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ADAPTATIONS TO TIDAL MARSHES IN BREEDING POPULATIONS OF THE SWAMP SPARROW[1]

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Abstract. The Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) was originally described from a small number of specimens from the tidal marshes of the Nanticoke River in southeastern Maryland. Based on our quantitative analysis of a larger series of specimens, we found that Swamp Sparrows collected during the breeding season from the Chesapeake and Delaware bays (and tributaries) and near the mouth of the Hudson River are generally less rusty, have more black in the crown and nape, and have larger bills than other Swamp Sparrows. Contrary to earlier accounts, we found *M. g. nigrescens* to be migratory, arriving after the spring migration and departing before the fall migration of the inland subspecies through the tidal marshes. The location of the wintering grounds of *M. g. nigrescens* is unknown. We argue that the morphological and life history differences characterizing *M. g. nigrescens* reflect adaptation to tidal marshes. We base this hypothesis on the nature of the morphological differences, which are convergent with other tidal marsh breeding sparrows and other terrestrial vertebrates.

Key words: Melospiza georgiana; *subspecies; tidal marsh; clutch size; color analysis; adaptation; Emberizidae; salt marsh melanism.*

INTRODUCTION

Almost 40 years ago Bond and Stewart (1951) described a new subspecies of Swamp Sparrow (*Melospiza georgiana nigrescens*) on the basis of a small number of specimens collected near Vienna, Maryland. Those authors believed it to be permanently resident in tidal marshes of the Delmarva Peninsula. The existence of such a morphologically distinct population was surprising from several perspectives: Swamp Sparrows were thought to epitomize species that are ecologically and morphologically homogeneous over their entire breeding range (Miller 1956); breeding Swamp Sparrows are generally restricted to freshwater marshes (Wetherbee 1968); and Swamp Sparrows were regarded as largely, if not wholly, migratory. The Coastal Plain Swamp Sparrow (*M. g. nigrescens*) was recognized by the AOU (1957) and aspects of its natural history and distribution were briefly summarized by Wetherbee (1968). More recently Paynter (1970) synonymized *M. g. nigrescens* with *M. g. georgiana,* the subspecies that breeds throughout much of northeastern North America. Based on nine variable loci, Balaban (1988) found no statistically significant difference in allele frequencies between a putative *nigrescens* population and several populations of the nominate race.

Recent breeding bird atlas projects have focused intensive efforts towards mapping the distribution of locally breeding birds in several of the mid-Atlantic states, including Delaware, Maryland, and New Jersey. These efforts have led to the discovery of previously undocumented populations of breeding Swamp Sparrows in the tidal marshes of the Chesapeake and Delaware bays. These discoveries prompted us to reexamine several questions pertaining to Swamp Sparrow populations that breed in tidal marshes: (1) What is the known distribution of tidal marsh populations along the mid-Atlantic coast; (2) what, if any, plumage and mensural characters distinguish these populations; (3) how morphologically distinct are these populations from those of *M. g. georgiana* and *M. g. ericrypta* (the northern + western populations); and (4) are similar morphological features found in other terrestrial vertebrates occupying tidal marshes? We also examined the evidence that the Coastal Plain Swamp Sparrow is a permanent resident of Delaware and Chesapeake Bay marshes and we com-

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pared the clutch sizes of nests from tidal and freshwater populations.

METHODS

DISTRIBUTION

The known distribution of Swamp Sparrows along the tidal zone of the major eastern estuaries is based on several sources: specimen records, published and unpublished breeding bird atlas maps (Anderle and Carrol 1988; E. Blom, pers. comm.; D. Hughes, pers. comm.; D. Brauning, pers. comm.; R. West, pers. comm.; S. Ridd, pers. comm.) for New York, Maryland, New Jersey, Pennsylvania, Delaware, and Virginia, and our own observations during the summers of 1986–1989. The general distribution of Swamp Sparrows was determined from atlas project and Breeding Bird Survey data as well as historical records summarized in the AOU (1957, 1983) checklists.

SPECIMENS USED IN ANALYSIS

We measured museum specimens and mist-netted individuals collected in marshes along the Chesapeake and Delaware bays and the mouth of the Hudson River and compared these measurements with those taken from individuals collected at numerous sites within the breeding ranges of *georgiana* and *ericrypta*. Only specimens collected or measured and released between 15 May–15 September were used for the breeding season analysis. For *nigrescens* we measured 82 museum specimens and eight mist-netted individuals; an additional 11 were hand-raised at the U.S. National Zoo. The museum specimens are at the Museum of Zoology, University of Michigan ($n = 19$), U.S. Museum of Natural History ($n = 38$, including National Zoo birds), Philadelphia Academy of Natural Science ($n = 19$), and the American Museum of Natural History ($n = 9$). Feather samples were collected from mist-netted individuals and have been retained by the senior author. Most of the measured *nigrescens* (73/93) were males. Therefore, the detailed morphological analyses have been restricted to males; females have been compared for differences between *nigrescens* and a pooled sample of the other two subspecies.

The amount of time since the collection of the specimens can affect their color. Specimens of *nigrescens* were collected during three periods over the past century. One-third of the specimens (32) were collected (or measured and released) in 1987–1988, all of which were captured or collected near Chesapeake and Delaware bays. Another 28% of the specimens (27) were collected around the Chesapeake and Delaware bays during the 20 years subsequent to the discovery of the subspecies (1947–1967). The remaining one-third of the specimens (34) was collected around the turn of the century; 24 of these specimens were collected from marshes near the mouth of the Hudson River and 10 from the upper Delaware Bay.

MORPHOLOGICAL MEASUREMENTS

Specimens and netted individuals were measured using dial calipers accurate to 0.1 mm. All specimens were measured by one person (RG) to ensure consistency. We measured bill length from, and bill depth and width at, the anterior edge of the exterior nares. To quantify overall bill size, we estimated bill volume based on the formula for the volume of a cone ($1/3\pi$ L $\times$ W $\times$ D). In addition, we recorded unflattened wing chord and tarsus length. The extent of crown color was measured on breeding plumage male specimens (with typical solid crown patches—Greenberg 1988a) along the midline of the crown from the bill to the end of continuous dark pigmentation on the nape. In addition, the proportion of rust (as opposed to black) along this cross section was calculated by dividing the length of the rusty patch by the total length of continuous black or rusty pigment.

To quantify plumage coloration, we compared specimens to a Munsell Soil Color Chart (Wood and Wood 1972, Munsell 1975, Atkinson and Ralph 1980), which provides three notations for the appropriate color chip: hue (departure from red or yellow), value (lightness ranging from white, 10, to black, 0), and chroma (departure from gray, which has a value of 0). Because all specimens were matched to the 10 Yellow-Red (YR) hue series we omit this variable from further discussion; we present pigment data as value/chroma. We measured back coloration by estimating the color of the feathers closest to the rump that have black feather bases. In particular we matched the portion of the feather closest to the black base to minimize the effect of feather wear (see below). In addition, the color of brightest portion of the flanks was measured and the presence of buff on the auriculars was recorded as present or absent.

PLUMAGE WEAR

Swamp Sparrows complete a molt in the autumn (late August–October; Dwight 1900, pers. observ.) replacing most of the contour feathers in juveniles and, additionally, the flight and tail feathers in adults. A prenuptial molt involves primarily the head, nape, and throat feathers (pers. observ. of captive Swamp Sparrows). Therefore, summer specimens have relatively worn body, wing, and tail feathers, yet have relatively fresh plumage over the head region. We have attempted to remove the potential biases in comparing plumages found in worn individuals by examining feathers and locations on feathers least subject to wear. The best way to eliminate the problem for contour feathers is to collect specimens in fresh plumage during September and October. However, *nigrescens* becomes very difficult to locate immediately after the breeding season. Fortunately, we were able to obtain several specimens of *nigrescens* from this period in addition to examining the first basic plumage of the 11 birds raised in captivity.

CLUTCH SIZE

Data on clutch size for *georgiana* were taken from completed clutches reported on nest record cards from Cornell Laboratory of Ornithology and for *nigrescens* from both nest record card data and our personal field notes.

RESULTS

DISTRIBUTION

The distribution of Swamp Sparrows in the mid-Atlantic region is shown in Figure 1. Coastal and montane populations are separated by nearly 120 km in Maryland, except for a few small breeding populations in the piedmont; this gap continues into southeastern Pennsylvania. The presence of such a hiatus between montane and coastal populations is also indicated by the breeding density map generated from BBS data (Fig. 2). Inland and coastal populations are conterminously distributed in central and northern New Jersey and New York. We were unable to find specimen material from across this zone of contact. However, we did capture and measure two males from a small population located in the piedmont of Carroll County, Maryland.

Swamp Sparrows are currently distributed in nearly continuous bands along both shores of the brackish portions of Delaware Bay and lower portions of the Delaware River. In these brackish marshes Seaside Sparrows (*Ammodramus maritimus*) are abundant in stands of *Juncus* and *Spartina* while Swamp Sparrows are more numerous in the shrub zone (*Iva fructescens* and *Baccharis hamifolia*). The shrub-*Spartina patens* association supports the highest densities of breeding Swamp Sparrows with territories ranging between 0.04–0.5 ha; such high and variable densities are comparable to those found in inland populations of Swamp Sparrows (Reinert and Golet 1978, Greenberg 1988a). Swamp Sparrows are not restricted to this association, and we found sizable populations in *Phragmites* and *Lythrum* under tidal influence.

Breeding Swamp Sparrows are much more localized along the Chesapeake than the Delaware Bay. There are no confirmed nesting records for localities on the Delmarva Peninsula south or east of the Nanticoke River drainage. On the western shore of Chesapeake Bay, Swamp Sparrows have been only reported breeding south to Fishing Creek near Chesapeake Beach, Calvert County. We know of no valid breeding season reports for the coastal plain of Virginia (S. Ridd, pers. comm.). Most Chesapeake Bay populations, including those at Eastern Neck Island, Edgewater, Sandy Point, Fishing Creek, Patapsco River, and Vienna, consisted of only a few pairs. The largest population that we could locate on the Chesapeake Bay was in Black Marsh, Baltimore County, where 50–70 singing males were present during the breeding seasons of 1988 and 1989.

The distribution outlined here represents a major range extension since Stewart and Robbins (1957). Whether this results from a true range expansion or better ornithological coverage is unclear. The patchy distribution and late arrival and early departure of this subspecies (see below) may contribute to it being overlooked. One piece of evidence that supports a range expansion is the recent colonization of tidal habitats by Swamp Sparrows on Cape Cod (Blair Nikula, pers. comm.).

MORPHOLOGICAL CHARACTERISTICS

Univariate analysis. Table 1 presents measurements for five samples of Swamp Sparrow specimens: (1) Delaware Bay, (2) Chesapeake Bay, (3) Hudson River-coastal New Jersey, (4) inland West Virginia, Pennsylvania, New York, and New England (e.g., *georgiana*), and (5) the northern

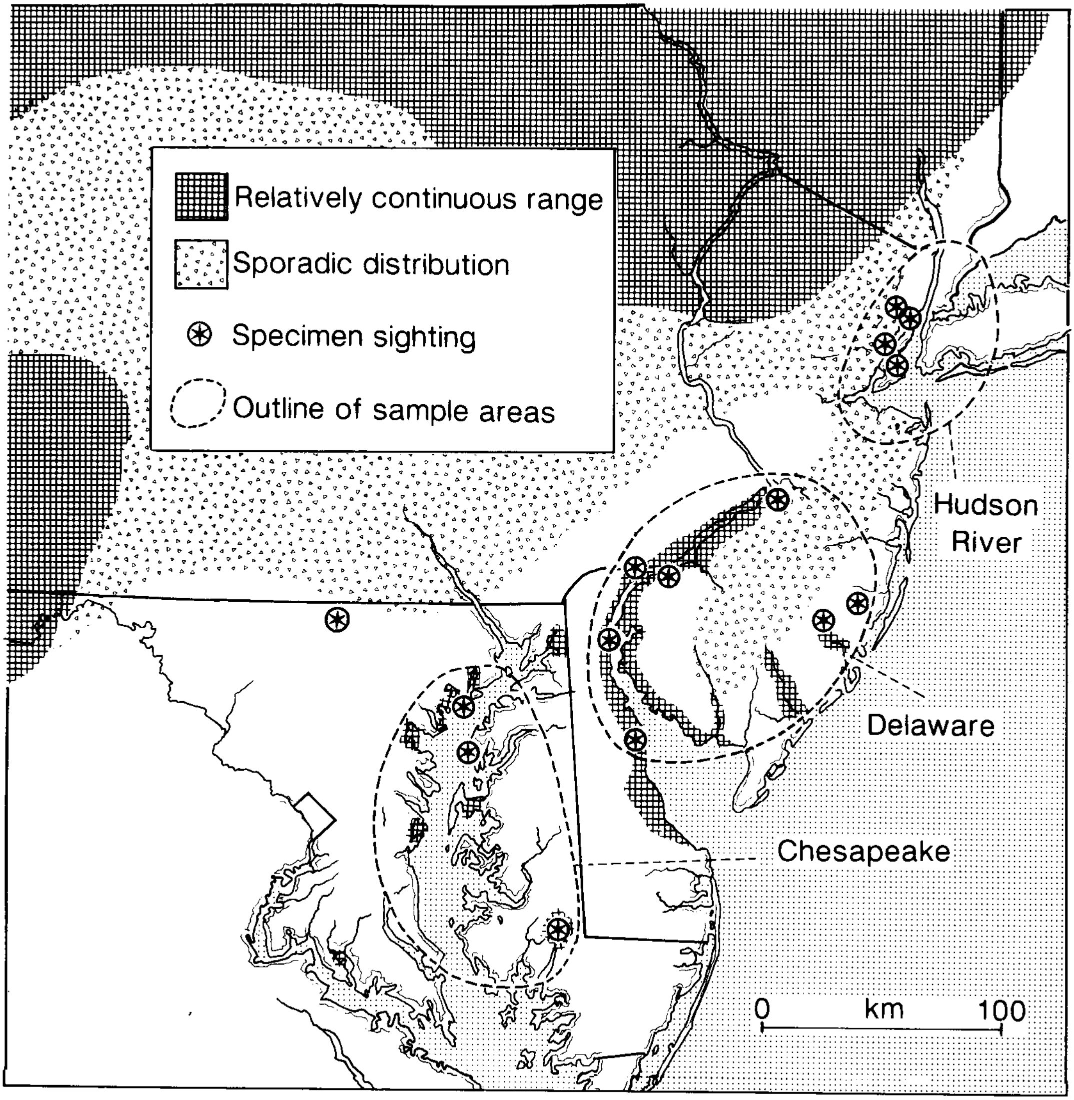

FIGURE 1. A map of the distribution of Swamp Sparrows along the mid-Atlantic coast with dots representing sites from which specimens were collected or birds netted and measured.

Great Plains to Newfoundland-Nova Scotia (*ericrypta*). The sampling areas and specimen locations for the first three populations are indicated in Figure 1. Univariate analyses (one-way ANOVA) detected no significant differences in mensural characteristics between the Delaware, Chesapeake, Hudson populations, and the only difference between *ericrypta* and *georgiana* populations was in the value (lightness) of back color (t-test, $P < 0.05$). Therefore we pooled the *nigrescens* populations and the *georgiana* and *ericrypta* samples in further analyses.

Three features distinguished Coastal Plain Swamp Sparrows from interior populations: less rust and more black in crown and nape ($P < 0.001$), the lack of rust in back and sides (lower values for chroma, $P < 0.001$), and the overall larger size of the bill ($P < 0.001$). A small, but significant difference in tarsus length ($P < 0.05$) and no difference in wing chord reflects the fact that bill size is relatively greater in the Coastal Plain Swamp Sparrow. A bivariate scatter plot of bill volume vs. tarsus length displays an almost complete lack of overlap in bill volumes between *nigrescens* and interior Swamp Sparrow specimens but considerable overlap in tarsus length (Fig. 3).

Female *nigrescens* also differ significantly ($P < 0.001$) from the inland subspecies in having larger bills and less rusty coloration on the back and sides (Table 1).

Degree of morphological overlap based on DFA. A Discriminant Function Analysis (DFA, SAS 1985) based on bill volume, crown color, and back color chroma (tarsus length and wing chord were entered but did not contribute significantly to the function) distinguished 117 out of 120 specimens correctly in an a posteriori classification of the *nigrescens* vs. interior specimens. The two misidentified *nigrescens* were from central and northern New Jersey; all Delaware and Chesapeake bay birds were correctly classified.

A similar DFA using *georgiana* and *ericrypta* specimens was not significant and was only able to correctly classify 75% of the specimens. Back color value was the only contributing variable to the function. Each of the three measures that contributed to the *georgiana-ericrypta* vs. *nigrescens* discrimination could individually be used to separate 92–97% of the specimens. For example, a bivariate scatter diagram of bill volume on percentage rust in crown shows almost complete separation between the coastal and interior forms (Fig. 4). This difference is graphically portrayed in sketches of the heads of typical specimens of interior and coastal Swamp Sparrows (Fig. 5). Specimens showing 70% or less rust along the midline of the head, bill volumes of more than 195 mm^3, and back colors of 5/3–5/4 or 4/3–4/4 have over a 98% probability of being *nigrescens*. Based on the two fresh-plumaged wild-caught and the 11 hand-raised *nigrescens* (see below) we believe that back color differences are even more pronounced in winter birds.

We examined two males netted at the sites in the Maryland Piedmont (Carroll County) between the coastal and interior breeding populations. Both males had a low proportion of rust in the crown with values well within a range of typical *nigrescens* (38 and 59%), one male had a large *nigrescens* bill (235 mm^3) and the other had a smaller bill (185 mm^3) typical of interior forms.

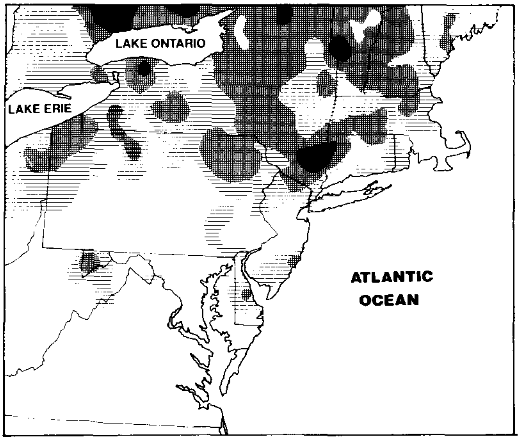

FIGURE 2. A map of the distribution of Swamp Sparrows based on Breeding Bird Survey data. Regions with similar shading represent areas of similar average density (Surfer: Golden Software). White areas have densities less than 0.1 bird/route, light gray = 0.1–1.0, medium gray = 1.1–4.0, and black = 4.1+. The plotting algorithm is based on the starting point of 40-km routes. Therefore the distribution away from the coast along Chesapeake and Delaware bays is exaggerated.

Both specimens had rusty backs and sides characteristic of interior forms.

MORPHOLOGY OF CAPTIVE-REARED COASTAL PLAINS SWAMP SPARROWS

Eleven nestlings (4–6 days old) of five broods of Swamp Sparrows were collected from Black Marsh, Baltimore County, Maryland and reared in aviaries at the National Zoological Park, Washington, DC, and fed a standard laboratory meat and cereal mash. After postjuvenal molt (October) these individuals were morphologically similar to adult *nigrescens* collected in the wild (Table 1). The back and side colors showed the same tendency towards gray neutral brown as the adults in more worn plumage (4/4–5/4). Immature *georgiana* collected at the same time of year all showed back colors of 4/7 to 5/7, which were much rustier shades than found in the hand-reared *nigrescens*. Furthermore, the five hand-raised male *nigrescens* that completed their first prenuptial molt had crown rust values of 27–52%, consistent with adult male *nigrescens* collected in the wild.

PLUMAGE WEAR AND SPECIMEN AGE

Fresh fall plumage *nigrescens* differ from worn summer specimens by having darker back and

TABLE 1. Measurements for different samples of Swamp Sparrows.

Sample	Sex	n	Crown % rust $\bar{x}$ (SE)	Back Value $\bar{x}$ (SE)	Back Chroma $\bar{x}$ (SE)	Sides Value $\bar{x}$ (SE)	Sides Chroma $\bar{x}$ (SE)
ericrypta	M	26	82.9 (1.2)	4.7 (0.5)	6.1 (0.9)	6.0 (0.2)	6.0 (0.5)
georgiana	M	28	83.5 (1.5)	4.3 (0.2)	6.2 (0.6)	5.9 (0.1)	6.2 (0.8)
nigrescens:							
Chesapeake Bay	M	14	50.6 (3.1)	4.9 (0.2)	3.8 (0.2)	6.8 (0.4)	3.6 (0.6)
Delaware Bay	M	29	47.8 (3.8)	5.0 (0)	3.8 (0.4)	6.6 (0.2)	3.3 (0.5)
New Jersey	M	23	51.6 (4.0)	4.9 (0.3)	3.8 (0.5)	6.7 (0.5)	3.8 (0.6)
Laboratory reared[a]	M	7	–	4.1 (0.1)	4.0 (0)	4.9 (0.1)	4.0 (0)
ericrypta-georgiana	F	22	–	4.5 (0.3)	6.1 (0.5)	5.7 (0.1)	6.1 (0.4)
nigrescens[b]	F	20	–	4.9 (0.1)	4.0 (0.2)	6.8 (0.1)	3.7 (0.1)

[a] Laboratory-reared category includes data on the seven males; data from the four females are lumped with the data from female museum skins.
[b] Data for color characteristics do not include measurements from laboratory-reared specimens. This is based on the known heterogeneity between fresh and worn plumaged males. The female specimens all had color value and chroma of 4/4 for back and 5/4 for sides.

flank coloration as indicated by lower color value. This is particularly true of the hand-raised sparrows, which had a back coloration of 4/4 (as opposed to 5/4 for summer) and side coloration of 5/4 (vs. 7/4 for summer). The two fresh specimens collected in the field had conspicuously darker sides as well, but were otherwise similar to summer specimens in their lack of rust. In contrast, fall *georgiana* are darker and rustier having higher color value and chroma than summer specimens: nine of 10 specimens had back coloration of 6/7 vs. 4/6 for summer specimens (one specimen was 7/5).

We also examined the effect of specimen age on its coloration. We found no significant difference in coloration between the 10 Delaware Bay specimens collected approximately 90 years ago, the 11 collected approximately 25 years ago, and the 10 taken during 1987–1988.

CLUTCH SIZE

The Coastal Plains Swamp Sparrow has an unusually small clutch for *Melospiza*; 34 completed clutches located during late May and June at Black Marsh and Delaware Bay localities averaged 3.45 eggs/clutch (range = 2–4). During the same part of the breeding season, interior populations of Swamp Sparrows in New York and Pennsylvania had an average clutch size of 4.6 (3–6, $n = 52$) with clutches of five and six comprising 40% of the nests located. The difference in clutch size between the two samples is highly significant (Mann-Whitney U-test, $P < 0.001$).

MIGRATORY STATUS

Melospiza g. nigrescens has been considered to be permanently resident (Bond and Stewart 1951, AOU 1957, Wetherbee 1968). This was apparently based on November specimens collected at the originally discovered breeding site at Vienna, Maryland. We examined these specimens and found them to be typical of *georgiana* with bill length of 7.9 mm (SE = 0.4) and depth of 5.1 mm (SE = 0.2) and back color of 4/7–6/7 for all individuals. In addition, several other specimens discussed in the literature (Ocean City, Maryland; Allentown, North Carolina; and Billy Williams Delta, Arizona; AOU 1957, Wetherbee 1968) also represent *georgiana* or *ericrypta.*

We believe that most individuals can be correctly identified to subspecies at close range through binoculars. Based on this, we censused Black Marsh on a weekly basis from 25 April to 6 June 1986 to determine the time of occupancy of this known breeding site for *nigrescens.* We found an abundance (15–25 males) of *georgiana* or *ericrypta* (inland Swamp Sparrows) during 20 April–15 May. On 15 May, these inland Swamp Sparrows were aggressively defending small territories in the same areas that would later be occupied by *nigrescens.* Several males were regularly performing flight songs, a display that usually occurs in the presence of females without completed clutches during the breeding season (pers. observ.). We observed only two *nigrescens* in this locality on 15 May, but found them to be common on 22 May when inland Swamp Sparrows were absent. Backdating the observations of fledging and clutch completion, we determined that the earliest nests were initiated between 20–30 May which is consistent with a mid-May arrival date. During the winter at known breeding sites (Edgewater, Eastern Neck Island) we observed only inland Swamp Sparrows. Ob-

TABLE 1. Extended.

Buff auriculars % individuals	Bill Length (mm) $\bar{x}$ (SE)	Bill Depth (mm) $\bar{x}$ (SE)	Bill Width (mm) $\bar{x}$ (SE)	Bill Volume (mm³) $\bar{x}$ (SE)	Wing (mm) $\bar{x}$ (SE)	Tarsus (mm) $\bar{x}$ (SE)
77	8.2 (0.07)	5.1 (0.05)	4.0 (0.01)	176 (4)	61.2 (0.3)	20.7 (0.3)
89	8.2 (0.02)	5.2 (0.02)	4.0 (0.05)	180 (3)	61.1 (0.3)	21.2 (0.8)
0	8.8 (0.05)	5.9 (0.05)	4.4 (0.06)	237 (6)	60.6 (0.7)	21.6 (0.2)
16	8.7 (0.07)	5.7 (0.04)	4.4 (0.09)	232 (5)	59.8 (0.4)	21.3 (0.1)
13	8.6 (0.07)	5.8 (0.04)	4.4 (0.06)	229 (7)	61.0 (0.3)	21.1 (0.2)
0	8.8 (0.04)	5.8 (0.07)	4.7 (0.07)	251 (5)	59.8 (0.7)	20.9 (0.2)
96	8.1 (0.07)	5.1 (0.05)	4.1 (0.05)	178 (3)	58.5 (0.3)	20.4 (0.2)
0	8.6 (0.07)	5.6 (0.08)	4.4 (0.04)	228 (5)	57.2 (0.3)	20.7 (0.2)

servation of breeding sites in the autumn by ourselves and Mark Robbins (pers. comm.) suggest that *nigrescens* is largely gone by September and October.

DISCUSSION

DISTRIBUTION

Swamp Sparrows are locally common breeders in marshes around the major estuaries of the mid-Atlantic Coast. These populations are largely restricted to brackish marshes under tidal influence. However, birds observed in bogs in the pine barrens of New Jersey (including three collected) were typical *nigrescens* in all measurements. The paucity of records from the lower portions of Delaware and Chesapeake bays, except those found along brackish tributaries, suggests that Swamp Sparrows do not breed in tidal marshes of high salinity. Within the Chesapeake Bay there are vast areas of shrub-*Spartina* marshes along the Delmarva Peninsula shore south of the Choptank River where Swamp Sparrows are apparently absent as a breeding species.

Away from the coast, the mid-Atlantic region Swamp Sparrows breed primarily in montane shrub-sedge bogs. There are only a few scattered piedmont and no interior coastal plain records for Maryland and southwestern Pennsylvania. Thus, the Swamp Sparrow populations in the fresh and brackish tidal marshes are largely disjunct from interior populations in the southern portion of the species' range. However, tidal and interior populations probably are not disjunct in New Jersey and New York. The location and nature of the contact zone has not been determined.

Inland and coastal populations show marked morphological differences. This occurs despite the potential for genetic swamping from potential contact between inland and coastal populations in the North, the possibility of occasional breeding away from montane bogs in the South, and the potential of mating between migrating inland Swamp Sparrows that occur in tidal marshes for a period narrowly overlapping the onset of breeding of the Coastal Plain Swamp Sparrows. The consistent morphological and life history differences in the face of potential gene flow suggest a prima facie case for a distinct selective pressure on Swamp Sparrows breeding in tidal marshes. This would be further supported by the apparent lack of divergence reported for allozymes by Balaban (1988). However, the samples were collected during 10–12 May 1984 without supporting morphological material (Balaban, pers. comm.). Given the territorial behavior characteristic of migrating Swamp Sparrows (pers. observ.), it is possible that at least some of this material represents migrants from other subspecies.

ADAPTATIONS

The hypothesis that geographical differences result from adaptation to local conditions requires critical testing. One approach is to study in detail the genetic structure, pattern of morphological divergence, and environmental correlates within a single species (Zink 1986). However, an alternative strategy for testing adaptive hypotheses is to search for convergent responses of unrelated species to similar environmental challenges. We will now argue that morphological differences that characterize *nigrescens* from other Swamp Sparrows are similar to those found in other tidal marsh dwelling sparrows (as well as other terrestrial vertebrates) and comprise convergent adaptations to the tidal environment.

Coastal Plain Swamp Sparrows differ from all other breeding populations of Swamp Sparrows

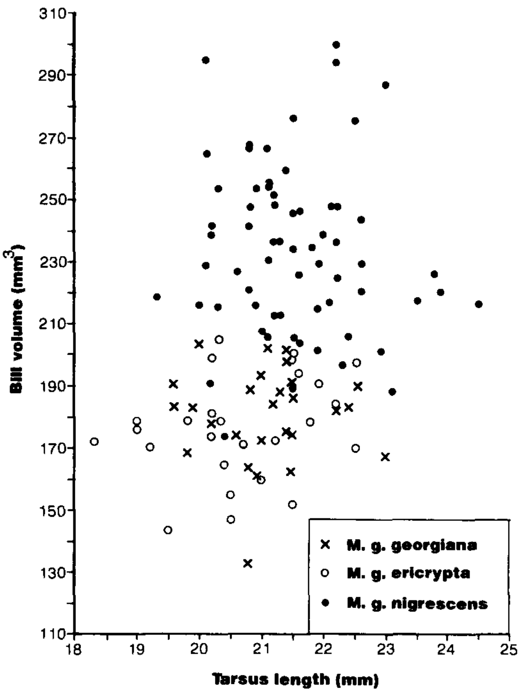

FIGURE 3. Scatter plot of tarsus length vs. bill volume in male *Melospiza georgiana georgiana, M. g. ericrypta,* and *M. g. nigrescens.*

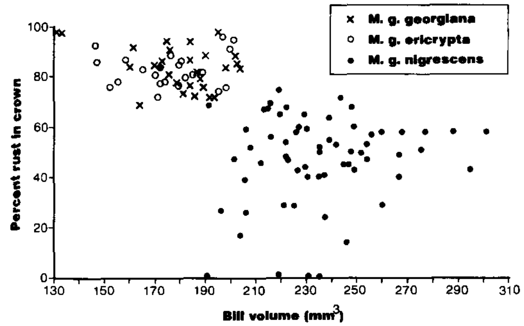

FIGURE 5. Scatter plot of Swamp Sparrow bill volume vs. percentage rust in crown.

in three major, and probably independent, characteristics: they have larger bills, their rusty browns are replaced by gray-browns, and they have a greater amount of black in their plumage, particularly around the crown and nape. None of these characters show significant within-population cross-correlations. The occurrence of the same plumage and bill size differences in laboratory-reared individuals implies a genetic basis for this geographic variation (Beebe 1907, James 1982, Zink and Remsen 1986).

Bill size. A number of taxa of emberizine sparrows that inhabit estuarine marshes have relatively larger bills than relatives in freshwater marshes (Murray 1969). Seaside Sparrows have distinctly larger bills than their congeners (Murray 1969). The salt-marsh breeding populations of Sharp-tailed Sparrow (*A. c. caudacutus* and *A. c. subvirgatus*) have larger bills than does the interior *A. c. nelsoni* subspecies (Murray 1969). The Suisun Bay subspecies of Song Sparrow (*Melospiza melodia maxillaris*) has the largest relative bill size of any Song Sparrow, with a full 40% greater bill depth than the closest interior subspecies (Marshall 1948). Finally, the subspe-

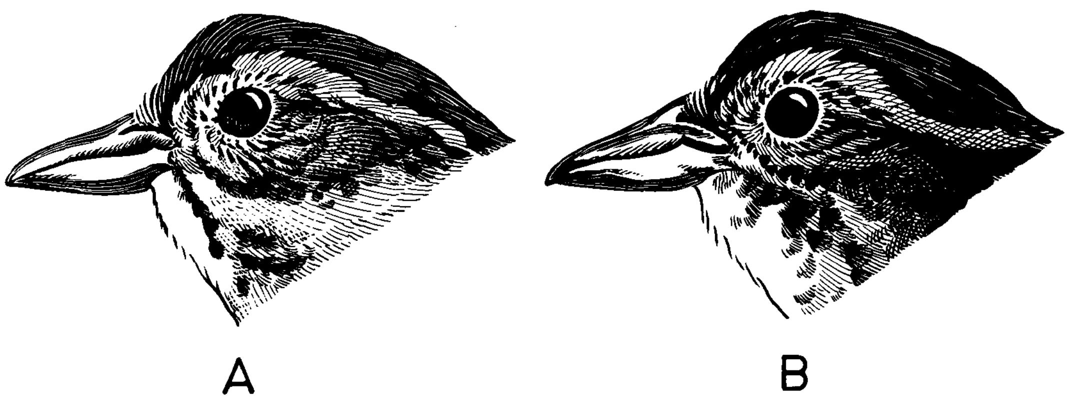

FIGURE 4. Line drawings of the heads of typical adult male (A) *Melospiza georgiana georgiana* and (B) *M. g. nigrescens.*

cies of Savannah Sparrows (*Passerculus sandwichensis*) most restricted to tidal marshes (*rostratus* subspecies group and *beldingi*) are characterized by relatively massive bills compared to other subspecies (Ridgeway 1901). Although not all salt-marsh populations or subspecies show such differentiation, we know of no populations in which the salt-marsh form has a relatively smaller bill than the most closely related inland forms. The functional significance of the larger bill size, however, is not known; it is likely that sparrows that live in estuarine habitats forage extensively on nonarthropod invertebrates in tidal mud.

Reduction of rust in plumage. The reduction of rust in the overall coloration of salt-marsh sparrows is also common. Seaside Sparrows are much less rusty than other species of *Ammodramus*. The general dorsal coloration of Coastal Plain Swamp Sparrows is quite similar to that of the Seaside Sparrow. The dorsal coloration of the Atlantic Coast Sharp-tailed Sparrow is also much less rusty than the interior subspecies (pers. observ.). The three salt-marsh subspecies of Song Sparrow that breed around San Francisco Bay are either grayer or darker than the local upland subspecies, but all three are distinctly less rusty (Grinnell 1909, Marshall 1948). Similarly, the weakly marked *M. melodia atlantica* of coastal marshes along the eastern seaboard is characterized as grayer with dark streakings and reduced rust when compared with eastern Song Sparrows (*M. m. melodia,* Nolan 1968). The four races of Marsh Wrens (*Cistothorus palustris*) found in tidal marshes of the Atlantic Coast are substantially less rusty than inland populations, either by being grayer, blacker, or both (Phillips 1986). In addition, the King (*Rallus elegans*) and Clapper (*R. longirostris*) rails provide an example of a pair of closely related terrestrial bird species where the salt-marsh form is grayer than the rusty interior form.

Melanism. The tendency towards dark coloration on the dorsal surface is also characteristic of several forms of salt-marsh sparrow including the mid-Atlantic subspecies of Sharp-tailed Sparrow (*Ammodramus caudacutus caudacutus*), various populations of Seaside Sparrow, particularly *A. m. nigrescens,* and the Suisun Bay Song Sparrow (*M. m. maxillaris*). We know of no case where a well-marked tidal marsh sparrow is distinctly paler than its closest relatives. As noted in the previous section, salt-marsh subspecies of Marsh Wren are frequently darker than inland races (Phillips 1986). Grinnell (1913) first noted the tendency for terrestrial vertebrates in tidal marshes to be darker than conspecifics in upland or freshwater habitats. He found that all 13 subspecifically distinct mammals and birds in the Suisun Marshes of upper San Francisco Bay were darker than their closest relatives. Grinnell (1913) and Von Bloeker (1932) both noted that whereas tidal estuary forms are usually darker than their closest relatives, the darkening is most pronounced in the least saline marshes. For example, Suisun Bay, near the mouth of the Sacramento River, supports more examples of salt-marsh melanism that does lower San Francisco Bay. Based on this observation, Von Bloeker suggested that salt-marsh melanism results not from salinity but from selection for background matching of the gray-black muds characteristic of tidal estuaries. It is therefore interesting that among small mammals salt-marsh melanism is found most commonly in those because they are often active during the day, e.g., *Sorex* spp. and *Microtus* spp. These species probably share the same threat from diurnal predators with largely visible hunting tactics that face terrestrial song birds. Melanistic forms of *Sorex* and *Microtus* that are endemic to salt and brackish marshes occur in a number of disjunct localities including San Francisco-Suisun Bay (Grinnell 1913, Rudd 1955, Thaeler 1961), Southern California (Von Bloeker 1932), Puget Sound (Jackson 1928), and coastal Florida (Wood et al. 1982). The small mammal fauna of the tidal marshes of the Delaware Bay estuary also includes distinct melanistic forms of *Sorex cinereus* and *Microtus pennsylvanicus* (Green 1932, Hall and Kelson 1959).

Based on the overall occurrence of grayer or darker dorsal coloration in tidal marsh vertebrates we suggest that background matching is a likely explanation for the plumage differences found between *nigrescens* and *georgiana.* Coastal Plain Swamp Sparrows were commonly observed foraging at the edge of tidal sloughs and mudflats where background colors tend towards grays and black (pers. observ.).

LIFE HISTORY

Clutch size. Because most of the data from clutches of the nominate race were taken in Pennsylvania and New York, it appears unlikely that the one egg difference in clutch size is simply a reflection of an overall increase in clutch size with latitude found in many species of birds (Lack 1968). It is possible that the reduction results from the reduced seasonality of maritime environments which reduce the resources available for reproduction (Cody 1968). Alternatively there may be an increase in the stochastic risk of total nest failure by flooding due to the combined effects of onshore winds, high tides, and high river flow after major storms. If nesting efforts represent a major energy drain for a female sparrow, then reduced clutch size might allow for the production of more nesting attempts. A similar argument has been developed for small clutch size in tropical birds (Foster 1974). To test these hypotheses, it would be necessary to study the pattern and abundance of food availability in freshwater vs. tidal marshes, as well as the probability of nest loss due to flooding. The generality of reduced clutch size in tidal marsh forms also needs further study. The smaller clutch size found in *M. g. nigrescens* parallels that found in the salt-marsh subspecies of Song Sparrow (Johnston 1956a, 1956b).

Migratory status. The late arrival and breeding of Coastal Plain Swamp Sparrows at Black Marsh are noteworthy for two reasons. First, Swamp Sparrows of other subspecies were present at this site throughout the winter and were common during April and early May; therefore resources are present to support adult Swamp Sparrows at any time outside the breeding season. Second, we have observed color-marked Swamp Sparrows on territory in northwestern Pennsylvania (an area with considerably harsher winters) in mid-April. In addition, Reinert and Golet (1978) reported territorial establishment began in mid-April for a peat bog in Rhode Island. This suggests that Coastal Plain Swamp Sparrows may actually arrive on the breeding grounds several weeks after more inland populations.

One possible explanation for the late arrival of the Coastal Plain Swamp Sparrow is based on susceptibility of Swamp Sparrow nests to flooding. Floods represent a major hazard for all nesting Swamp Sparrows (Wetherbee 1968, Greenberg 1988b). Floods are usually more common in April and May than later in the spring and summer and therefore may select for late breeding in Swamp Sparrows (Greenberg 1988b). As in other Swamp Sparrow populations, the Coastal Plain Swamp Sparrow places its nests in dense grass at the base of shrubs (88% of 34 nests were so placed and all were under 1 m from the ground) and nest placement farther above the flood line would probably make their nests conspicuous. For flooding to select for later breeding in coastal vs. inland populations of Swamp Sparrow, the threat of flooding must be greater later in the spring at the coastal sites. The timing and frequency of marsh flooding and its relation to nesting season in sparrows deserves further study. Other salt-marsh-nesting sparrows, such as Seaside and Sharp-tailed sparrows, also nest relatively late and this too has been attributed to the threat of flooding (M. MacDonald, pers. comm.). The distinct breeding season of the San Francisco Bay salt-marsh Song Sparrows also seems shaped by the threat of spring tides (Johnston 1956a, 1956b). Interestingly, the Salt Marsh Song Sparrow begins nesting well ahead of upland populations so that the first breeding effort can be completed before spring flooding. Presumably this option is not available to birds occupying the less climatically benign habitats along the mid-Atlantic coast.

Late breeding to avoid flooding does not explain why Coastal Plain Swamp Sparrows do not arrive on the breeding grounds until the bulk of the other Swamp Sparrows have left. And, it certainly does not explain the early exodus from breeding sites in the fall, well ahead of the arrival of migrants from the north. Such a pattern of late arrival is unusual for migratory birds in which local breeders usually arrive on territory before the bulk of the more northern nesting migrants pass through (Alerstam and Hogstedt 1980). The sharp turnover from one subspecies to another presents an interesting pattern that needs further confirmation. However, breeding season tenure may be determined by the point at which increased fitness due to superior survivorship on the winter range no longer exceeds the reproductive advantages of breeding grounds occupancy. Therefore, in order to understand the short breeding season, it may be necessary to discover and characterize the subspecies' wintering grounds.

CONCLUSIONS

The Coastal Plain Swamp Sparrow is a well-marked subspecies that breeds primarily in the tidal fresh and brackish marshes associated with major river systems of the mid-Atlantic Coast of North America. It is virtually nonoverlapping with other subspecies of Swamp Sparrows in three major aspects of its external morphology; it has a relatively larger bill, grayer plumage, and more black on the head and nape. It also has a distinctive life history characterized by having a short period of breeding grounds occupancy and a reduced clutch size when compared with inland populations. The location of the wintering grounds of the Coastal Plain Swamp Sparrow remains on ornithological mystery.

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