WINTER ECOLOGY OF SHARP-TAILED AND SEASIDE SPARROWS IN NORTH CAROLINA

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ABSTRACT

Although the Seaside Sparrow (*Ammodramus maritimus*), the Nelson’s Sharp-tailed Sparrow (*A. nelsoni*), and the Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*) maintain distinct breeding ranges, all three species are sympatric in winter in the coastal saltmarshes of southeastern North Carolina. Each species is of conservation concern due to habitat loss and a poor understanding of their natural history and ecology, particularly in the winter, nonbreeding season. This study provides new information on the migratory timing and winter distribution of each species, and supports observations of site fidelity.

Comparisons of foraging ecology among these species and subspecies using stable isotope analysis of δ¹³C and δ¹⁵N in feather and blood indicate a seasonal (breeding to nonbreeding) dietary shift in Saltmarsh and Nelson’s Sharp-tailed Sparrows. Saltmarsh Sharp-tailed Sparrows feed at a higher trophic level during the breeding season than nonbreeding season. Nelson’s Sharp-tailed Sparrows shift from a C₄ plant-based diet during the nonbreeding season to one incorporating more C₃ plants during the breeding season. Stable isotope analysis did not provide unique identification and cannot be used independently to recognize subspecies of Nelson’s Sharp-tailed Sparrows.
ACKNOWLEDGEMENTS

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INTRODUCTION

The southeastern North Carolina saltmarsh is home to three species of sparrows, two of which are found here only in winter. The Seaside Sparrow (*Ammodramus maritimus*) is a year-round resident while the Nelson’s Sharp-tailed Sparrow (*A. nelsoni*) and the Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*) are winter migrants (Fig. 1). Saltmarsh Sharp-tailed Sparrows (SSTS) breed along the Atlantic Coast from the North Carolina-Virginia border north through Maine (Greenlaw and Rising 1994, Rising and Avise 1993). The breeding range of the Seaside Sparrow (SESP) extends along the coast from New Hampshire south to Florida (Post and Greenlaw 1994). The Nelson’s Sharp-tailed Sparrow (NSTS) has three geographically distinct breeding populations, corresponding to three subspecies. *Ammodramus nelsoni nelsoni* breeds from the southern Mackenzie Province of the Northwest Territories to northern South Dakota and eastward to northwestern Wisconsin (Post 1998). A second population, *A. n. alterus*, breeds along the southern shores of Hudson and James Bays, Ontario, Canada. The third population, *A. n. subvirgatus*, breeds along the Atlantic Coast from southern Maine north through the Atlantic Provinces to Quebec along the St. Lawrence Estuary (Post 1998). The co-occurrence of SESP, NSTS, and SSTS in North Carolina during the winter season provides a unique opportunity to investigate the winter ecology of these three species.
Figure 1: Breeding Range of SESP, NSTS, and SSTS. The breeding range of each species is shown, including subspecies population range of NSTS. Map adopted from Greenlaw and Rising (1994).
All three of these species are of conservation concern. NSTS is listed as a Species of Conservation Concern by Bird Life International and is designated as a Yellow List species on the most recent National Audubon Society’s Watchlist (USFWS 2002, National Audubon Society 2007). NSTS and SSTS are listed on the Partners in Flight Watch List in their North American Land Bird Conservation Plan (Rich et al. 2004). SSTS and SESP are designated as Red List species on the National Audubon Society’s Watchlist 2002-2007 (National Audubon Society 2007). Additionally, the office of Migratory Bird Management considers SESP a migratory nongame bird of management concern (Post and Greenlaw 1994).

These birds need protection because of habitat loss and a general lack of knowledge of their natural history and ecology. Fragmented wetlands, particularly Atlantic Coast saltmarsh, affect both breeding and nonbreeding populations (DiQuinzio et al. 2001, Greenlaw and Woolfenden 2007). As with any migratory species, effective conservation efforts must account for year-round behavior and habitat use. While limited work has focused on the breeding season, few studies have addressed the winter ecology of these birds (Emery 1968, Gjerdrum et al. 2005, Greenlaw 1993, Greenlaw and Woolfenden 2007, Nocera et al. 2007, Post 1998, Shields 1982).

The objective of this study was to enhance understanding of the winter ecology of SESP, NSTS, and SSTS. Specifically, I investigated the timing of migration, winter site fidelity based on banding and recapture data, and foraging ecology using stable isotope analysis of blood and feathers to compare both winter and summer diets for each species. I hypothesized that these species will exhibit ecological segregation in diet during winter, when all three are sympatric, and that summer diet $\delta^{13}C$ and $\delta^{15}N$ isotopes will reflect
geographic differences in species and subspecies breeding grounds. Three study sites in coastal saltmarshes near Wilmington, North Carolina, were chosen to complete these investigations over two winter seasons (2006/2007 and 2007/2008).

Stable Isotope Analysis

Stable isotope analysis (SIA), a process now common in ecological studies of migratory birds, enables dietary inferences through non-destructive means (Hobson 1999b). SIA is based on isotope ratios in consumer tissues that reflect fractionation of these isotopes from their diet (Forero et al. 2002, Marra et al. 1998, Sydeman et al. 1997). Previous studies using δ^{13}C and δ^{15}N have demonstrated the ability to track migration through geographic trends in isotope values, as well as infer trophic level based on the isotopic enrichment occurring at each step (Hobson 1999a, Hobson et al. 1997).

Important to this project, plant sources are identified through SIA based on signatures typical of different photosynthetic pathways. C₃ plants such as *Juncus roemerianus* maintain lower δ^{13}C values than do C₄ plants, including *Spartina alterniflora*, and these sparrows have both options available as a food source (Hobson 1992a and b, Greenlaw and Rising 1994, Marra et al. 1998, Post and Greenlaw 1994).

SIA also permits the study of a wide temporal scale that would otherwise be difficult using standard techniques such as gut content analysis, which only shows recent food consumption based on ingested, not necessarily assimilated, food (Hobson and Clark 1992a). Different tissues possess distinct isotopic turnover rates, and are indicative of separate time frames (Hobson 1992a and b and 1999b, Thompson and Furness 1995).
Feather is an inert tissue and maintains the isotopic signature corresponding to the time and location of synthesis (Podlesak et al. 2005, Robertson 2004). Blood, however, has a much faster turnover of several days to a few weeks, particularly in small birds such as sparrows (Hobson 1999a, Podlesak et al. 2005). Here, breast feathers grown at the end of summer are assumed to reflect summer diet while blood should represent winter diet, or food consumption within the two-week period prior to collection of the sample.

Accordingly, the stable isotope data was used to investigate any seasonal dietary shifts, as well as to assess trophic relationships in diet of each species. Winter diets were also compared among the three species to determine if ecological segregation occurs when these species are sympatric in winter. Last, the potential of using SIA to aide in subspecies identification was tested by comparing NSTS subspecies feathers, which should reflect geographically distinct breeding grounds.

METHODS

Study Site Selection

Three study sites were selected to provide three sampling locales known to hold sharp-tailed sparrows during the winter (Fig. 2). Each site was accessible from the Intracoastal Waterway. Site were designated as follows: Lea-Huttaf (34°19’45.74” N, 77°41’30.48” W), Parnell (34°11’04.69” N, 77°50’17.74” W), and Estuarine Reserve (34°08’17.24” N, 77°50’48.64” W). All sites were marsh islets reachable at high tide by boat. Vegetation at each site was dominated by Spartina alterniflora (C₄) as well as small patches of Salicornia sp. (C₃) and Limonium sp. (C₃).
Figure 2: Winter Sampling Sites in North Carolina. Site acronyms are as follows: LH, Lea-Hutaff; P, Parnell; ER, Estuarine Reserve.
Banding

Banding efforts began in October 2006 after earlier visits to each study site to identify the arrival of migrating sparrows in the Wilmington area. Each sampling trip was completed at high tide, when birds were concentrated on the small, exposed islets. Birds were captured in mist-nets (6 and 12 m nets with 20-mm mesh) and banded with the appropriate species-specific size band (1B for SESP, 1 for NSTS/SSTS) in accordance with the U. S. Geological Survey (USGS) Bird Banding Lab. Only one subspecies of SESP and SSTS was identified during these operations while at least two subspecies of NSTS were identifiable using published criteria in plumage and bill size (Greenlaw and Rising 1994, Sibley 1996).

A series of measurements was taken from all captured birds (including weight, fat score, bill length, wing chord, and molt score), while blood and feather samples were collected from a subset of birds. The initial aim was an equal number of samples (60) from each species at each site. This was not always possible due to differences in species abundance per site, as well as ability to collect blood. Some birds sampled did not provide enough blood for SIA, and this was more apparent on colder days. In addition to timing affecting blood capture, it also affected species abundance. During the fall migratory period, the number of birds using each site was much higher than during the winter, and included more birds than could be effectively banded and sampled during a single trip. Some birds were thus released without being sampled. During these periods of high migration, blood samples were avoided to speed up the banding process and to ensure that blood samples reflect wintering ground isotope values rather than migratory
stopping points. Banding continued through April 2008 and the data were used to evaluate migratory timing and site fidelity.

Blood and Feather Sampling

Less than 50 μl of blood was collected from each bird through a brachial blood draw using a sterile syringe needle to induce bleeding and a 70-μl heparinized capillary tube to capture the blood. Blood was stored for isotopic analysis in 70% ethanol (Forero et al. 2002, Hobson et al. 1997). Three to four breast feathers were collected and stored in a small, plastic Ziploc bag. Digital photos were taken of birds (NSTS and SSTS only) sampled for blood and any birds with questionable species identification.

Blood and feathers were stored at room temperature until prepared for isotope analysis. Blood was first oven-dried at 45º C before freeze-drying, then powdered with mortar and pestle and transferred into tin cups to be analyzed in the mass spectrometer (Forero et al. 2002, Hobson et al. 1997). Feathers were rinsed in distilled water and acetone to remove contaminants and left to dry for 24 hours (Nisbet et al. 2002). Dry feathers were cut into small fragments, weighed, and placed in tin cups for analysis in the mass spectrometer.

Samples were processed in a Thermo DELTA V Plus Isotopic Ratio Mass Spectrometer (IRMS) interfaced with a Costech 4050 Elemental Analyzer located at the Center for Marine Science, University of North Carolina Wilmington. Each sample was combusted in the elemental analyzer, converting C to CO₂ and N initially to NOX. The NOX was reduced to N₂ in a net CO reduction furnace. N₂ and CO₂ were
chromatographically separated on a Purepak Q GC column at 60°C. The N₂ and CO₂ peaks were analyzed by continuous flow IRMS. Final δ values of $^{13}$C and $^{15}$N were normalized to known reference materials, glutamic acid USGS 40 and 41, which bracketed the enrichments of the samples. Isotope ratios were reported as δ values when $\delta = (R/R_1-1)*100$.

Breeding Ground Blood Samples

In July 2008, blood samples were collected at three SSTS breeding sites near Milford, Connecticut along the East, Housatonic, and Quinnipiac Rivers. Each of the banding locales were sites currently used by researchers at the University of Connecticut. Connecticut marsh sites were more expansive than North Carolina sites, and two of the three sites had been ditched for drainage purposes. Sites were also closer to human development than North Carolina locations; in some areas homes flanked the marsh. Dominant vegetation at each site was *Spartina patens* (C₄) with patches of *S. alterniflora* (C₄) and *Phragmites australis* (C₃).

Diet Samples

During the fall of 2008, potential diet source samples were collected at each of the three North Carolina study sites and included four samples of *S. alterniflora* and one sample of *Limonium* sp. While *Limonium* itself is an unlikely food item for the sparrows, it was selected as a C₃ plant within the marsh that could be a diet source for
other sparrow prey items. Sections of each plant were cut to include *S. alterniflora* seeds and exposed segments of *Limonium*. Plant and seed samples were rinsed with distilled water and dried before being powdered for isotopic analysis (Haines and Montague 1979).

Potential prey samples were also collected. Fourteen invertebrate samples, including specimens from the classes Arachnida and Insecta (orders Diptera, Hemiptera, Lepidoptera, and Orthoptera) were collected with a sweep net and stored in 70% ethanol before being rinsed with distilled water, dried, and ground with mortar and pestle. Samples were then analyzed in the mass spectrometer.

Statistical Analyses

Analyses of δ¹³C and δ¹⁵N values were performed using the statistical software program NCSS (Hintze 2006). After examining data for patterns of normality and equal variance, the lack of normality required non-parametric tests. Sampling site differences were evaluated using the Kruskal-Wallis One-Way ANOVA on Ranks with the Multiple Comparison Z-Value Test. Sampling sites were compared to test for differences in δ¹⁵N and δ¹³C among the three North Carolina sites. The Kruskal-Wallis One-Way ANOVA on Ranks with the Multiple Comparison Z-Value Test was used to compare breeding ground samples collected in Connecticut to samples collected in North Carolina, looking for differences in δ¹⁵N and δ¹³C of Connecticut blood samples relative to North Carolina blood and feather. This test was also used to identify possible patterns of ecological segregation during the winter season, comparing δ¹⁵N and δ¹³C values among all three
species’ blood samples. The Mann Whitney U Test/Wilcoxon Rank-Sum Test for Differences in Medians was used to compare year-to-year variation in each species’ δ¹⁵N and δ¹³C values, as well as to compare NSTS subspecies feather values, looking for differences in δ¹⁵N and δ¹³C between two subspecies. In addition, blood and feather samples were compared within each species using the Wilcoxon Signed-Rank Test for Difference in Medians, testing for differences in δ¹⁵N and δ¹³C between tissues. Statistical significance was assumed at p < 0.05 for all tests.

RESULTS

Banding Data

A total of 523 birds were banded over two banding seasons (September 2006-March 2007 and September 2007-March 2008). Monthly trends in the number of birds captured of each species were consistent from the 2006-07 to the 2007-08 season. Totals (with recaptures) include 272 SESP, 196 NSTS, and 127 SSTS (Fig. 3). Of the 196 NSTS, 119 were A. n. nelsoni and 76 A. n. subvirgatus, with one unidentified.
Figure 3: Individuals of each species captured and banded per month; September 2006-March 2008. Because monthly trends were consistent between the 2006-07 and 2007-08 seasons, monthly totals were combined. Values include recaptured birds.
Recapture Data

Sixty-two birds were recaptured over two winter seasons, including several individuals that were recaptured multiple times, leading to a total of 72 recaptures. All 72 recaptures occurred at the site at which the bird was initially banded. Recaptured individuals included 43 SESP, 10 NSTS, and 9 SSTS. Of the 72 recaptures, 44 occurred within the same season as the initial banding and 28 occurred in the following season.

Annual Differences in $\delta^{15}$N and $\delta^{13}$C

Blood and feather $\delta^{15}$N and $\delta^{13}$C values were compared between years by defining winter from October to April when the birds are on the wintering sites, and summer (May to September) when they are on the breeding sites. No significant variation was found between summer feather samples of SESP or NSTS between years (Figures 4 and 5). However, differences in $\delta^{13}$C and $\delta^{15}$N values between years were apparent in blood and feather tissue in SSTS (Fig. 6). SSTS mean feather $\delta^{13}$C values were greater in the 2007-08 season by 0.85 ‰ ($\text{Mann-Whitney U Test/Wilcoxon Rank-Sum Test}$, $U_{2006-2007} = 138$, $U_{2007-2008} = 304$, $p = 0.04$). SSTS mean blood $\delta^{13}$C was also higher in the 2007-08 season, by 0.67 ‰ ($U_{2006-2007} = 138$, $U_{2007-2008} = 304$, $p = 0.04$) and $\delta^{15}$N by 0.89 ‰ ($U_{2006-2007} = 132$, $U_{2007-2008} = 310$, $p = 0.03$).
Figure 4: Comparison of $\delta^{15}$N and $\delta^{13}$C in SESP tissues between the 2006-07 and 2007-08 banding seasons. Samples included 24 samples of both blood and feather from 2006-07, and 28 samples of each from the 2007-08 season.
Figure 5: Comparison of $\delta^{15}$N and $\delta^{13}$C in NSTS tissues between the 2006-07 and 2007-08 banding seasons. Samples included 19 samples of both blood and feather from 2006-07, and 31 samples of each from the 2007-08 season.
Figure 6: Comparison of $\delta^{15}$N and $\delta^{13}$C in SSTS tissues between the 2006-07 and 2007-08 banding seasons. Samples included 17 samples of both blood and feather from 2006-07, and 26 samples of each from the 2007-08 season.
Site Differences in $\delta^{15}$N and $\delta^{13}$C

Winter site variation was apparent in $\delta^{15}$N values in all three species’ blood samples. SESP blood $\delta^{15}$N values at site ER (10.5±0.47 ‰) differed from both sites LH (8.1±0.48 ‰) and P (8.98±0.41 ‰) (*Kruskal-Wallis One-Way ANOVA on Ranks with Multiple-Comparison Z-Value Test, H = 37.43, p < 0.01*), but no differences were seen among feathers or in $\delta^{13}$C (Fig. 7). Similarly, NSTS blood samples varied between ER (10.47±0.68 ‰) and LH (8.78±0.85 ‰) in $\delta^{15}$N only (H = 27.54, p = 0.01), while showing no feather variation (Fig. 8). SSTS $\delta^{15}$N values differed among blood samples, with significant differences between sites ER (9.73±1.11 ‰) and LH (8.15±1.03 ‰) (H = 10.19, p = 0.01), and feather samples, with differences between LH (10.36±1.56 ‰) and P (12.05±1.59 ‰) (H = 8.20, p = 0.02). SSTS samples did not differ in $\delta^{13}$C values (Fig. 9).
Figure 7: Comparison of $\delta^{15}$N and $\delta^{13}$C in SESP tissues among three NC study sites.

Samples included 12 samples of both blood and feather from site ER, 9 from site LH, and 11 from site P.
Figure 8: Comparison of δ\textsuperscript{15}N and δ\textsuperscript{13}C in NSTS tissues among three NC study sites.

Samples included 21 samples of both blood and feather from site ER, 25 from site LH, and 4 from site P.
Figure 9: Comparison of $\delta^{15}$N and $\delta^{13}$C in SSTS tissues among three NC study sites.

Samples included 6 samples of both blood and feather from site ER, 19 from site LH, and 18 from site P.
Tissue Comparison

The difference in δ^{15}N and δ^{13}C between feather and blood was compared for each species where both were available. To alleviate problems of small sample size, each species’ data were combined from all study sites.

In SESP, there was a significant difference between blood and feather δ^{15}N values (Wilcoxon Signed-Rank Test for Difference in Medians, \(W_{\text{Sum Ranks}} = 152, p = 0.01\)), but no variation in δ^{13}C between tissues (Table 1, Fig. 10). NSTS showed no difference in blood and feather δ^{15}N, but δ^{13}C values varied significantly between tissues (\(W_{\text{Sum Ranks}} = 1246, p < 0.01\)) (Table 1, Fig. 11). SSTS tissues differed both in δ^{13}C (\(W_{\text{Sum Ranks}} = 176, p = 0.000335\)) and δ^{15}N (\(W_{\text{Sum Ranks}} = 6, p < 0.01\)) (Table 1, Fig. 12).

Table 1: Comparison of δ^{15}N and δ^{13}C between tissues for each species. Means and standard deviations (SD) in δ^{13}C and δ^{15}N values are given in ‰. Differences were calculated as means of blood minus feather from birds sampled during winter. An asterisk (*) denotes significant tissues differences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample Size</th>
<th>Tissue Difference δ^{15}N ±SD</th>
<th>Tissue Difference δ^{13}C ±SD</th>
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<td>-1.34 ±1.71*</td>
<td>0.09 ±2.94</td>
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<td>NSTS</td>
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<td>8.02 ±5.38*</td>
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<td>SSTS</td>
<td>43</td>
<td>-2.69 ±1.59*</td>
<td>-1.05 ±2.27*</td>
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Figure 10: Comparison of $\delta^{13}$C and $\delta^{15}$N between tissues in SESP. Mean $\delta^{13}$C and $\delta^{15}$N from *Spartina alterniflora* collected in North Carolina (N = 4) is shown, designated C4. C3 represents the value of *Limonium* sp. (N = 1) $\delta^{13}$C and $\delta^{15}$N, also collected in North Carolina.
Figure 11: Comparison of $\delta^{13}$C and $\delta^{15}$N between tissues in NSTS. Data are presented as in Fig. 3.
Figure 12: Comparison of $\delta^{13}$C and $\delta^{15}$N between tissues in SSTS. Data are presented as in Fig. 3.
Diet Samples:

Plant and invertebrate samples collected at North Carolina sites possessed $\delta^{13}C$ values typical of both $C_3$ and $C_4$ plants (Table 2).

Table 2: Potential diet source $\delta^{15}N$ and $\delta^{13}C$ values from samples collected at winter sites in North Carolina. $\delta^{15}N$ and $\delta^{13}C$ values are given in $\%_o$. Arthropods of class Insecta were further identified by order.

<table>
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<td>Lepidoptera</td>
<td>4.34</td>
<td>-12.93</td>
</tr>
<tr>
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</tr>
<tr>
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<td>3.16</td>
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</tr>
<tr>
<td>Limonium sp. (plant)</td>
<td>4.1</td>
<td>-23.0</td>
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<tr>
<td>Spartina alterniflora (seed)</td>
<td>7.1 +/- 0.9</td>
<td>-13.2 +/- 0.4</td>
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</table>
NSTS Subspecies Comparison

NSTS subspecies A. n. nelsoni and A. n. subvirgatus, identified by plumage characteristics in the field, varied significantly in $\delta^{13}$C values (Mann-Whitney U/Wilcoxon Rank-Sum Test for Difference in Medians, $U_{\text{net}}=770$, $U_{\text{sub}}=2350$, $p = 0.01$), but not $\delta^{15}$N. A. n. nelsoni mean $\delta^{13}$C values were 5.17 ‰ lower than A. n. subvirgatus (Fig. 13).
Figure 13: Comparison of $\delta^{15}$N and $\delta^{13}$C in feathers of NSTS subspecies (A. n. nelsoni and A. n. subvirgatus). Also included are mean feather values for each subspecies.
Breeding Ground Sampling

SSTS blood $\delta^{15}$N values collected during the breeding season in Connecticut varied significantly from blood collected in winter in North Carolina (*Kruskal-Wallis One-Way ANOVA on Ranks, H = 51.86, p < 0.01*) (Table 3). CT Blood $\delta^{15}$N exceed NC blood by approximately 3.09 ‰. In addition, $\delta^{13}$C values of feathers collected during summer in Connecticut were approximately 1.5 ‰ lighter than NC feathers (H = 21.49, p = 0.01).

Table 3: Comparison of breeding ground (Connecticut) blood samples to wintering ground (North Carolina) blood and feather samples. Means and standard deviations (SD) of $\delta^{15}$N and $\delta^{13}$C values are given in ‰ for each tissue. Samples include only that of SSTS. An asterisk (*) denotes means significantly different from Connecticut blood samples.
Winter Blood Comparison

NSTS blood $\delta^{13}$C values differed from SSTS and SESP, with a mean value of $-13.41 \pm 1.14\%$ for NSTS, which is higher than that of SESP ($-13.9 \pm 1.23\%$) and SSTS ($-14.39 \pm 1.4\%$) (Kruskal-Wallis One-Way ANOVA on Ranks, $H = 17.15$, $p = 0.01$). SSTS blood $\delta^{15}$N ratios also differed from NSTS ($9.56 \pm 1.11\%$) and SESP ($9.8 \pm 1.08\%$), with SSTS lowest at $8.6 \pm 0.96\%$ ($H = 29.59$, $p < 0.01$) (Table 4). To avoid problems of small sample size in certain cases, samples were compared collectively rather than per site.

Table 4: Comparison of winter blood samples among all species. Means and standard deviations of $\delta^{15}$N and $\delta^{13}$C values are given in $\%$ for each tissue. An asterisk (*) denotes means significantly different from other species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample Size</th>
<th>$\delta^{15}$N ± SD</th>
<th>$\delta^{13}$C ± SD</th>
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<td>SESP</td>
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<td>SSTS</td>
<td>44</td>
<td>8.6 ± 0.96*</td>
<td>-14.39 ± 1.4</td>
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</tbody>
</table>
DISCUSSION

Migratory Timing and Abundance

Sharp-tailed sparrow migration spans from late August to early October (DiQuinzio et al. 2001, Greenlaw and Rising 1994, Rising and Avise 1993). Fall migration is thought to cease by mid-November (Greenlaw and Woolfenden 2007). Museum specimens collected in North Carolina suggest the arrival of birds to North Carolina in late September; data gathered here confirm this arrival time (Greenlaw and Woolfenden 2007). Results from this study, however, contradict the end of fall migration in mid-November. Banding numbers were highest for all species during the months of October, November, and December before dropping in January (Fig. 3). This pattern suggests that, during the month of December, birds were continuing to migrate south. This prolonged migration may be the outcome of limited study of the nonbreeding season ecology of these species, or perhaps represents an effect of climate change enabling the birds to remain at the breeding grounds longer into the fall. Identifying the cause of this difference is not possible within the scope of this project, but warrants future investigation and may carry implications for the population of each species.

October, November, and December have the highest numbers of sparrows present on wintering sites likely due to large groups of birds passing through as they travel farther south, as well as those birds arriving to their wintering grounds in North Carolina. Because SESP numbers are included in these data, it is possible that non-resident SESP are migrating through North Carolina as well. While SESP are found year-round in
North Carolina, it is unknown if the local breeding population remains in winter or is replaced by migrants from the north (Post and Greenlaw 1994, Robbins 1981). Banding data, supported by isotopic evidence, suggest that wintering SESP are year-round residents. Continued banding during the breeding season is needed to further address this question.

In addition to migratory timing, banding data provides information on species and subspecies distribution contrary to previous work. Post (1998) documented that the majority of sharp-tailed sparrows wintering in Waccasassa Bay, along the Gulf Coast of Florida, were NSTS and suggested that SSTS dominate habitats along the Atlantic Coast. Studies based on specimens collected in North Carolina indicated that 66% of wintering sharp-tailed sparrows are SSTS, and that NSTS prevail at coastal wintering sites further south (Greenlaw and Woolfenden 2007). *A. n. subvirgatus*, in particular, is noted by some to have the most restricted range from South Carolina to Florida (Burleigh 1958, Greenlaw and Woolfenden 2007). Banding data contradicts such trends and shows NSTS to be more abundant in southeastern North Carolina than SSTS (196 NSTS banded versus 127 SSTS). In addition, of 196 NSTS banded, 76 were identified as *A. n. subvirgatus*. This result is in concordance with winter ranges suggested by Sibley (1996). Banding further north along the North Carolina coast is recommended to compare numbers of wintering sharp-tailed sparrows and suggest an extension of the presupposed winter strongholds of NSTS.

All three species remained at the study sites through March each year as the winter season ended. Numbers at the end of the season were never as high as during the fall migration, suggesting spring migration had not yet begun. This pattern coincides

Site Fidelity

Recapture data supports the hypothesis that SESP, NSTS, and SSTS are site-faithful during the winter season. Here, recaptures demonstrated 100% site fidelity by each species at the three study sites at high tide. The study sites are separated from each other by over 7 km, well outside of the mean foraging area of 1039 m$^2$ given for SESP (Post and Greenlaw 1994). During the breeding season elsewhere, SSTS demonstrated moderate site fidelity as most were observed to move within and among marshes (DiQuinzio et al. 2001). DiQuinzio et al. (2001) suggested that patterns of site fidelity in promiscuous species such as SSTS and NSTS are affected by limited suitable habitat, thus fragmented wetlands in North Carolina may increase winter site fidelity among these birds. Further investigation is recommended, including banding at sites closer to one another, potentially within the same marsh system. Incorporating more banding locations could show how far individual birds travel within the marsh.

Annual Differences in $\delta^{13}$C and $\delta^{15}$N

Summer to summer variation, as well as winter to winter, in $\delta^{13}$C and $\delta^{15}$N, was significant only in SSTS (Fig. 4, 5, 6). The cause of annual variation cannot be specifically identified, but climate effects are a possible source. As suggested by Graves
et al. (2002), annual variation in δ^{13}C and δ^{15}N may be influenced by soil nitrogen dynamics, water availability, and plant nitrogen storage strategies, all of which vary interannually and regionally. Investigation of weather patterns, particularly droughts, could offer insight into δ^{13}C and δ^{15}N trends, but the migratory nature of the species is problematic as the specific breeding site of sampled SSTS must be known to investigate climatic effects (and thus their effect on feather isotope values) during the breeding season. While annual differences were not the focus of this project, their effects on other comparisons were evaluated.

Study Site Differences in δ^{13}C and δ^{15}N

Blood δ^{15}N varied within SESP, NSTS, and SSTS by study site (Fig. 7, 8, 9). Samples from ER possessed the most enriched δ^{15}N signature for each species, followed by P and LH. The dominant vegetation at all three sites is *Spartina alterniflora* and there are no obvious vegetative distinctions that could explain the cause of this isotopic variation. Marsh age may affect δ^{15}N, but all three sites are similar in age (Rozema et al. 2000). Moreover, while highly disturbed ecosystems show enriched values of δ^{15}N, all three sites are relatively undisturbed (Hobson 1999b). Intrusion of human and animal waste, as well as fertilizer, can also lead to high values of δ^{15}N (Hobson 1999b, McClelland et al. 1997, Wigand et al. 2007). The site most likely to be affected by waste or fertilizer is P because of its proximity to the mainland, but δ^{15}N was less enriched here than at ER.
Food source availability may have affected blood $\delta^{15}N$ values at each site, but this is unlikely. If insect availability varied per site, birds feeding on more insects would possess a higher $\delta^{15}N$ signature due to observed stepwise trophic enrichment (Sydeman et al. 1997, Thompson and Furness 1995). $\delta^{13}C$ values also follow a pattern of trophic enrichment, but at a much smaller scale (Thompson and Furness 1995). Thus, even if too small to be statistically significant, $\delta^{13}C$ results should correspond to the site trend as in $\delta^{15}N$, but do not. Additionally, during the winter insect availability is minimal and would have limited effect on blood isotope values.

If food availability varied among sites, to the extent that birds were nutritionally stressed at certain sites, this would be displayed in blood sample isotopes. $\delta^{15}N$ is enriched in vertebrates when fasting (Hobson et al. 1993). Thus, if birds were facing limited resources at a site, then $\delta^{15}N$ should increase and this effect would not be displayed in $\delta^{13}C$ ratios. This option, however, is also unlikely as $\delta^{15}N$ ratios were lower during the winter season than the breeding season when high quality food is more abundant. Consequently, there at present is no likely explanation for the variation in $\delta^{15}N$ in blood among the three study sites.

Variation among SSTS feather $\delta^{15}N$ was also observed among the three winter sampling sites. This variation may be an effect of small sample size at ER and several outlier values recorded at LH and P. If the variation is real, it suggests that SSTS are migrating from specific breeding locations, where individuals share a common isotopic signature in molted and new feathers, to specific wintering sites and maintain site fidelity at both. Additional research of feather $\delta^{15}N$ at breeding sites would be needed to verify this pattern.
While study site differences are evident in blood $\delta^{15}$N values, it is impossible within this project to identify the source of variation, nor is it the objective. The number of variables affecting $\delta^{15}$N within each marsh system prevents determining the cause of site differences, but as with annual differences, the pattern was incorporated into other isotope analyses.

Winter and Summer Diet Comparison

Blood and feather tissues were compared to measure the difference between tissue types (Table 1). Variation in $\delta^{13}$C and $\delta^{15}$N between tissues could represent a seasonal dietary shift. It has been suggested that all three species maintain a summer diet comprised of predominantly animal matter and incorporate more seed during the winter season. Gut content analyses support this summer diet, but to what extent winter diet differs is unknown (Greenlaw and Rising 1994, Post and Greenlaw 1994). Accordingly, isotope values should reflect a diet based on some combination of C$_3$ and C$_4$ plants and consumers. Typical $\delta^{13}$C values of a C$_3$ plant such as *Juncus roemerianus* are near -23 ‰ (Pain et al. 2004, Peterson and Howarth 1987). C$_4$ plant-based food webs, including *Spartina alterniflora*, maintain much more enriched $\delta^{13}$C signatures around -13 ‰ (Haines and Montague 1979, Pain et al. 2004, Peterson 1987, Wainright et al. 2000).

SESP blood and feather samples differed significantly in $\delta^{15}$N, with feathers more enriched than blood by 1.3 ‰. While statistically significant, this does not necessarily indicate a dietary shift. Previous studies show evidence of isotopic discrimination within
tissues, referring to differences in isotopic assimilation rates among tissue types (Hobson and Bairlein 2003, Bearhop et al. 2002, Cherel et al. 2005). Hobson and Bairlein (2003) demonstrated a difference between feather and blood discrimination factors of 1.6 ‰ for $\delta^{15}$N and 1 ‰ for $\delta^{13}$C, based on feather discrimination factors of 2.7 ‰ for $\delta^{13}$C and 4 ‰ for $\delta^{15}$N, with blood discrimination factors of 1.7 ‰ for $\delta^{13}$C and 2.4 ‰ for $\delta^{15}$N. Such an offset suggests that feathers naturally possess heavier or higher $\delta^{15}$N and $\delta^{13}$C values than blood. Accounting for this inherent tissue offset, $\delta^{15}$N between blood and feathers does not differ or support a seasonal dietary shift in SESP.

While the winter and summer diet of SESP may not vary, the data do provide dietary information (Fig. 10). Most birds showed a reliance on a C$_4$ plant-based diet year-round, as $\delta^{13}$C and $\delta^{15}$N values have signatures typical of C$_4$ plants (Haines and Montague 1979, Peterson 1987, Wainright et al. 2000, Wigand et al. 2007). SESP are known to breed in habitat of Spartina alterniflora and Juncus roemerianus (Post and Greenlaw 1994). Results indicate that wintering birds relied primarily on S. alterniflora, while there is some variation from this diet during the breeding season. Birds possessing $\delta^{13}$C values that are less enriched than those characteristic of C$_4$ plants rely on C$_3$ plants for a portion of their diet (Peterson 1986 and 1987, Wainright et al. 2000, Wigand et al. 2007). Thus, the data indicate that a small portion of SESP wintering in North Carolina rely on a C$_3$-plant based diet during the breeding season. Potential breeding sites in North Carolina would be Juncus-dominated marshes found along rivers and away from the tidal amplitude of the coast (Post and Greenlaw 1994). The majority of SESP samples, however, surround values typical of C$_4$ S. alterniflora, supporting the thought that the SESP population in southeastern North Carolina represent a resident group.
Isotope data support previous dietary content assumptions that SESP feed on a diet based on plant and animal matter located within *S. alterniflora* stands (Post and Greenlaw 1994). There is also evidence that SESP feed within *Salicornia sp.* patches (Post and Greenlaw 1994). *Salicornia*, a C$_3$ plant, can be found within two of the study sites, and blood samples indicate that SESP may be feeding on consumers of *Salicornia* during the winter season as some samples possess $\delta^{13}$C values below those characteristic of C$_4$-based diets. Invertebrate SIA confirms the presence of both C$_3$ and C$_4$ consumers at winter sites (Table 2).

NSTS tissue samples showed a $\delta^{13}$C difference of 8.02 ‰ between feathers and blood. It exceeds the expected tissue offset, and is not likely due to a shift in trophic level feeding. Samples show a wide range of $\delta^{13}$C values, with most blood samples converging on the isotopic signature for *S. alterniflora* (Fig. 8). Feather values include $\delta^{13}$C signatures near -13 ‰, resembling that of *S. alterniflora*, but span well beyond -20 ‰, indicating a C$_3$ food source (Haines and Montague 1979, Peterson 1986 and 1987, Wainright et al. 2000, Wigand et al. 2007).

Winter blood values were not significantly different, as expected, since all birds were presumably feeding upon a similar diet in North Carolina. The spread of feather samples may indicate more opportunistic feeding during the breeding season, but more likely reflects the breeding range of the three subspecies of NSTS (Greenlaw and Rising 1994). Within each range, birds occupy varied habitats that differ in the dominant vegetation, with *Spartina pectinata*, *Hordeum jubatum*, *Scolochloa festucacea*, and *Phragmites australis* found more inland, while coastal populations are found in *S. alterniflora*, *S. patens*, *J. roemerianus*, and *Triglochin maritime* dominated habitats.
NSTS populations as a whole encounter both C$_3$ and C$_4$-based habitat, and this was seen in their isotope signatures.

In SSTS, $\delta^{15}$N was more enriched in feathers than blood by 2.7 ‰, which is outside of the tissue discrimination factor (Fig. 9). $\delta^{13}$C was also more enriched in feathers, but only by 1.05 ‰, slightly higher than the suggested discrimination factor. $\delta^{13}$C and $\delta^{15}$N values suggest that SSTS do undergo a seasonal dietary shift, albeit minor, feeding on more higher trophic level items during the summer. This shift corresponds with previous hypotheses that the SSTS summer diet is largely insect-based and more seed is consumed during winter months (Greenlaw and Rising 1994).

Samples show that SSTS rely on a C$_4$-based diet year-round, which is expected as birds both breed and winter in S. alterniflora marshes along the coast (Fig.9; Greenlaw and Rising 1994, Rising 1996). In some locations, birds breed in marshes dominated by J. roemerianus, which would explain some of the depleted $\delta^{13}$C values in the data (Greenlaw and Rising 1994; Rising 1996).

NSTS Subspecies Comparisons

NSTS individuals were identified to subspecies using plumage and morphological characteristics at time of capture. Two of three known subspecies were confirmed in North Carolina at the three study sites and included A. n. nelsoni and A. n. subvirgatus. The third subspecies, A. n. alterus, was not recognized due to difficulty in identification based on similarities in plumage and morphology with the other subspecies (especially A. n. subvirgatus) and this difficulty may explain its reported limited occurrence in North
Carolina (Sibley 1996). Thus, I do not discount the possibility that this subspecies is more common in North Carolina than has been reported in the literature. Based on subspecies designation in the field, feather $\delta^{13}$C varied significantly among A. n. nelsoni and A. n. subvirgatus. Mean $\delta^{13}$C of A. n. nelsoni was much more depleted than A. n. subvirgatus (Fig. 13). The majority of A. n. nelsoni samples suggested a C$_3$ source in diet while A. n. subvirgatus values were more variable. Data on $\delta^{13}$C in this latter species were more indicative of a C$_4$-based diet, with some C$_3$ food as well. Many samples possessed $\delta^{13}$C values falling between that of a C$_3$ and a C$_4$ plant, and suggest that some A. n. subvirgatus rely on a mixed vegetation diet. These patterns in $\delta^{13}$C are probably due to the absence of C$_4$ plants over much of the breeding range of A. n. nelsoni, while A. n. subvirgatus does have both C$_3$ and C$_4$ plants available. Recent work has also shown that A. n. subvirgatus breeds in a variety of habitats, including hayfields, when more suitable habitats have been compromised (Nocera et al. 2007).

An alternate explanation for variation in feather $\delta^{13}$C is that birds may be molting during migration. If a bird left the breeding grounds before molt was complete, $\delta^{13}$C values would reflect the path of migration and stopover points (Podlesak et al. 2005). Although SIA may be helpful in identifying subspecies of NSTS, the wide range of $\delta^{13}$C values, particularly in A. n. subvirgatus feathers, suggest that SIA alone should not be used in subspecies identification due to variable habitat within each subspecies’ range.
Breeding Ground Blood Comparison

SSTS blood samples were collected on breeding grounds in Connecticut to evaluate tissue differences between blood and feathers during breeding. Assuming that SSTS feathers are molted before departure from the breeding grounds, Connecticut blood (hereafter CT blood) samples should reflect isotopic signatures similar to the feathers collected at wintering sites in North Carolina (NC).

CT blood was more similar to NC feather $\delta^{15}$N values than to NC blood. NC Feather samples were 0.4 ‰ lighter than CT blood, while NC blood was 3.09 ‰ lighter, which was a significant difference (Table 3). After accounting for the tissue discrimination offset, however, NC feathers were 1.2 ‰ lighter than CT blood. Even with the tissue offset, CT blood $\delta^{15}$N was more similar to NC feathers than to NC blood. $\delta^{15}$N values suggest that breast feathers are an appropriate indicator of breeding season diet in SSTS.

$\delta^{13}$C values did not follow a similar trend. The means of each group’s $\delta^{13}$C were within 1.5 ‰ of one another. NC feather and CT blood differed significantly by 1.5 ‰ (after offset, 0.5 ‰) while NC blood and CT blood differed by 0.45‰. While the two blood samples proved more similar, differences were minimal among all three. CT blood was less enriched in $\delta^{13}$C overall when compared to NC feathers. This effect is likely an outcome of habitat. Dominant vegetation at sampling sites in Connecticut included *Spartina alterniflora, S. patens,* and *Phragmites australis.* The last plant, an invasive C$_3$ species, was not present at the study sites in North Carolina. The incorporation of *P. australis,* directly or through consumers, influenced the lower $\delta^{13}$C values of CT blood.
Habitat differences also may have affected $\delta^{15}$N among samples. $\delta^{15}$N was more enriched in CT blood than either of the NC samples. As mentioned above, disturbance within a marsh system can lead to elevated $\delta^{15}$N values (Hobson 1999b, Wigand et al. 2007). Marsh sites in North Carolina, although accessible from the Intracoastal Waterway, were more secluded than those in Connecticut. Sampling sites in Connecticut were closer to human development, and also faced the effects of ditching. This type of marsh management may have influenced $\delta^{15}$N values in CT blood samples.

Overall, collecting both blood and feathers during a single season can provide an accurate representation of diet and location for a migratory songbird species. Habitat variability over the range of a species, however, may affect the outcome of a temporal comparison. As suggested by Hobson (1999b), an understanding of local foodweb signatures is necessary to relate dietary models at different locations. Expanded banding at both breeding and wintering grounds can provide essential habitat information to correspond with SIA. Inter-season (breeding to nonbreeding) recaptures may be critical to identify with certainty where individual populations migrate.

Winter Ecological Segregation

Winter blood samples of all three species were compared to investigate patterns of dietary segregation. Foraging differences were possible as these were three species that do not share summer resources, but were relying on common marsh patches during the winter. Isotope values of $\delta^{13}$C and $\delta^{15}$N were significantly different among species (Table 4). SSTS $\delta^{15}$N was lighter than both NSTS and SESP. This result suggests that SSTS
feeds on lower-trophic prey than NSTS or SESP, presumably by consuming fewer invertebrates (Hobson 1999a, Hobson et al. 1997). A more likely cause is sampling site differences. As shown above, ER showed significantly higher δ¹⁵N values and the smallest sample of SSTS was captured at ER (n=6). Thus, the difference in δ¹⁵N was likely an effect of site variation compounded by small sample size.

NSTS δ¹³C values were heavier than that of SSTS or SESP. Differences in δ¹³C were not significant among the study sites, so sampling size per site is not a factor. In addition, trophic level has a minimal effect on δ¹³C values, thus trophic level differences in prey are unlikely (Thompson and Furness 1995). NSTS samples show less variation among δ¹³C values than other species (Table 4). Differences in δ¹³C among species could be an outcome of NSTS feeding primarily on C₄ food sources during the winter, with little to no incorporation of any C₃ plants or C₃ plant consumers. Although δ¹³C and δ¹⁵N differences existed among species, patterns are not substantial enough to suggest ecological segregation among NSTS, SESP, and SSTS during the winter season.

CONCLUSION

While SIA demonstrates different plant sources at the base of each sparrow’s diet, continued study is crucial to further ecological understanding and conservation of SESP, NSTS, and SSTS. SIA showed that only SSTS demonstrated a minor seasonal trophic level shift in feeding from breeding to nonbreeding seasons, while NSTS undergo a C₃ to C₄ plant source shift. This study also demonstrated winter site fidelity among all three species, as well as provided novel information regarding migratory patterns and timing.
Whether current migratory patterns differ from those previously suggested due to a lack of study in North Carolina, or represent real effects of a warming climate is uncertain, but surely enhances concern for all three species.

Study of winter habitat use and greater investigation of each species’ winter range is encouraged to emphasize winter sites in need of protection. Additionally, estimates of wintering populations throughout the range would be helpful for management purposes. Specifically, year-round banding of SESP in North Carolina can help answer questions regarding migration and population trends, while NSTS and SSTS would benefit from banding studies at other locations, both winter and summer, to provide data essential for the conservation of each species.
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