

WINTER SURVIVORSHIP AND SITE FIDELITY OF NELSON'S, SALTMARSH, AND SEASIDE SPARROWS IN NORTH CAROLINA

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Abstract. Three species of coastal sparrows (*Ammodramus nelsoni*, Nelson's Sparrow; *A. caudacutus*, Saltmarsh Sparrow; and *A. maritimus*, Seaside Sparrow) reside in North Carolina salt marshes in winter during their nonbreeding periods. We analyzed the timing of migration, survivorship, and site fidelity of these species with mark–recapture data from five winters (2006–2010). By determining the percentage of individuals captured more than once, we documented a shift from transient to settled individuals during and following migration and used linear regressions to test whether this shift was related to mean monthly minimum temperatures. We also used MARK and capture histories over five winters to estimate probabilities of apparent survival and capture. On the basis of recapture data, the three species' populations were composed largely of transient individuals from October until the sparrows settled for the winter by late November. Our recapture data indicate that when coastal sparrows settle for the winter or return to the region in a subsequent year, they do so with high site fidelity. We found that the percent of Nelson's and Seaside sparrows captured more than once had a negative relationship with mean monthly minimum temperature. We estimated survival of Nelson's, Saltmarsh, and Seaside sparrows at 0.673, 0.520, and 0.483, respectively. Our data indicate that survival of these coastal sparrows through the nonbreeding season is comparable to existing estimates for their breeding populations. Surveys in the nonbreeding season and management plans should take into account the likely presence of a large proportion of transient individuals during migration.

Key words: *Ammodramus caudacutus*, *Ammodramus maritimus*, *Ammodramus nelsoni*, *migration*, *recapture*, *site fidelity*, *survival*

Supervivencia Invernal y Fidelidad de Sitio en *Ammodramus nelsoni*, *A. caudacutus* y *A. maritimus* en Carolina del Norte

Resumen. Tres especies de gorrión, *Ammodramus nelsoni*, *A. caudacutus* y *A. maritimus*, residen en el invierno en las marismas de Carolina del Norte, durante sus periodos no reproductivos. Analizamos el momento de migración, la supervivencia y la fidelidad de sitio de estas especies con datos de captura–recaptura provenientes de cinco inviernos (2006–2010). Mediante la determinación del porcentaje de individuos capturados más de una vez, documentamos un cambio de individuos transitorios a individuos establecidos durante y luego de la migración. Luego, usamos regresiones lineales para evaluar si este cambio estuvo relacionado con las temperaturas mínimas medias mensuales. También usamos MARK e historias de captura a lo largo de cinco inviernos para estimar las probabilidades de supervivencia aparente y de captura. Sobre la base de los datos de recaptura, las poblaciones de las tres especies estuvieron compuestas principalmente por individuos transitorios desde octubre hasta que los gorriones se establecieron para pasar el invierno a finales de noviembre. Nuestros datos de recaptura indicaron que cuando los gorriones de las especies estudiadas se establecen para pasar el invierno o regresan a la región en un año subsecuente, lo hacen exhibiendo una alta fidelidad de sitio. Encontramos que el porcentaje de individuos de *A. nelsoni* y *A. maritimus* capturados más de una vez tuvieron una relación negativa con la temperatura mínima media mensual. Estimamos la supervivencia de los individuos de *A. nelsoni*, *A. caudacutus* y *A. maritimus* en 0.673, 0.520 y 0.483, respectivamente. Nuestros datos indican que la supervivencia de estas especies a lo largo de la estación no reproductiva es comparable con los estimados existentes para sus poblaciones reproductivas. Los muestreos en la estación no reproductiva y los planes de manejo deberían considerar la presencia probable de una gran proporción de individuos transitorios durante la migración.

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INTRODUCTION

Studies of the nonbreeding winter ecology of migratory birds can provide insight into factors that could have significant influence on future breeding success and conservation (Sherry and Holmes 1995, Marra et al. 1998, Sandercock and Jaramillo 2002, Sillett and Holmes 2002, Holmes 2007). However, few studies have focused on survival and site fidelity of migratory passerines at their wintering sites (Ralph and Meewaldt 1975, Johnson et al. 2009). Basic population information such as survival estimates and site fidelity is particularly important for species in decline due to winter habitat loss or other effects that may reduce breeding success.

Here, we investigated the winter ecology of three coastal sparrows in North Carolina: Nelson's Sparrow (*Ammodramus nelsoni*), Saltmarsh Sparrow (*A. caudacutus*), and Seaside Sparrow (*A. maritimus*). These three closely related species occur in mixed flocks in winter in North Carolina salt marshes. All three inhabit salt marshes during their nonbreeding period, while salt marshes are the sole habitat year round for the Saltmarsh and Seaside sparrows (Greenlaw and Rising 1994, Post and Greenlaw 2009). In part because salt marshes represent some of the most functionally degraded habitats in North America (Greenlaw and Woolfenden 2007), each of these species is of conservation concern (Dettmers and Rosenberg 2000, U.S. Fish and Wildlife Service 2002, Rich et al. 2004). In particular, the Saltmarsh Sparrow is listed as "vulnerable" by the International Union for Conservation of Nature (2011).

To date, estimates of these species' survivorship have been based only on data from the breeding period. In marked populations, return rates can be used as a proxy for minimum survival. In this manner, Post and Greenlaw (1982) estimated survival of adult Saltmarsh Sparrows breeding in New York at 55–60% for males and 53–63% for females. DiQuinzio et al. (2001) calculated maximum-likelihood estimates of annual survival of adult Saltmarsh Sparrows breeding in Rhode Island at 27–66%. Neither of these studies found survival of males and females to differ statistically. In various parts of its range the Seaside Sparrow varies from fully migratory to nonmigratory; the North Carolina population is thought to include both year-round residents and winter visitors (Michaelis 2009, Post and Greenlaw 2009). Post et al. (1983) used rates of return of migratory Seaside Sparrows breeding in both the northern and southern regions of the species' range to estimate survival at 53–57% for males and 41–60% for females. Werner (1975) estimated survivorship of adult Seaside Sparrows resident in southern Florida at 88%. No information is currently available on survival rates of Nelson's Sparrow.

We used individually marked birds and banding records from five winters to examine timing of migration from the perspective of transient versus settled populations during the period from fall arrival to spring departure. We then used banding and recapture data to examine the site fidelity of each

species during its nonbreeding period in North Carolina. We also investigated whether patterns of the sparrows' abundance and recapture were related to mean monthly minimum temperature. Finally, using mark–recapture records, we estimated local apparent survival and capture probabilities for each species. Together, these data can aid conservation efforts for these species by providing novel information about their movements and minimum survival estimates.

METHODS

STUDY SITES AND CAPTURE METHODS

We captured Nelson's, Saltmarsh, and Seaside sparrows at three sites in salt marshes near Wrightsville Beach, North Carolina (Fig. 1), for five winters (2006–2010; Table 1). These relatively elevated sites represent areas where sparrows congregate at high tides when much of the surrounding marsh is flooded: Lea-Hutaff (LH, near Lea-Hutaff Island), Parnell (P, first sampled by J. Parnell in the 1960s and 1970s), and Estuarine Reserve (ER, near the Masonboro Island National Estuarine Research Reserve). We captured birds by actively funneling them from one side of the site toward one or two nets, which were set perpendicular to the long axis of the site. We banded each individual with a unique U.S. Geological Survey aluminum band.

Although we banded in September and April of some years, the core of our banding effort took place from October through March; during this core period, we completed a mean of 3.4 banding trips per month for the five winters we banded birds (usually at least one trip per site per month; Table 1). Each trip consisted of 1–3 hr of banding effort; the length and timing of trips were dictated by the tide and weather. Since sampling effort was identical for each species and net-hours were, for the most part, comparable across years and sites, we present raw capture data. In order to indicate that our sampling regime represented the entire period from fall arrival to spring departure as completely as was possible, we present data for all months in which we captured sparrows each year (Table 1), although we did not include data from all months in all analyses (see below). All netting, banding, and sampling were performed under the requisite institutional, state, and federal permits.

TIMING OF MIGRATION AND SITE FIDELITY

We define the winter nonbreeding period for Nelson's, Seaside, and Saltmarsh sparrows as beginning in late September, when migrants first appear in North Carolina salt marshes, to early April, when most migrants have departed for northern breeding grounds. Hereafter, we use year to refer to a single winter period spanning two calendar years. Our sampling regime relied on tide heights at or around the level of spring tides, which occur twice monthly and coincide with the full and new moon. This reliance on especially high tides to reach our sample sites resulted in two pulses of banding each month,



FIGURE 1. Sites of winter sampling of sparrows in coastal North Carolina: Lea-Hutaff (LH), $34^{\circ} 19' 46''$ N, $77^{\circ} 41' 31''$ W; Parnell (P), $34^{\circ} 11' 05''$ N, $77^{\circ} 50' 18''$ W; Estuarine Reserve (ER), $34^{\circ} 08' 17''$ N, $77^{\circ} 50' 49''$ W.

weather permitting. We divided each year of sampling into discrete blocks by month because of this relationship to the tide and to ensure that data from each of our three sites were included in each sampling block.

For each species, within each month of each year, we calculated the percent of individuals that were captured more than once (either in previous or subsequent months within the same year or across years, as in Johnson et al. 2009). We tracked changes in abundance per banding trip through each year along with the timing of the movement of transient individuals in and out of the study area each spring and fall. We considered periods in which the percentage of individuals that had been captured more than once was relatively low (<10%) to be periods of considerable movement of transients in and out of the study area. Conversely, in periods when the percentage of individuals captured more than once was relatively high (>10%), we considered these individuals to have “settled” locally for the duration of the nonbreeding period (Johnson et al. 2009). To formally test the relationship between sparrow abundance per trip and the percent

of individuals captured more than once for each species, we used Spearman correlations (proc corr, SAS version 9.1).

We obtained minimum daily temperature data archived by the North Carolina State Climate Office for the Wilmington International Airport station (station ID 319457; 12–20 km from our study sites) and calculated a mean monthly minimum temperature for each month within each of our five years of banding. We used separate linear regressions for each species to test for relationships between monthly abundance per trip and mean monthly minimum temperature as well as between monthly values of percent of individuals captured more than once (during either a previous or subsequent month in any year) and mean monthly minimum temperature (proc reg). Regressions including abundance per trip and percent of individuals captured more than once met the assumptions for parametric statistical analyses after \log_{10} transformation of these data; we present nontransformed values throughout.

We recorded whether each bird recaptured was caught at the site where it was first banded, then calculated the longest gap between its first and last captures. We compared the interval between first and last capture by species with non-parametric ANOVA (proc npar1way) because the data failed to fit a normal distribution. We set the level of significance at $P < 0.05$ for all tests.

ESTIMATION OF APPARENT LOCAL SURVIVAL AND CAPTURE PROBABILITIES

We assumed that our sample of netted birds was homogeneous with respect to sex, age, behavior, and habitat characteristics since our active flush-netting technique, unlike other capture methods such as baiting or passive mist netting, should be unbiased with respect to any of these characteristics (Tucker and Robinson 2003). To estimate apparent survival and capture probabilities, we followed the outline and notation of Lebreton et al. (1992). Using mark–recapture data, we built separate Cormack–Jolly–Seber (CJS) models for each species in MARK (White and Burnham 1999) to determine local annual survival and capture probabilities with the “sin link” function (Pollock et al. 1990, Lebreton et al. 1992). To avoid the complications introduced by migration, we limited the scope of our CJS analysis to individuals we defined as part of the settled nonbreeding population (captured between 1 November and 31 March; 392 Nelson’s Sparrows, 219 Saltmarsh Sparrows, and 398 Seaside Sparrows). Therefore, the capture history of each individual included its presence or absence for five years (2006–2010) with each year composed of banding data from a 5-month period spanning two calendar years.

First we built a global model, which included capture site (ER, LH, or P) and year as parameters [survival (years + site + years \times site) capture (years + site + years \times site)]. In our models, we use “years” to refer to the intervals (between consecutive years of banding) for which MARK

TABLE 1. Total number of captures and recaptures (including multiple recaptures of the same individual) during five winters of sparrow capture in NC. Refer to Fig. 1 for site abbreviations and locations. Numbers after site abbreviations indicate the number of times that site was visited in that month; if no number follows a site abbreviation, the site was visited once.

Month and year	Sites visited	Total net-hr	Nelson's Sparrow		Saltmarsh Sparrow		Seaside Sparrow	
			Total captures	Recaptures	Total captures	Recaptures	Total captures	Recaptures
Sep 2006	P	2	0	0	0	0	9	0
Oct 2006	ER, LH, P	6.5	26	0	20	0	49	0
Nov 2006	ER, LH	5.5	39	0	16	0	28	1
Dec 2006	ER, LH	5.5	25	1	9	0	27	3
Jan 2007	ER(2)	3.5	9	1	8	0	11	3
Feb 2007	LH, P	4	7	2	10	2	5	2
Mar 2007	ER, LH	4	5	3	2	2	6	1
Total year 1	14 trips	31	111	7	65	4	135	10
Oct 2007	LH(2)	5	10	0	5	0	19	0
Nov 2007	ER(2), LH(2)	10.5	40	3	14	0	30	6
Dec 2007	ER, LH, P(2)	9.5	22	2	28	1	31	11
Jan 2008	ER(2), LH, P(2)	9.5	6	2	11	1	45	18
Feb 2008	ER, LH, P(2)	6.25	4	2	4	1	7	3
Mar 2008	P	2	2	0	1	0	5	0
Total year 2	20 trips	42.75	84	9	63	3	137	38
Oct 2008	ER, LH, P	7	7	0	15	3	34	9
Nov 2008	ER, LH, P(2)	9.5	17	1	13	2	34	7
Dec 2008	ER, LH(2), P	9.5	19	6	19	5	38	13
Jan 2009	ER, LH(3)	8	6	1	6	1	22	10
Feb 2009	LH(3), P(3)	10.75	4	3	13	4	26	8
Mar 2009	P(3)	6	8	4	7	2	6	0
Apr 2009	LH, P	4	2	0	4	2	7	2
Total year 3	26 trips	54.75	63	15	77	19	167	49
Sep 2009	LH	2	0	0	0	0	6	0
Oct 2009	ER, LH(2), P(2)	11.25	11	0	1	0	44	1
Nov 2009	ER(2), LH(2), P(2)	12.75	75	5	22	3	39	7
Dec 2009	ER, LH, P	6.75	31	4	10	1	21	6
Jan 2010	LH, P	4.5	6	1	8	3	7	4
Feb 2010	ER, LH(2), P	7.5	17	2	0	0	17	7
Mar 2010	ER(2), LH, P	9.75	29	6	7	2	11	5
Apr 2010	ER	2	2	0	0	0	10	3
Total year 4	26 trips	56.5	171	18	48	9	155	33
Oct 2010	ER, LH(2), P	9.25	4	0	6	0	22	1
Nov 2010	ER(2), LH(2), P(2)	14.75	44	3	25	7	51	14
Dec 2010	ER, LH, P	7	13	6	9	3	13	8
Jan 2011	ER, LH	4	7	4	4	3	13	5
Feb 2011	ER, LH(2)	6.75	12	1	5	2	12	2
Mar 2011	ER, LH(2), P	9.25	3	1	7	1	30	12
Apr 2011	LH	1.5	0	0	0	0	1	1
Total year 5	23 trips	52.5	83	15	56	16	142	43
Total all years	109 trips	237.6	512	64	309	51	736	173

estimates parameters. Second, we tested this global model for violations of the assumptions of mark-recapture models (equal probabilities of catchability and survival). We used a bootstrap goodness-of-fit approach, which generated a distribution of expected deviances from the global model with 1000 random simulations of capture histories. We then calculated the variance-inflation factor (a measure of over-

underdispersion; \hat{c}) by dividing the observed deviance for the global model by the mean expected deviance from the bootstrap simulations (Table 2). We then ran 20 models for each species, testing a suite of alternative hypotheses incorporating variables we felt might reasonably influence survival and capture rates. The model with the most parameters in each set incorporated the effect of site, years, and the interaction

TABLE 2. Estimates of apparent survival and capture probability from the most parsimonious models using capture–recapture data in program MARK for three species of coastal sparrows in North Carolina salt marshes. Capture histories were compiled from banding and recapture data over five winters.

Species	Number of individuals	Most parsimonious model	Bootstrap <i>P</i>	Adjusted \hat{c}^a	Apparent survival	Capture probability
Nelson’s Sparrow	392	Survival (·) ^b Capture probability (·)	0.42	2.376	0.673	0.077
Saltmarsh Sparrow	219	Survival (·) Capture probability (·)	0.47	1.902	0.520	0.167
Seaside Sparrow	398	Survival (·) Capture probability (·)	0.35	1.745	0.483	0.284

^aVariance-inflation factor, a measure of the over- or underdispersion of the global model [survivorship (years + site + years × site) recapture probability (years + site + years × site)].

^bModel notation: (·) = parameter modeled as independent of site and years.

term between these two main effects on survival and the effect of site and years on capture probability. The remaining 19 models in each set were iterations of this model with one or more parameters removed (Appendix, available at <http://dx.doi.org/10.1525/cond.2012.110088>).

For each species, we ranked these 20 models by Akaike’s information criterion (AIC) adjusted for \hat{c} and small sample sizes (QAIC_c; Appendix). We considered models with $\Delta\text{QAIC}_c < 7.0$ possible candidates for the most parsimonious model (Burnham et al. 2011). We consider the MARK-derived estimates of apparent survival and capture probabilities to be minimal estimates of these parameters because of the indistinguishability of true mortality and permanent emigration from the study sites (Lebreton et al. 1992). Values reported under Results are means or estimates ± SE unless otherwise indicated.

RESULTS

CAPTURES, TIMING OF MIGRATION, AND SITE FIDELITY

During 109 banding trips over five winters, we captured 1269 individuals and had 288 recaptures (Table 1). The mean number of birds captured per year was 311 ± 37 SD. Of our 288 recaptures (including multiple recaptures of the same individual either within or across years), 64 were Nelson’s Sparrows, 51 were Saltmarsh Sparrows, and 173 were Seaside Sparrows (Table 1). The mean number of recaptures per year was 58 ± 24 SD. Recaptures in years 3–5 were 3–4 times more frequent than in year 1 (Table 1). Throughout the five years of this study, 229 individuals were captured more than once, with 99% of these (227 of 229) recaptures occurring at the site of the bird’s original banding (ER, LH, or P).

We calculated an annual percent return rate for each species by dividing the total number of individuals captured in at least two different years by the total banded. Return rates were 6% for Nelson’s Sparrow, 10% for the Saltmarsh Sparrow, and 11% for the Seaside Sparrow. When recaptures within and across years were included, recapture rates were 12%, 18%, and 23%, respectively. Two Nelson’s Sparrows were captured a total of five times each. Seven Seaside Sparrows and one Saltmarsh Sparrow were captured four times each (Table 3).

TABLE 3. Frequencies of capture of individuals by species across five winters.

Times individual captured	Nelson’s Sparrow	Saltmarsh Sparrow	Seaside Sparrow	Total
1	393	216	431	1040
2	46	42	96	184
3	5	3	26	34
4	0	1	7	8
5	2	0	1	3

Nelson’s Sparrows arrived at our sites consistently in October and remained through March or into April (Fig. 2a). Saltmarsh Sparrows arrived in October in four of the five years with an apparent delayed fall migration in 2009 when they were not captured until November; this species was present on our sites through March or into April (Fig. 2b). Seaside Sparrows were present on our sites in September in the two years in which we banded during this month and remained through the rest of the nonbreeding period (Fig. 2c).

On the basis of the percent of sparrows captured more than once, Nelson’s and Saltmarsh sparrows appear to be largely transient at our study sites until November, when the percentage of individuals captured more than once began to increase, indicating settlement of the nonbreeding population for the remainder of the winter. In contrast, we found no clear or consistent peak in the percentage of Seaside Sparrows captured more than once (Fig. 2). For all three species there was a significant negative correlation between monthly values of percent of individuals captured more than once and abundance per trip (Nelson’s: $r = -0.531$, $P = 0.004$; Saltmarsh: $r = -0.540$, $P = 0.003$; Seaside: $r = -0.418$, $P = 0.016$).

We found no significant relationship between abundance per trip, averaged by month, and mean monthly minimum temperature for any species ($r^2 < 0.05$, $P > 0.246$). However, monthly values of percent of individuals captured more than once were significantly negatively related to mean monthly

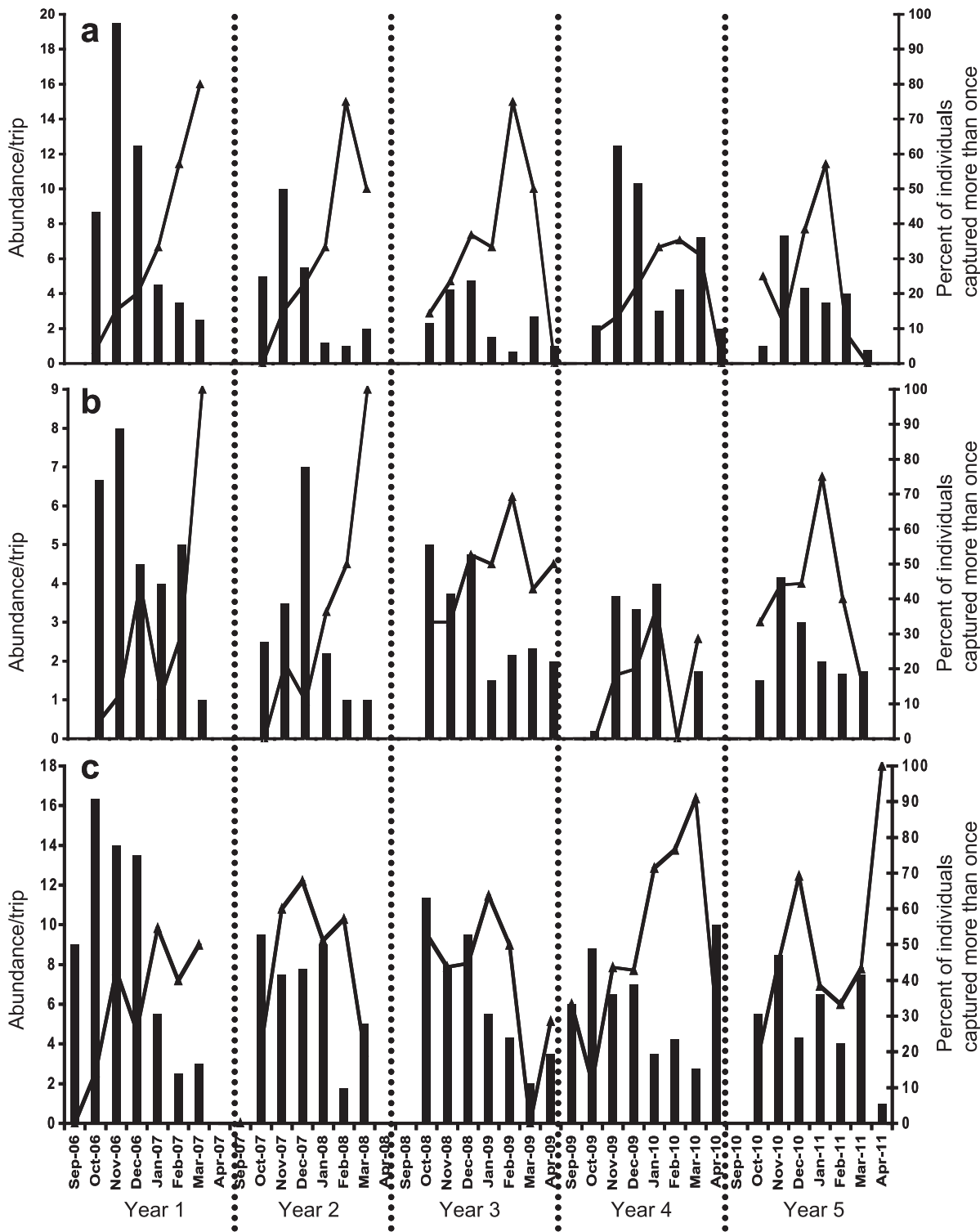


FIGURE 2. Trends in number of individuals captured and percentage of individuals captured more than once for each month of banding over five winters in North Carolina. Bars, abundance, on the basis of number captured per trip. Lines, the percentage of birds captured more than once, calculated by dividing the number of individuals captured in each month that were also recaptured at least once (in either the same year or a different year) by the total number of captures for that month of that species. (a) Nelson's Sparrow; (b) Saltmarsh Sparrow; (c) Seaside Sparrow. No banding was done in April 2007 and 2008 or September 2007, 2008, and 2010.

minimum temperature for Nelson's and Seaside sparrows ($r^2 = -0.285$, $P = 0.0034$ and $r^2 = -0.256$, $P = 0.0027$, respectively; Fig. 3) but not for the Saltmarsh Sparrow ($r^2 = 0.082$, $P = 0.140$).

For each species we identified the longest interval between recaptures, representing the oldest known individuals of each. Minimum age at final capture was 5.5 years for each species. The mean interval between first and last capture for all recaptured individuals was 350 ± 52 days for Nelson's Sparrow, 327 ± 46 days for the Saltmarsh Sparrow, and 298 ± 30 days for the Seaside Sparrow; time between captures did not vary by species ($df = 2$, $F = 0.5$, $P = 0.6$).

ESTIMATION OF APPARENT LOCAL SURVIVAL AND CAPTURE PROBABILITIES

The bootstrap goodness-of-fit tests ($P > 0.05$) and relatively low variance-inflation factors ($\hat{c} < 5$) indicated that our global model for each species met the assumptions of the CJS model (Table 2). For each species, the most parsimonious model describing capture history data displayed independence in both time and site, supporting the hypothesis that neither apparent survival nor capture probability varied by year or capture location. Since the model with the fewest parameters was the best-supported model for each species, we present this model as the single most parsimonious model in each case (Richards 2008, Arnold 2010, Richards et al. 2011). When the null model is ranked as the most supported model (as is the case for the MARK results for each species we studied), all of the other models in the candidate set incorporate noninformative parameters and so should not be used as a basis for inference (Richards 2008, Arnold 2010).

Apparent survival of Nelson's Sparrows was the highest at 0.673 ± 0.137 , of the Saltmarsh Sparrow was intermediate at 0.520 ± 0.119 , and of the Seaside Sparrow was the lowest at 0.483 ± 0.067 (Table 2). We estimated the probability of

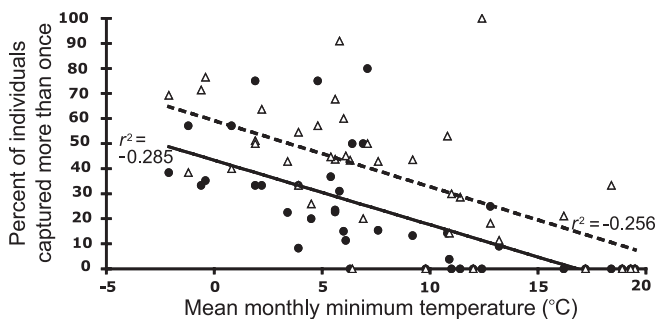


FIGURE 3. The relationship between the percent of individuals captured more than once (in either the same year or a different year; refer to legend for Fig. 2 for more detail) and mean monthly minimum temperature. Black circles and solid black line, Nelson's Sparrow; open triangles and dashed line, Seaside Sparrow. The relationship between these variables was not significant for the Saltmarsh Sparrow.

recapture at 0.077 ± 0.028 for Nelson's, 0.167 ± 0.064 for the Saltmarsh, and 0.284 ± 0.061 for the Seaside (Table 3).

DISCUSSION

RECAPTURE RATES AND SITE FIDELITY

Rates of band recovery for many migratory passerines are routinely low (Weatherhead and Forbes 1994, Brawn and Robinson 1996). For this reason, we consider our return rates based on band recoveries over the five years of this study (ranging from 12 to 23% when recaptures both within a season and in successive seasons are included) to be moderately high and believe that this allows us to address several characteristics of these species' nonbreeding ecology. DiQuinzio et al. (2001) reported band-recovery rates of 46% for Saltmarsh Sparrows breeding in Rhode Island, indicating high levels of site fidelity to fixed home ranges within the overall breeding range. Since 99% of our recaptures were at the site of original banding, we contend that the coastal sparrows that return to our region do so with high fidelity to a specific site.

TRANSIENT VERSUS SETTLED POPULATIONS

Between 59 and 86% of individuals of each species captured were netted between October and December every year. However, in pairing these abundance data with the percentage of individuals captured more than once for each species, we have identified trends for transient versus settled populations. We assume that the odds of recapturing a transient individual more than once within its lifetime are negligible within a banding schedule such as ours; therefore, when we captured the same individual more than once (either within the same year or in a subsequent year), we believe that it is reasonable to assume that this individual was not a transient but settled for the remainder of the nonbreeding period.

We have documented trends in the movement of transient Nelson's, Saltmarsh, and Seaside sparrows through our study area until November, when we observed an increased proportion of individuals captured multiple times, indicating settlement of the nonbreeding population for the remainder of the winter. Our detection of transients is consistent with a similar study by Johnson et al. (2009), who reported first fall arrival of Henslow's Sparrow (*Ammodramus henslowii*) in Louisiana in October but found the population composed mostly of transients until mid-November. In all four of these species of *Ammodramus*, it appears that of the large numbers that arrive on the nonbreeding grounds many filter out of the area to other sites over the next several weeks until a settled nonbreeding population is established by late November (Johnson et al. 2009).

For both Nelson's and Saltmarsh sparrows, the highest percentage of birds captured more than once began to rise in November and December, reaching a maximum from January to March (Fig. 2a, 2b). The trend for movement of transient Seaside Sparrows was more variable among years (Fig. 2c). These observations are in agreement with our more formal test of these trends in that for Nelson's and Saltmarsh sparrows, the negative

relationship between the percent of individuals captured more than once and abundance per trip was roughly 20% stronger than for the Seaside Sparrow. Analyses of stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and of mercury in the feathers and blood of nonbreeding Seaside Sparrows support the hypothesis that some portion of this population is resident in these salt marshes year round (Michaelis 2009; Winder, unpubl. data). This partially resident population may be a contributing factor to the relatively weak relationship we observed in the Seaside Sparrow between the percent of individuals captured more than once and abundance per trip. The capture and recapture of year-round resident Seaside Sparrows early in the nonbreeding period (when Nelson's and Saltmarsh sparrow populations are composed primarily of transients) may be the source of this species' increased variability in population trends. Additional work is necessary to determine what proportion of the nonbreeding Seaside Sparrows in coastal North Carolina is migratory and subsequently on how this species should be managed and studied in the future.

In Delaware, Greenberg et al. (2010) found that the winter abundance of the Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) was closely related to the frequency of days with temperatures at or below freezing ($r^2 = 0.66$). They concluded that the Coastal Plain Swamp Sparrow, which is thought to migrate away from the study area when not breeding, uses temperature cues to time its migration. While Greenberg et al. (2010) sought to determine whether the timing of the Coastal Plain Swamp Sparrow's departure from breeding sites is related (perhaps facultatively) to the frequency of days with minimum temperatures below freezing, we addressed a slightly different question—to determine whether the settlement of nonbreeding populations (and concomitant exit of transients from the population) was related to mean monthly minimum temperatures. For both Nelson's and Seaside sparrows, all five winters of our data support the hypothesis that settlement of nonbreeding populations (measured by an increased percent of individuals captured more than once) is negatively related to mean monthly minimum temperature (Fig. 3). Decreasing temperature may be the driver of the decision to settle or continue migrating, or this decision may be the result of other factors related to temperature change (e.g., photoperiod). It is possible that our sample size for the Saltmarsh Sparrow was not adequate to address this question or that transients of this species are responding to an unknown environmental cue.

ESTIMATES OF APPARENT SURVIVAL AND CAPTURE PROBABILITY

Our results provide the first estimates of apparent survival and capture probability for Nelson's, Saltmarsh, and Seaside sparrows based on capture histories from their nonbreeding period. Published estimates of apparent survival of North America passerines range from 29 to 63% with a mean of 53% (Johnston et al. 1997); our survival estimates for coastal sparrows in North Carolina range from 48 ± 7 to $67 \pm 14\%$ and thus compare well with published values for other species.

Relatively high survivorship in some passerine populations has been attributed to their being nonmigratory (Morrison et al. 2004), while other studies have found no difference in survivorship between migratory and resident populations (Sandercock and Jaramillo 2002). Our data fall into the latter category, as survival estimates for the partially resident Seaside Sparrow were similar to those for the closely related, fully migratory Nelson's and Saltmarsh sparrows. Our apparent survival rates for the Saltmarsh and Seaside sparrows are similar to those from previous studies of breeding populations of these species (Werner 1975, Post and Greenlaw 1982, Post et al. 1983, DiQuinzio et al. 2001).

MARK models cannot distinguish mortality from permanent emigration; for this reason parameter estimates from these procedures are typically considered as minimum estimates (Lebreton et al. 1992, DiQuinzio et al. 2001). A lower level of fidelity to a particular nonbreeding site or region from year to year could cause the survival estimate for the Saltmarsh and Nelson's sparrows to be more variable than that for the Seaside Sparrow. Since the presence of transients has resulted in underestimation of survival in other studies (Pradel et al. 1997, Nur et al. 2004), we worked to minimize this potentially confounding factor by analyzing capture data from what appear to be settled populations. Therefore, we present our values of apparent survival as conservative estimates. To this end, further study to connect specific nonbreeding and breeding populations and sites is warranted and could lead to a better understanding of causes and patterns of these species' mortality throughout the year.

Holmes (2007) asserted that to conserve and manage migratory bird populations effectively, we must understand as much as possible about where and how these populations are limited and regulated. Our results provide a portion of this information for Nelson's, Saltmarsh, and Seaside sparrows in one region within their wider nonbreeding ranges. Strong fidelity to a specific patch of marsh could have important implications for the health and persistence of local populations of these species based on levels of toxic contaminants, habitat fragmentation, food availability/quality, predation, or disease. Thus studies that provide basic information such as the level of site fidelity in a species can be integral to determining the status of migratory populations (Sherry and Holmes 1995, Sandercock and Jaramillo 2002, Winder and Emslie 2011). Continued banding and recapture studies, direct determination of reproductive success, and an examination of connectivity between breeding and nonbreeding populations will be necessary for these coastal sparrow populations to be adequately understood and conserved.

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Supplementary Online Material for
 WINTER SURVIVORSHIP AND SITE FIDELITY OF NELSON’S, SALTMARSH,
 AND SEASIDE SPARROWS IN NORTH CAROLINA

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APPENDIX. Results and rankings of 20 models used to estimate apparent survival and capture probability for three species of sparrows in North Carolina coastal salt marshes. Capture histories were compiled from banding and recapture data over five winters. Model notation follows White and Burnham (1999); () indicates that neither capture location nor time varied for a given parameter estimate; ΔQAIC_c indicates simple differences in quasi-Akaike’s information criterion adjusted for \hat{c} (variance-inflation factor; Table 3); w_i indicates Akaike’s model weight; K indicates the number of parameters included in a given model. In our models, we use “years” to refer to the intervals (between consecutive years of banding) for which MARK generates parameter estimates and “site” to refer to banding site.

Species and model	ΔQAIC_c	w_i	K	Deviance
Nelson’s Sparrow				
Survivorship (·) capture (·)	0.00 ^a	0.663	3	20.566
Survivorship (·) capture (site)	3.59	0.110	5	20.070
Survivorship (site) capture (·)	3.99	0.090	5	20.469
Survivorship (years) capture (·)	5.47	0.043	6	19.894
Survivorship (·) capture (years)	5.63	0.040	6	20.048
Survivorship (site) capture (site)	6.98	0.020	7	19.332
Survivorship (years) capture (site)	8.81	0.008	8	19.074
Survivorship (·) capture (years + site)	9.05	0.007	8	19.318
Survivorship (years + site) capture (·)	9.39	0.006	8	19.659
Survivorship (site) capture (years)	9.60	0.005	8	19.864
Survivorship (years) capture (years)	11.33	0.002	9	19.501
Survivorship (years + site) capture (site)	11.67	0.002	10	17.232
Survivorship (site) capture (years + site)	12.43	0.001	10	18.489
Survivorship (years) capture (years + site)	14.61	0.000	11	18.553
Survivorship (years + site) capture (years)	15.14	0.000	11	19.076
Survivorship (years + site) capture (years + site)	17.28	0.000	13	16.942
Survivorship (years + site + years × site) capture (·)	19.80	0.000	14	17.296
Survivorship (years + site + years × site) capture (site)	21.83	0.000	16	14.962
Survivorship (years + site + years × site) capture (years)	25.75	0.000	17	16.691
Survivorship (years + site + years × site) capture (years + site)	28.32	0.000	19	14.821
Saltmarsh Sparrow				
Survivorship (·) capture (·)	0.00 ^b	0.444	3	24.212
Survivorship (site) capture (·)	1.69	0.191	5	21.753
Survivorship (·) capture (site)	1.82	0.179	5	21.888
Survivorship (years) capture (·)	5.04	0.036	6	23.005
Survivorship (·) capture (years)	5.11	0.035	6	23.072
Survivorship (site) capture (site)	5.67	0.026	7	21.507
Survivorship (years) capture (site)	6.63	0.016	8	20.321

(Continued)

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APPENDIX. Continued

Species and model	ΔQAIC_c	w_i	K	Deviance
Nelson's Sparrow				
Survivorship (site) capture (years)	6.89	0.014	8	20.576
Survivorship (·) capture (years + site)	6.97	0.014	8	20.661
Survivorship (years) capture (years)	7.23	0.012	9	18.747
Survivorship (years + site) capture (·)	7.28	0.012	8	20.972
Survivorship (years) capture (years + site)	7.46	0.011	11	14.563
Survivorship (years + site) capture (site)	9.33	0.004	10	18.650
Survivorship (years + site) capture (years)	10.45	0.002	11	17.551
Survivorship (years + site) capture (years + site)	10.48	0.002	13	13.079
Survivorship (site) capture (years + site)	11.00	0.002	10	20.319
Survivorship (years + site + years × site) capture (·)	13.74	0.000	14	14.042
Survivorship (years + site + years × site) capture (site)	18.19	0.000	16	13.837
Survivorship (years + site + years × site) capture (years)	19.06	0.000	17	12.349
Survivorship (years + site + years × site) capture (years + site)	23.11	0.000	19	11.585
Seaside Sparrow				
Survivorship (·) capture (·)	0.00 ^c	0.328	3	32.778
Survivorship (·) capture (site)	1.08	0.191	5	29.781
Survivorship (site) capture (·)	1.83	0.132	5	30.533
Survivorship (years) capture (·)	2.46	0.096	6	29.101
Survivorship (·) capture (years)	3.21	0.066	6	29.853
Survivorship (years) capture (site)	3.91	0.046	8	26.400
Survivorship (·) capture (years + site)	4.41	0.036	8	26.909
Survivorship (years + site) capture (·)	4.71	0.031	8	27.202
Survivorship (site) capture (site)	4.95	0.028	7	29.522
Survivorship (site) capture (years)	5.18	0.025	8	27.672
Survivorship (years + site) capture (site)	8.00	0.006	10	26.304
Survivorship (site) capture (years + site)	8.08	0.006	10	26.376
Survivorship (years) capture (years)	8.59	0.004	9	28.994
Survivorship (years) capture (years + site)	10.01	0.002	11	26.195
Survivorship (years + site) capture (years)	10.35	0.002	11	26.529
Survivorship (years + site) capture (years + site)	14.10	0.000	13	26.017
Survivorship (years + site + years × site) capture (·)	15.53	0.000	14	25.296
Survivorship (years + site + years × site) capture (site)	18.94	0.000	16	24.362
Survivorship (years + site + years × site) capture (years)	21.88	0.000	17	25.108
Survivorship (years + site + years × site) capture (years + site)	25.19	0.000	19	24.000

^aQAIC_c = 102.284.^bQAIC_c = 101.574.^cQAIC_c = 246.793.