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WINTER COMPOSITION OF NELSON'S SPARROW (*AMMODRAMUS NELSONI*) AND SALTMARSH SPARROW (*AMMODRAMUS CAUDACUTUS*) MIXED FLOCKS IN COASTAL VIRGINIA

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ABSTRACT.—We captured 1,055 Nelson's (*Ammodramus nelsoni*) and Saltmarsh (*Ammodramus caudacutus*) sparrows during the winter season (2006–2014) within the outer Coastal Plain of Virginia to determine the composition of subspecies. Birds were captured using mist nets in 24 tidal salt marshes and identified to subspecies using a plumage-based, syntopic key. Contrary to previous assessments, both species of sharp-tailed sparrows were common. All five subspecies were present and appeared to form mixed flocks within patches. The north-Atlantic Saltmarsh Sparrow (*A. c. caudacutus*) was the most common form, accounting for 45% of all birds identified to subspecies. The three Nelson's Sparrow forms including the "Acadian" Nelson's Sparrow (*A. n. subvirgatus*), "James Bay" Nelson's Sparrow (*A. n. alter*) and the "Nelson's" Sparrow (*A. n. nelsoni*) were equally common and collectively accounted for 47% of the subspecies identified. The highly restricted, mid-Atlantic Saltmarsh Sparrow (*A. c. diversus*) was the least common, accounting for only 8% of individuals. Subspecific composition did not vary with geography in the region. Age ratios for both Nelson's and Saltmarsh sparrows were significantly skewed to hatching-year (HY) rather than after-hatching-year (AHY) birds. However, age ratios varied dramatically across years for both species. The annual portion of birds accounted for by the HY class ranged from 31.3 to 77.5% and 36.7 to 70.3% for Nelson's and Saltmarsh sparrows, respectively. Information from Virginia represents a significant extension of current perceptions about the winter distribution of these forms. *Received 19 September 2014. Accepted 15 February 2015.*

Key words: age ratio, *Ammodramus caudacutus*, *Ammodramus nelsoni*, Nelson's Sparrow, Saltmarsh Sparrow, Virginia, winter range.

The sharp-tailed sparrow complex is a superspecies that has had a complicated taxonomic history (AOU 1931, 1957; Greenlaw and Rising 1994). Current subdivisions reflect breeding distribution, habitat use, morphology, behavior, and genetic differences (Greenlaw 1993, Rising and Avise 1993, Hodgman et al. 2002) and recognize two species (Nelson's Sparrow, *Ammodramus nelson*; Saltmarsh Sparrow, *A. caudacutus*) and five subspecies (*A. n. nelsoni*, *A. n. alter*, *A. n. subvirgatus*, *A. c. caudacutus*, *A. c. diversus*; AOU 1995). The breeding ranges of all subspecies have been recognized for more than a century (Greenlaw and Rising 1994, Hodgman et al. 2002). Selected subspecies pairs overlap on the breeding grounds with documented hybrid zones (Hodgman et al. 2002, Shriver et al. 2005). The winter ranges have received much less attention (Post 1998, Greenlaw and Woolfenden 2007).

Greenlaw and Woolfenden (2007) utilized a synoptic key to classify more than 660 specimens that had been collected during the winter season to assess distribution along the Atlantic and Gulf coasts. They demonstrate that all five subspecies converge on the south Atlantic Coast and that for most forms this location represents the center of occurrence. One limitation of the Greenlaw and Woolfenden (2007) study is the lack of specimens available along the Atlantic Coast north of North Carolina. Only 25 specimens were available north of this area, including only a single Nelson's Sparrow. While the possibility exists that the lack of specimens to the north is consistent with the distribution of birds, it is also possible that the void reflects a lack of collecting activity. If the latter, this void may severely limit our perception of subspecific composition and associated distribution within the northern reach of the winter range.

Clarifying the winter range of this species complex is of particular interest because all forms appear to be saltmarsh obligates during the winter period and, as such, are confined to a thin veneer of tidal habitat that is being subjected to increasing threats from sea-level rise (Church et al. 2001). Concern is especially high for both forms of Saltmarsh Sparrows that have relatively small global population sizes and are confined to saltmarsh habitats throughout their entire annual cycle (Gjerdrum et al. 2005). Our objectives here were to assess the use of saltmarsh habitats by the sharp-tailed sparrow complex during the winter season in Virginia. The assessment will extend the

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information provided by Greenlaw and Woolfenden (2007) and contribute to our understanding of winter distribution in this species complex.

METHODS

Study Area.—We studied Nelson's and Saltmarsh sparrows within the outer Coastal Plain of Virginia during six winter seasons (2006–2007, 2008–2009, 2009–2010, 2010–2011, 2012–2013, 2013–2014). We worked within 24 patches of salt marsh (defined as marshes exposed to 18–30 ppt salinity) composed of smooth cordgrass (*Spartina alterniflora*), black needlerush (*Juncus roemerianus*), salt meadow hay (*S. patens*), saltgrass (*Distichlis spicata*), and saltbush (*Baccharis hamilifolia*). Field sites were distributed among two ecological units (Fig. 1), including the Delmarva coastal bay ($n = 14$) and the Chesapeake Bay ($n = 10$). The Delmarva coastal bay includes the seaward margin of the Delmarva Peninsula from the mouth of the Chesapeake Bay to the Maryland-Virginia border. An outer chain of 14 barrier islands protects an extensive lagoon system that contains more than 85,000 ha of tidal marsh, mudflats and open water. The Chesapeake Bay is the largest estuary in North America, containing more than 19,000 km of tidal shoreline. The Bay supports extensive tidal marshes that vary in vegetational composition and associated bird communities depending on salinity exposure (Wilson et al. 2007), with salt marsh representing the most prevalent type within the lower Chesapeake Bay study area (Stevenson et al. 2000).

Bird Sampling.—We banded sparrows during a total of 103 field days (15 Nov through 20 Mar) including 20, 16, 27, 15, 10, and 15 days during the 2006–2007, 2008–2009, 2009–2010, 2010–2011, 2012–2013, 2013–2014 winter seasons respectively. We captured sparrows using up to three 12-m mist nets (32 mm mesh) placed along vegetation used as cover. Teams of three to eight individuals walked marshes to locate sparrows and erected nets adjacent to patches of high cordgrass, black needlerush or salt bush that represented conspicuous sources of cover. Teams pulled 60-m, weighted ropes to drive sparrows toward cover patches and into nets. Once extracted, birds were identified, aged, banded with United States Geological Survey aluminum bands and released.

We identified sparrows to the lowest taxonomic level possible with a plumage-based dichotomous key (Greenlaw and Woolfenden 2007). All individuals were identified to the species level. We attempted to designate subspecies for the majority (89.5%) of individuals captured. We took high resolution photographs of three views, including frontal, profile and back, for later reference in reviewing plumage characters. We employed a conservative approach to subspecific designations. As indicated in Greenlaw and Woolfenden (2007), the level of overlap in plumage characters varies such that some subspecies pairings (i.e., interior Nelson's Sparrows) are more difficult to separate. We placed individuals with clear plumage characters in exclusive subspecies groups. We placed individuals with characters that favored two subspecies in an overlap group. All individuals examined were narrowed down to at least a subspecies pairing.

We designated age as either hatch-year (HY) or after-hatch-year (AHY). Our usage here differs from typical banding nomenclature where these terms reflect the calendar year. HY in the current usage refers to individuals that were hatched during the previous breeding season. AHY refers to individuals that were hatched before the previous breeding season. We determined sparrow age using a combination of skull ossification and plumage characters (Pyle 1997). We designated birds with incomplete skull ossification as HY. For birds with completely ossified skulls, we referred to plumage characters for age designations. We considered birds with retained primary coverts and replaced secondary coverts as HY after Pyle (1997). Birds that had undergone definitive prebasic molt, with primary and secondary coverts uniform in color and wear, were designated as AHY.

Data Analysis.—We summarize species and subspecies composition to provide the most information possible. In addition to species and subspecies categories, we also grouped Nelson's Sparrows into inland (*A. n. nelsoni*, *A. n. alter*) and coastal (*A. n. subvirgatus*). Because many individuals could not be classified to the subspecies level using the plumage key (exhibited characters of two forms), we provide classification rates for all subspecies pairings. Classification rates presented as percentages were calculated for each pairing as [(identified form 1 + identified form 2)/(identified form 1 + identified form 2 + overlap form 1 and 2)] × 100. This gives the percentage of each pairing that could be classified to the subspecies level. We also provide classification rates on the subspecies level calcu-

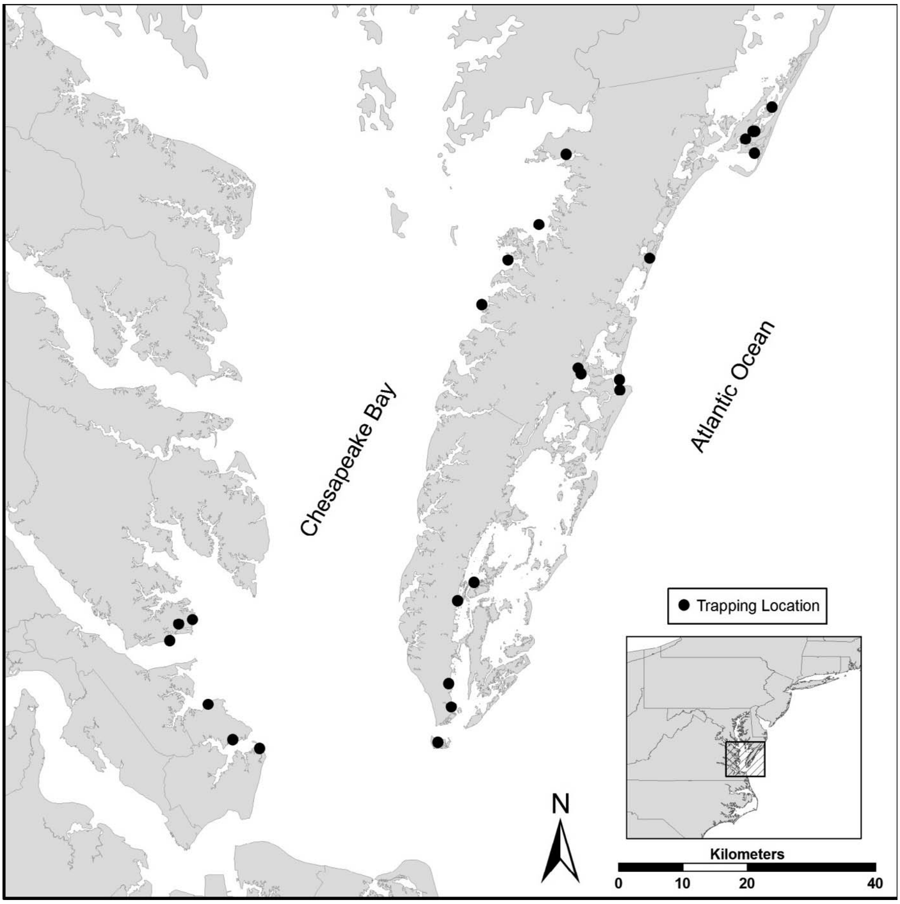


FIG. 1. Map of sharp-tailed sparrow trapping sites in coastal Virginia. Sites along the Atlantic Coast are considered within the "coastal bay" study area. All other sites are within the Chesapeake Bay.

lated as [(identified form 1)/(identified form 1 + overlap form 1 and 2)] × 100. We compared species composition by geographic area, age distribution by species, and age distribution across years using a likelihood ratio test for goodness-of-fit.

RESULTS

Both Nelson's and Saltmarsh sparrows were common within the study area and represented comparable (52.5% and 47.5%, respectively) portions of the total birds captured (n = 1,055; Table 1). Samples included all 5 subspecies. For the individuals for which subspecific designations were possible, the north-Atlantic (*A. c. caudacutus*) and mid-Atlantic (*A. c. diversus*) Saltmarsh Sparrows were the most and least common at 45 and 8% of the total, respectively (Fig. 2). All Nelson's Sparrow forms were of similar abundance. As a group, interior Nelson's Sparrows (*A. n. nelsoni* and *A. n. alter*) were much more common than Acadian Nelson's Sparrows (*A. n. subvirgatus*; Table 1).

Ability to separate subspecies in the field varied across pairings (Table 2). For the three Nelson's subspecies, the Acadian form could be separated from both interior forms more than 90% of the time. However, interior subspecies were very similar and more than 40% of individuals exhibited characteristics of both forms. The overlap between Saltmarsh Sparrow subspecies was also considerable, though the influence on classification rates differed between the forms due to a disparity in abundance. Collectively, the patterns of overlap suggest that three groups, including interior Nelson's, Acadian Nelson's and

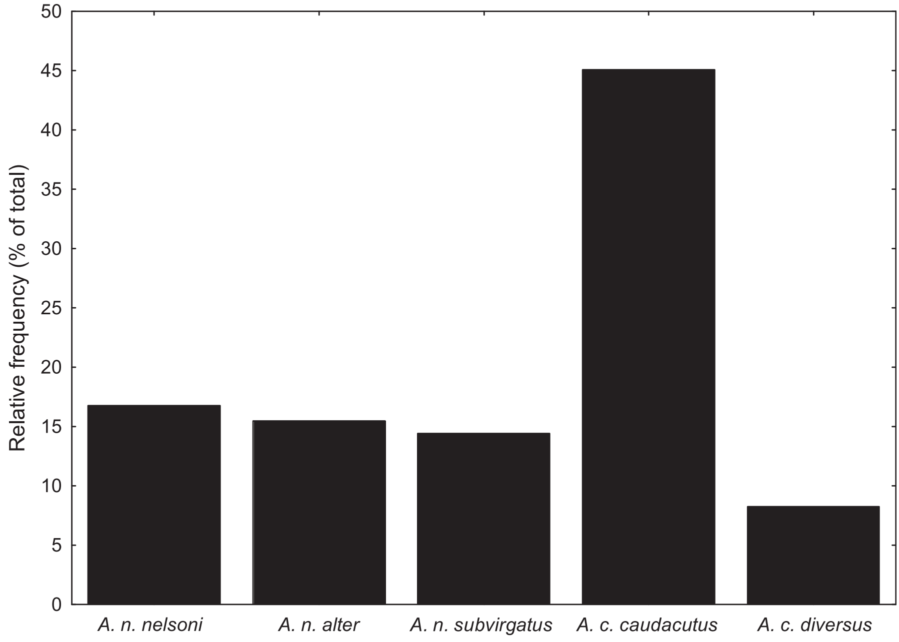


FIG. 2. Relative frequencies of sharp-tailed sparrow subspecies captured within tidal saltmarshes in coastal Virginia (2006–2014). Values represent percentage of all individuals identified to the subspecies level.

Saltmarsh sparrows, are distinct enough that more than 90% of individuals may be successfully separated in the field.

Relative abundance of Nelson's and Saltmarsh sparrows did not vary between geographic areas (coastal bay versus Chesapeake Bay; $G = 0.35$, df = 1, $P = 0.55$). Composition of subspecies groups (interior Nelson's, Acadian Nelson's, saltmarsh) was also similar for the two areas ($G = 2.58$, df = 2, $P = 0.27$). In addition, the small number of overlaps between Acadian and interior Nelson's Sparrows had no influence on this result.

When all years were considered collectively, both Nelson's (HY = 59.6% versus AHY = 40.4%) and Saltmarsh (HY = 61.9% versus AHY = 38.1%) sparrows were significantly biased toward the HY age class in Virginia (both $G > 16.0$, df = 1, $P < 0.001$). However, age ratios varied dramatically across years for both

TABLE 1. Frequency of sharp-tailed sparrow forms identified within geographic areas of coastal Virginia. Percentages reflect comparisons within categories indicated by common indentation and superscripts.

Species/form	Coastal Bay	Chesapeake Bay	Total
Nelson's Sparrow	483 (52.8%)[a]	71 (50.4%)[e]	554 (52.5%)[i]
Interior	360 (82.2%)[b]	57 (53.8%)[f]	417 (76.7%)[j]
A. n. nelsoni	108 (51.2%)[d]	20 (57.1%)[h]	128 (52.0%)[l]
A. n. alter	103 (48.8%)[d]	15 (42.9%)[h]	118 (48.0%)[l]
Coastal (*A. n. subvirgatus*)	68 (15.5%)[b]	42 (39.6%)[f]	110 (20.2%)[j]
Unknown	10 (2.3%)[b]	7 (6.6%)[f]	17 (3.1%)[j]
Saltmarsh Sparrow	431 (47.2%)[a]	70 (49.6%)[e]	501 (47.5%)[i]
Northern (*A. c. caudacutus*)	299 (80.2%)[c]	45 (66.2%)[g]	344 (78.0%)[k]
Southern (*A. c. diversus*)	50 (13.4%)[c]	13 (19.1%)[g]	63 (14.3%)[k]
Unknown	24 (6.4%)[c]	10 (14.7%)[g]	34 (7.7%)[k]
Total	914	141	1055

TABLE 2. Overlap matrix for sharp-tailed sparrow subspecies trapped during the winter in coastal Virginia. Values represent the proportion of the individuals from subspecies (left column) that could not be separated from corresponding subspecies (header) on the basis of plumage characters.

	A. n. nelsoni	*A. n. alter*	*A. n. subvirgatus*	*A. c. caudacutus*	*A. c. diversus*
A. n. nelsoni	–	57.1	0.0	0.0	0.0
A. n. alter	59.2	–	7.0	0.0	0.0
A. n. subvirgatus	0.0	10.6	–	0.0	0.0
A. c. caudacutus	0.0	0.0	0.0	–	8.9
A. c. diversus	0.0	0.0	0.0	35.0	–

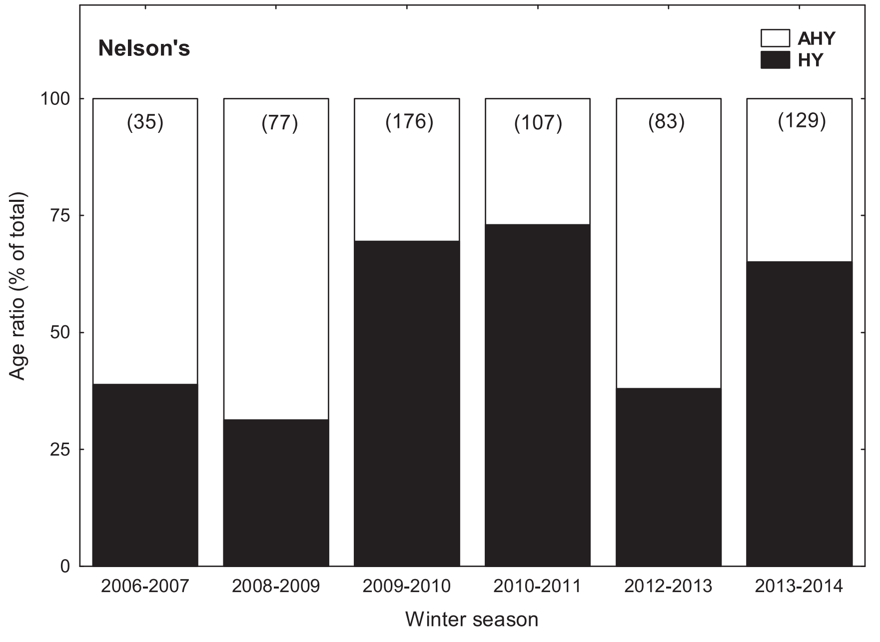
species (both $G > 39.0$, df = 5, $P < 0.001$; Fig. 3). The annual portion of birds accounted for by the HY age class varied from 31.3 to 77.5% and 36.7 to 70.3% for Nelson's and saltmarsh, respectively.

DISCUSSION

Results presented here add to a growing body of work that is beginning to clarify the winter distribution of the sharp-tailed sparrow complex (e.g., Post 1998, Greenlaw and Woolfenden 2007, Michaelis 2009). Virginia supports extensive salt marsh habitat and appears to play an important role during the winter period for the complex as a whole. All five subspecies converge within this geographic location and form mixed flocks within marsh patches. The paucity of historic information on the complex within this location has constrained previous understanding of distribution. Greenlaw and Woolfenden (2007) had access to only 25 specimens taken north of North Carolina, severely limiting their treatment of composition in the northern reaches of the winter range and, by association, inferences about distribution. Only 9 specimens were available from Virginia and all were taken from the southern portion of the barrier island/lagoon system (referred to here as Delmarva coastal bay).

Greenlaw and Woolfenden (2007) suggest a latitudinal gradient in species composition, with Nelson's becoming more prominent to the south. The frequencies of Nelson's and Saltmarsh Sparrows were similar (554, 52.5% versus 501, 47.5%, respectively) in captures made in Virginia. This finding, along with recent captures in North Carolina (196, 60.7% versus 127, 39.3%, respectively; Michaelis 2009), extends support to the north for a gradient in composition along the south Atlantic Coast. The relatively even occurrence of the three Nelson's subspecies was contrary to previous perceptions of distribution. The eastern breeding "James Bay" (*A. n. alter*) and "Acadian" (*A. n. subvirgatus*) subspecies are believed to winter primarily along the Atlantic Coast, while the interior (*A. n. nelsoni*) subspecies is believed to winter primarily along the Gulf Coast. Greenlaw and Woolfenden (2007) found no specimens of either interior or James Bay Nelson's and only one specimen of Acadian Nelson's north of North Carolina. In addition, these forms were poorly represented within the set of specimens from North Carolina. These voids have led to the suggestion that the eastern breeding forms were compressed along the south Atlantic Coast between South Carolina and north Florida. Post (1998) reports on the frequency of Nelson's forms from a marsh in South Carolina as 15%, 11% and 17% for *A. n. alter*, *A. n. subvirgatus*, and *A. n. nelson,* respectively. These values are comparable to the 15.5%, 14.4%, and 16.8% relative frequencies reported here (Fig. 2).

The breeding range of the Saltmarsh Sparrow is confined to the Atlantic Coast from Virginia north to the Canadian Maritimes (Greenlaw and Rising 1994, AOU 1995), and birds are believed to move south of this range for the winter season (Greenlaw and Woolfenden 2007). Both north-Atlantic (*A. c. caudacutus*) and mid-Atlantic (*A. c. diversus*) forms were well represented in Virginia from winter samples, with the north-Atlantic form accounting for a large portion of the overall sample. The majority (93.4%) of specimens of this group available to Greenlaw and Woolfenden (2007) were taken between North Carolina and Florida, with none coming from the Gulf Coast. Delineation of winter range is particularly important for these forms because both are saltmarsh obligates throughout their entire annual cycles and are considered to be of high conservation concern (Watts 1999, Dettmers and Rosenberg 2000). This is particularly true of *A. c. diversus,* which has a very restricted a)



b)

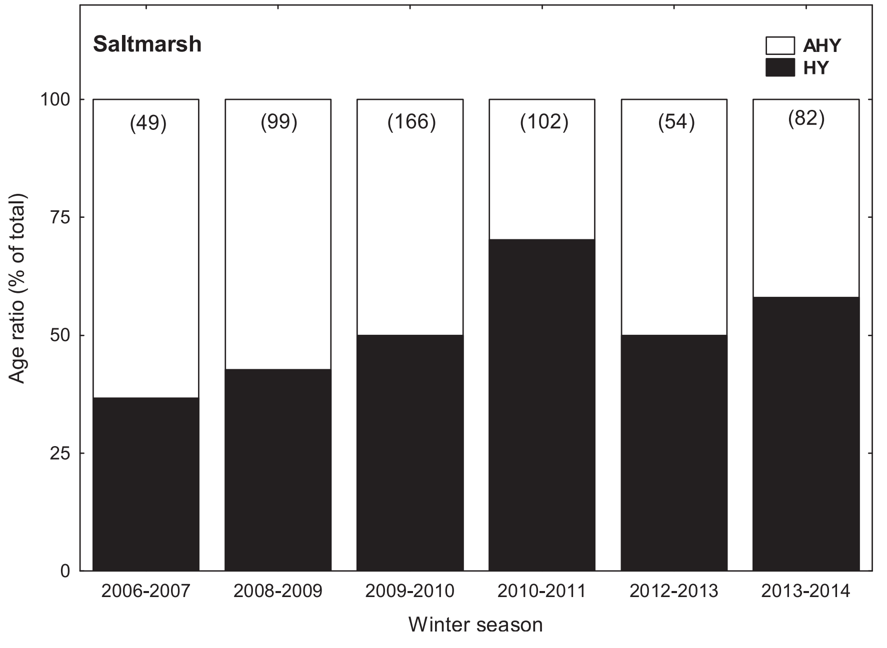


FIG. 3. Age ratios of (a) Nelson's Sparrows and (b) Saltmarsh Sparrows presented across winter seasons (2006–2014). Parenthetic values represent sample sizes. All birds were captured within tidal saltmarshes in coastal Virginia (2006–2014).

breeding range and likely a correspondingly small population.

One of the impediments to understanding connectivity on the population level within this sparrow complex has been a limitation on our ability to effectively separate subspecies. Following earlier treatments (Parkes 1952, Post 1998), the development of a dichotomous key by Greenlaw and Woolfenden (2007) has improved our ability to separate forms in the field. However, as indicated in their treatment, separation of some subspecies couplets continues to be a challenge. This is particularly true for the *A. n. nelsoni* and *A. n. alter* pairing and the *A. c. caudacutus* and *A. c. diversus* pairing, presumably reflecting their recent ancestry (Rising and Avise 1993) and continued contact (Hodgman et al. 2002, Shriver et al. 2005). More than 40% and 8% of the individuals exhibited characters of both forms for the former and latter pairings, respectively. Greenlaw and Woolfenden (2007) do not provide statistics on classification rates. The clear result of the classification problem is to increase the uncertainty for both spatial and temporal comparisons for some subspecies.

The interest in age ratios collected during the nonbreeding season for demographic monitoring has increased in recent years (e.g., Green 1999, Piersma and Lindström 2004, Robinson et al. 2005), and is proving useful in isolating the role of reproductive rates in population trends for some species (e.g., Boyd and Piersma 2001). Age class is easily determined for birds in the hand within this sparrow complex. Age ratios varied widely across years for both species. Although the direct relationship between age ratios on the winter grounds and breeding performance has not been established, ratios do provide insight into the recruitment of young into the winter population. Given the broad spatial extent of the breeding grounds and the concentration of forms within a relatively small winter range, winter monitoring may ultimately be the most efficient strategy for tracking population trends. Winter demographic monitoring would be most informative if tied to the level of subspecies.

Previous efforts (Post 1998, Greenlaw and Woolfenden 2007) have contributed a great deal to our understanding of both the subspecific composition and distribution of sharp-tailed sparrows during winter south of Virginia. However, the lack of both specimens and dedicated fieldwork north of North Carolina severely limit our understanding of occurrence within the northern reaches of the winter range. Evidence presented here confirms that both species and all five subspecies are relatively common in the coastal salt marshes of Virginia. Additional fieldwork is needed to extend our understanding of winter distribution throughout the mid-Atlantic and southern New England physiographic areas.

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