/2/2022	FI03
80070781	SALS	12/10/2022	FI05	244164231	SESP	1/21/2023	FI03
80070782	NESP	1/15/2021	FI01	244164232	SESP	1/15/2021	FI03
80070783	NESP	1/15/2021	FI01	244164232	SESP	2/2/2022	FI03
80070784	SWSP	1/15/2021	FI04	244164232	SESP	12/10/2022	FI03
80070784	SWSP	2/27/2021	FI04	244164232	SESP	2/19/2023	FI03
80070785	SALS	1/15/2021	FI04	244164233	SESP	12/5/2021	BM03
80070785	SALS	2/27/2021	FI04	244164234	SESP	12/5/2021	BM03
80070786	NESP	1/15/2021	FI04	244164235	SESP	12/5/2021	BM03
80070787	SALS	1/15/2021	FI04	244164235	SESP	1/31/2022	BM03
80070787	SALS	1/21/2023	FI05	244164235	SESP	11/26/2022	BM03
80070788	NESP	1/15/2021	FI03	244164236	SESP	12/5/2021	BM03
80070789	SALS	1/15/2021	FI03	244164237	SESP	12/6/2021	FI03
80070789	SALS	12/10/2022	FI03	244164237	SESP	2/2/2022	FI03
80070790	NESP	2/25/2021	BR01	244164237	SESP	12/10/2022	FI03
80070791	NESP	2/25/2021	BR04	244164237	SESP	1/21/2023	FI03
80070791	NESP	12/9/2022	BR01	244164237	SESP	2/19/2023	FI03

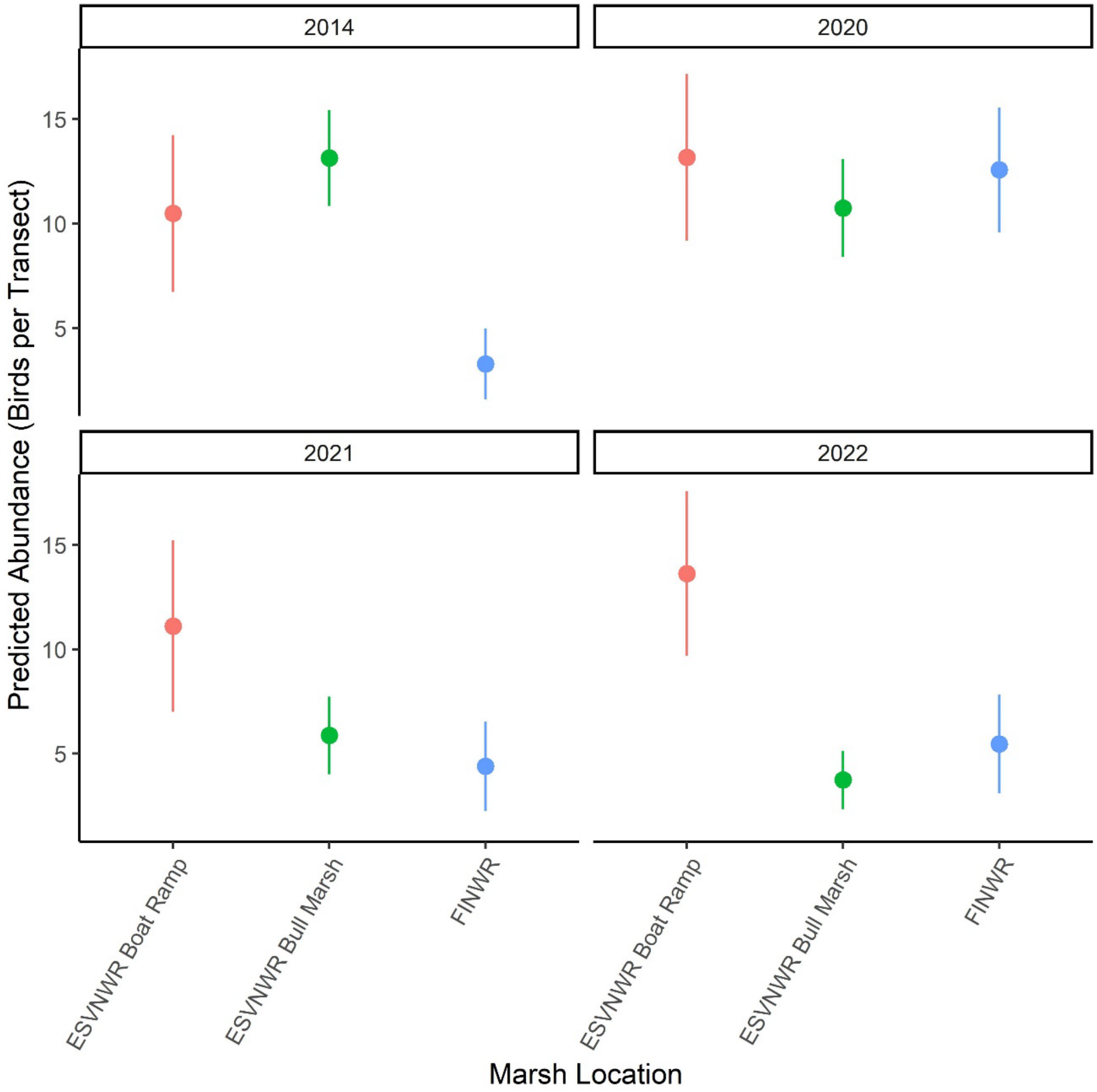
Band Number	Species	Capture Date	Capture Location	Band Number	Species	Capture Date	Capture Location
80070791	NESP	1/23/2023	BR01	244164238	SESP	12/6/2021	FI03
80070792	SALS	2/26/2021	BM01	244164239	SESP	12/6/2021	FI03
80070793	NESP	2/26/2021	BM05	244164240	SESP	1/31/2022	BM03
80070794	NESP	2/26/2021	BM05	244164241	SESP	1/31/2022	BM03
80070795	NESP	2/26/2021	BM05	244164241	SESP	11/26/2022	BM03
80070796	NESP	2/26/2021	BM05	244164242	SESP	1/31/2022	BM03
80070797	NESP	2/26/2021	BM05	244164243	SESP	1/31/2022	BM03
80070798	NESP	2/26/2021	BM05	244164244	SESP	1/31/2022	BM03
80070799	NESP	2/26/2021	BM02	244164245	SESP	1/31/2022	BM03
80070800	SALS	2/26/2021	BM02	244164246	SESP	2/1/2022	BR01
174189401	NESP	12/4/2021	BR01	244164246	SESP	12/9/2022	BR01
174189402	NESP	12/5/2021	BM03	244164258	SESP	11/26/2022	BM03
174189403	SALS	12/5/2021	BM03	244164259	SESP	11/26/2022	BM03
174189403	SALS	2/27/2022	BM05	244164259	SESP	1/22/2023	BM03
174189404	SALS	12/5/2021	BM03	244164260	SESP	11/26/2022	BM03
174189405	NESP	12/5/2021	BM03	244164260	SESP	2/18/2023	BM03
174189406	NESP	12/5/2021	BM03	244164261	SESP	12/10/2022	FI02
174189406	NESP	1/31/2022	BM03	244164262	SESP	2/19/2023	FI03
174189406	NESP	1/22/2023	BM03	244164263	SESP	2/19/2023	FI03
174189407	SALS	12/5/2021	BM03	244164264	SESP	2/19/2023	FI03
174189407	SALS	2/27/2022	BM05	281138486	SALS	1/14/2021	BM03
174189407	SALS	1/22/2023	BM03	174189408	NESP	12/5/2021	BM03

Appendix II. Candidate model list for CJS survival modeling including parmaters within the survival (Phi) and recapture probablity (p) functions, number of parmaters (K), log-likelihood (-2logLik), AIC score, ΔAIC, and model weight used to predict abundance and densities for sharp-tailed sparrows on the eastern shore of Virginia.

Model Parameters	K	AIC	ΔAIC	weight	-2logLik
Phi(~Site + time + Species + Species * Site)p(~1)	8	335.49	0.00	0.23	319.49
Phi(~Site + time + Species + Species * Site)p(~Site)	9	336.59	1.10	0.13	318.59
Phi(~Site + time + Species + Species * Site)p(~tide)	9	337.48	1.98	0.08	319.48
Phi(~Site + time + Species + Species * Site)p(~tide+ Site)	10	338.49	3.00	0.05	318.49
Phi(~Site + time + Species)p(~Site)	7	338.59	3.10	0.05	324.59
Phi(~time)p(~Site)	4	338.82	3.33	0.04	330.82
Phi(~time)p(~Site)	4	338.82	3.33	0.04	330.82
Phi(~Site + time + Species + Species * Site)p(~time + tide)	10	339.42	3.93	0.03	319.42
Phi(~Site + time + Species + Species * Site)p(~Species)	10	339.45	3.96	0.03	319.45
Phi(~Site + time + Species)p(~tide + Site)	8	339.56	4.06	0.03	323.56
Phi(~Site + time)p(~1)	4	339.56	4.07	0.03	331.56
Phi(~time)p(~tide + Site)	5	340.34	4.85	0.02	330.34
Phi(~time)p(~tide + Site)	5	340.34	4.85	0.02	330.34
Phi(~time + Species)p(~Site)	6	340.57	5.08	0.02	328.57
Phi(~Site + time)p(~Site)	5	340.74	5.25	0.02	330.74
Phi(~Site + time)p(~tide)	5	341.47	5.98	0.01	331.47
Phi(~Site + time + Species)p(~1)	6	341.63	6.14	0.01	329.63
Phi(~Site + time)p(~time + tide)	6	341.83	6.34	0.01	329.83
Phi(~Site + Species)p(~time + tide)	7	341.84	6.35	0.01	327.84
Phi(~Site + time)p(~Species)	6	342.24	6.75	0.01	330.24
Phi(~Site + time)p(~tide + Site)	6	342.29	6.80	0.01	330.29
Phi(~time + Species)p(~tide + Site)	7	342.33	6.84	0.01	328.33
Phi(~time)p(~1)	3	342.38	6.88	0.01	336.38
Phi(~time)p(~1)	3	342.38	6.88	0.01	336.38
Phi(~1)p(~Site)	3	342.39	6.89	0.01	336.39
Phi(~1)p(~tide + Site)	4	342.41	6.92	0.01	334.41
Phi(~Site + Species)p(~Species)	7	342.49	7.00	0.01	328.49
Phi(~Site + Species)p(~1)	5	342.60	7.10	0.01	332.60
Phi(~Site + time + Species)p(~time + tide)	8	342.78	7.28	0.01	326.78
Phi(~1)p(~time + tide)	4	343.03	7.54	0.01	335.03
Phi(~Site + Species)p(~tide)	6	343.05	7.56	0.01	331.05
Phi(~time + Species)p(~1)	5	343.09	7.60	0.01	333.09
Phi(~time)p(~tide)	4	343.21	7.72	0.00	335.21
Phi(~time)p(~tide)	4	343.21	7.72	0.00	335.21

Model Parameters	K	AIC	ΔAIC	weight	-2logLik
Phi(~Site + time + Species)p(~Species)	8	343.47	7.98	0.00	327.47
Phi(~Site + time + Species)p(~tide)	7	343.60	8.11	0.00	329.60
Phi(~Species)p(~tide + Site)	6	343.81	8.31	0.00	331.81
Phi(~Species)p(~Site)	5	343.91	8.41	0.00	333.91
Phi(~time + Species)p(~tide)	6	344.48	8.98	0.00	332.48
Phi(~Site + Species)p(~Site)	6	344.57	9.08	0.00	332.57
Phi(~time)p(~Species)	5	344.59	9.09	0.00	334.59
Phi(~time)p(~Species)	5	344.59	9.09	0.00	334.59
Phi(~Species)p(~time + tide)	6	344.82	9.32	0.00	332.82
Phi(~Site + Species)p(~tide + Site)	7	344.89	9.40	0.00	330.89
Phi(~1)p(~1)	2	345.00	9.50	0.00	341.00
Phi(~time)p(~time + tide)	5	345.03	9.54	0.00	335.03
Phi(~time)p(~time + tide)	5	345.03	9.54	0.00	335.03
Phi(~Species)p(~1)	4	345.64	10.15	0.00	337.64
Phi(~1)p(~tide)	3	346.07	10.58	0.00	340.07
Phi(~time + Species)p(~time + tide)	7	346.35	10.86	0.00	332.35
Phi(~Species)p(~tide)	5	346.59	11.10	0.00	336.59
Phi(~1)p(~Species)	4	346.59	11.10	0.00	338.59
Phi(~time + Species)p(~Species)	7	346.98	11.49	0.00	332.98
Phi(~Species)p(~Species)	6	349.47	13.98	0.00	337.47

Appendix III. Predicted Sharp-tailed Sparrow abundance at all marshes during the 2014 and 2021-2022 winters. Error bars represent standard error.



Appendix IV. Predicted Sharp-tailed Sparrow availability at all transects surveyed during the 2014 and 2020-2022 winters. Error bars represent standard error.