BEHAVIORAL AND MORPHOLOGICAL DIVERSIFICATION IN SHARP-TAILED SPARROWS (*AMMODRAMUS CAUDACUTUS*) OF THE ATLANTIC COAST

JON S. GREENLAW

Department of Biology, Long Island University, Brookville, New York 11548, USA

ABSTRACT.—Among Sharp-tailed Sparrows (*Ammodramus caudacutus*), a northern group of populations can be distinguished from a southern group. The northern group, comprising the races *nelsoni, alterus,* and *subvirgatus,* occurs in three disjunct populations distributed from the continental interior to the north Atlantic coast. The southern group, including the nominate race and *diversus,* is found only along the mid-Atlantic coast south to northern Virginia. The two groups, which are in limited contact in southwestern Maine, are defined by uniquely derived behavioral (song-related) characteristics, as well as by differences in morphology (bill size and ventral streakiness) and habitat. In the southern group, song-related behaviors are divergent compared to such behaviors in congeneric relatives. Instead of loud primary songs uttered repetitively in discrete bouts (the usual pattern in *Ammodramus* and other emberizines, and in males of the northern group within the species), southern males sing a continuous series of variable, muted phrases and sharp notes in a single display called "complex whisper song." They also have largely "suppressed" a typical emberizine flight song and display that are frequently employed by northern males. Males in both groups are nonterritorial and lack male parental care. A morphological reanalysis of two populations (Scarborough Marsh and Popham Beach) in the contact zone in Maine suggests that there is gene flow between the two groups, but that it is limited geographically, and perhaps in intensity. Phenotypic males of both groups, each exhibiting their characteristic song-related behaviors, co-occur at Popham Beach, with no evidence of behavioral intermediacy in the population. Since the two groups are distinct phylogenetic species, I suggest that the Maine contact is a zone of secondary intergradation. A cladistic hypothesis of relationship in the complex, together with geographic considerations, suggests a history of vicariance in which widely distributed interior-to-coastal populations were split apart during a Pleistocene glaciation. The northern group evidently evolved as an isolate in freshwater wetlands south of the glacial ice front in the interior of the continent, while the southern group differentiated in salt marshes along the Atlantic coast. Most recently, the interior isolate dispersed eastward during early Holocene time, perhaps via a James Bay/Gulf of St. Lawrence route to the Atlantic coast, where it met the northward-advancing southern group in Maine. I recommend that the two groups be treated taxonomically as allospecies of a superspecies. *Received 21 October 1991, accepted 6 September 1992.*

THE NORTHERLY distribution of the Sharp-tailed Sparrow (*Ammodramus caudacutus*) in North America consists of three disjunct populations that extend from the continental interior to the Atlantic coast (Murray 1969, AOU 1983). Interior birds (*A. c. nelsoni*) inhabit freshwater marshes and meadows of the northern Great Plains. This population is separated by over 900 km (Peters 1942) of unsuitable habitat in the Canadian Shield uplands from a second population (*A. c. alterus*) in the coastal marshes of James Bay and lower Hudson Bay. Populations along the Atlantic coast in turn are isolated from *alterus* by about 600 km of forested wilderness and low hills. They occupy grassy estuarine wetlands and tidal marshes from the

Gulf of St. Lawrence to northern Virginia. The Atlantic coastal birds are geographically variable, with pale, indistinctly patterned birds occurring to the north (*A. c. subvirgatus*), and dark, sharply patterned birds to the south (*A. c. caudacutus* and *A. c. diversus*). These differentiates are in limited contact in southwestern Maine (Norton 1897, Montagna 1940, 1942).

This species exhibits a highly unusual social system that features nonterritoriality and a bondless form of polygyny in which males provide no parental care (Woolfenden 1956, Greenlaw and Post unpubl. manuscript). Present evidence supports the view that these are specieswide traits (Murray 1969, Greenlaw and Post unpubl. manuscript). However, recent field

work indicated that other behavioral characteristics, notably songs and the manner of singing, distinguished the northern birds as a group (*nelsoni, alterus,* and *subvirgatus,* hereafter the "northern group") from southern birds ("southern group") along the Atlantic coast. These observations impelled me to explore song structure and vocal behavior of sparrows in the coastal marsh at Popham Beach, Maine, where northern and southern populations are in contact and morphological intermediates are thought to occur (Montagna 1940).

In this paper, I characterize the marked differences between the songs and song-related behavior of northern and southern male sparrows. Also, I consider the possibility that the limited junction between these populations in southwestern Maine represents a narrow secondary contact between two vicariates, rather than a zone of primary intergradation as currently implied (Beecher 1955). The resolution of this problem can influence how we think about the evolution of Sharp-tailed Sparrows with respect to their historical biogeography. Also, I examine patterns of variation in plumage color and bill size across the contact in Maine, as an independent assay of diversification, using samples of birds collected at Popham Beach by Montagna (1940) and at Scarborough Marsh by Norton (1897). Finally, I develop biogeographic and phylogenetic models that may account for the behavioral, morphological, and geographic patterns evident in the species.

METHODS

Field methods.—The social behavior of color-banded sparrows was studied on salt marshes in southwestern Long Island, New York, from 1977 to 1985, and on the Tantramar marshes near Sackville, New Brunswick, in 1977 and 1978. All captured birds were routinely measured and weighed. Observations spanning a total of 10 field days were made on unmarked birds at Popham Beach State Park, Town of Phippsburg, Sagadahoc County, Maine, in mid-June 1983 and late June 1989, and at Scarborough Marsh near Scarborough, Cumberland County, Maine, in mid-June 1983. Recordings of vocalizations were made using a Uher-4000 Report tape recorder and Dan Gibson E.P.M. electronic parabolic microphone.

Song vocalizations.—Samples of primary songs and flight songs were recorded in populations from New York, southwestern Maine, and Canadian Maritime provinces (New Brunswick, Nova Scotia). In addition, tapes of primary songs of birds representing interior plains, James Bay, and southern New Jersey popu-

lations were supplied by sound libraries at the Florida Museum of Natural History (FMNH) and Cornell Laboratory of Ornithology (CLO). Thus, songs of all races of this species (AOU 1957) were represented in these samples. Voucher recordings of sparrow songs illustrated here are on deposit in the FMNH archives. Sound spectrograms of songs were prepared using a wide-band filter on a Kay Elemetrics 7029A Sona-Graph. Representative spectrograms characterize general song structure in populations and illustrate qualitative differences among them. Terminology of song structural components follows Baptista (1977).

Morphology and coloration.—Traditional skin characters from specimens in museum collections were used to address the question of possible congruence in variation of behavioral and morphological traits across the racial contact zone. Two historically significant series of specimens from southwestern coastal Maine were available for reevaluation. The 16 specimens collected by Montagna (1940) at Popham Beach in 1937 were deposited in the Cornell University collection. Two of these were later transferred to the Carnegie Museum. A series of 19 usable, breeding-season specimens obtained by Norton (1897) from Scarborough Marsh was located in the Zoology Department of the University of Maine (Orono) as part of the old Portland Society of Natural History collection. These specimens were compared with typical (including topotypical) *caudacutus* and *subvirgatus* specimens obtained on loan from the American Museum of Natural History (AMNH), U.S. National Museum, and Museum of Comparative Zoology. To minimize the effects of wear on plumage characteristics as a variable, only specimens obtained during June and early July were used in comparisons.

Two sets of comparisons were undertaken in analyses of morphological and coloration data. One concerned the possible existence of clinal variation in characters between New York and Maine populations. The other focused on variation across the contact zone in Maine. Percent measurement error (%ME) was assessed separately following the procedure of Lougheed et al. (1991) before these analyses were undertaken.

I measured four morphometric and two plumage (color, pattern) characters from available museum study skins. The morphometric traits were: (1) bill length (three alternative variables were evaluated in a preliminary analysis [length from base, length from anterior nares, and gonys length]), (2) bill depth at base of culmen, (3) wing chord, and (4) tarsus length from nuchal notch to lowest undivided scute. Among these characters, only wing chord exhibited significant sexual size dimorphism (ANOVA, df = 109, F = 190.4, P < 0.001). Consequently, sex-specific data were pooled in all analyses not involving wing chord. Correlation analyses showed strongly positive relationships of the three bill-length variables (narial and basal length, r = 0.42, n = 92, P < 0.01; basal and

gonys length, $r = 0.23$, $n = 74$, $P < 0.05$; narial and gonys length, $r = 0.61$, $n = 75$, $P < 0.01$. Since %ME values for basal bill length and gonys length exceeded 20% in some population samples, while those for narial bill length were low (see Results), I have dropped the two former variables from further consideration. To minimize the effects of measurement error in all analyses of the remaining variables, each dimension of a specimen was measured twice independently and the two values were averaged. These means were treated as sample data in final analyses. In several data sets where %ME for a character was large (>15%), one or two "obvious" mistakes within samples were discovered by replication. These outliers were not corrected in %ME analyses, but they were corrected by remeasurement before final analyses were undertaken. Bill measurements were made with a dial caliper (nearest 0.01 mm), while wing and tarsus measurements were obtained using a divider (nearest 0.5 mm).

Plumage characters were midback hue and ventral streakiness (two alternative variables were considered initially, breast streaking and flank streaking). These were assessed by comparing skins directly in natural light with reference specimens selected from AMNH series to represent natural variation in New York (*caudacutus*) and Nova Scotia (*subvirgatus*) populations. Back hue and ventral streaking offered the most consistent differences between these "endpoints" along a linear (coastal) geographic gradient. Other characteristics either were too variable in all populations, or subject to excessive influence from feather wear (Peters 1942). Streakiness pertained only to intensity of hue and definition of pattern, not to the density (amount) of streaks. Back hue concerned the general background color of the midback feather coat and not the amount of melanistic intrusion in these feathers, which is quite variable within and between populations. In a preliminary analysis, breast and flank streakiness were found to be positively correlated ($r_s = 0.56$, $t = 6.16$, $P < 0.001$). Thus, only data on breast streaking are reported here.

For each plumage trait, four reference specimens spanning observed variation were assigned arbitrary integer values to produce an index scale. Values 1.0 and 2.0 represented variation in dark, distinct streakiness of the breast in southern (nominate) birds, and 4.0 and 5.0 represented variation in pale, indistinct streakiness of northern coastal birds (*subvirgatus*). The median integer (3.0) reflected "missing" variation in the reference series and other specimens from the endpoint localities. Midback hue along the Atlantic coast was best represented by a scale of 1 to 4, with 1.0 and 2.0 assigned to the more brownish-olive condition of southern sparrows, and 3.0 and 4.0 to the more grayish-olive hue of northern ones. Specimens were ranked twice independently against the reference series and assigned values based on each comparison to the nearest 0.5. Analysis is based on the average of the two rankings.

Statistics.—Means and measures of sample variation were obtained routinely for all parameters in each geographic data set. Differences among populations were evaluated using a single-classification model I ANOVA with *a priori* hypotheses (Sokal and Rohlf 1969). Expectations of differences between populations, which determined whether one- or two-tailed tests were used, were derived from accepted taxonomic rankings of the different populations in the literature. The Scarborough Marsh population was considered to represent *A. c. caudacutus* (Norton 1897), and the Popham Beach population was treated as (most similar to) *A. c. subvirgatus* (Montagna 1940, 1942). Statistical significance was accepted at $P < 0.05$.

RESULTS

VOCAL BEHAVIOR

Songlike vocalizations in the Sharp-tailed Sparrow include primary song, flight song, and "complex whisper song." The primary song (sensu Thorpe 1961) is present as an independent display only in northern populations, while the complex whisper song occurs only in southern populations. The complex whisper song contains elements of ritualized primary song and flight song observed in northern birds and in other emberizines but, overall, it is distinctive and unique. Primary song is not employed as a separate display by southern birds. A true flight song rarely expresses itself in routine social contexts in southern populations. I witnessed such a display only twice during 10 years of field observations on sparrows in New York. Yet, this display is employed on a daily basis during the breeding season by northern birds and is expressed in a form commonly found in many other emberizines.

Primary song.—This is the song that is generally described as representative of the species as a whole (e.g. Borror 1961, National Geographic Society 1987), but as noted it is restricted to birds of the Canadian Maritime, coastal Maine, James Bay, and Northern Plains. Figure 1 shows sound spectrograms of representative songs from each of these populations. This song is given by transients during vernal migration and on the breeding grounds.

Song structure varies principally in relation to the introductory and terminal notes and syllables, and some of these variants may be widespread in certain populations (Borror 1961). Still, the overall structural pattern of this vocalization is similar in all northern birds (Fig. 1).
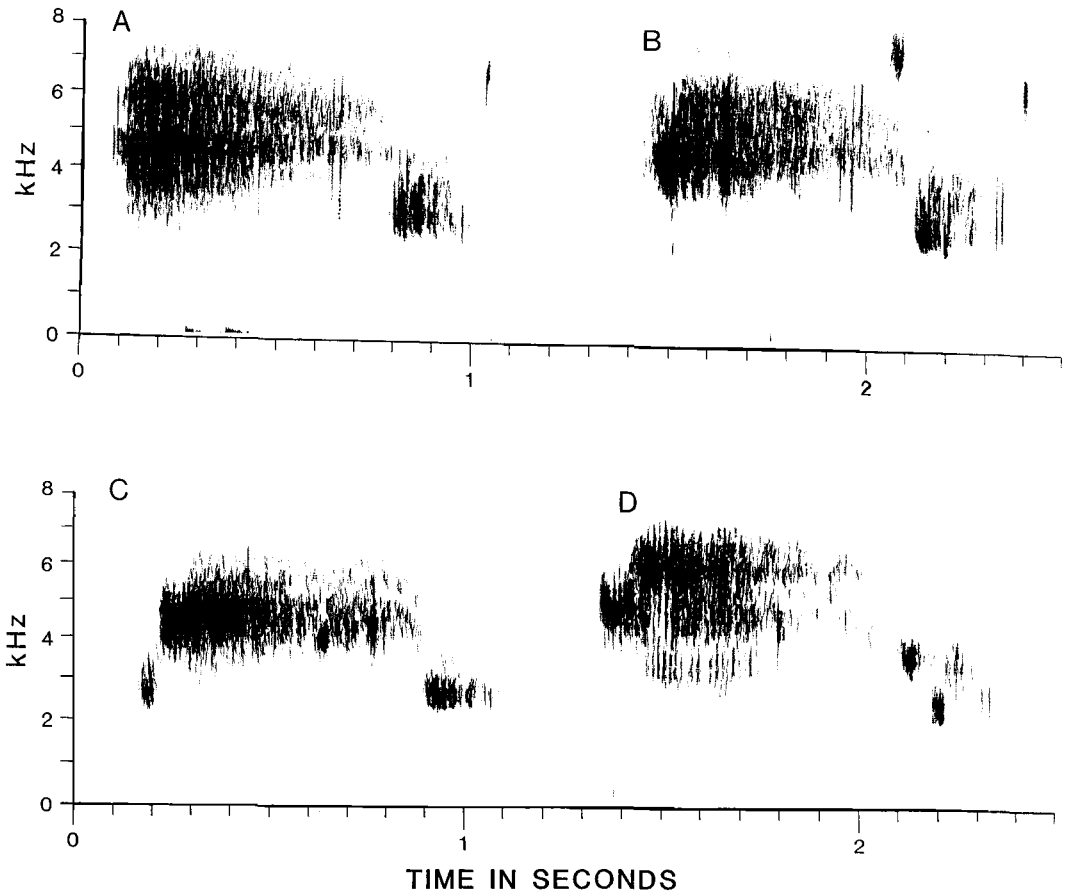
Songs consist mainly of two frequency-mod-

Fig. 1. Representative sonagrams of male primary songs in four northern populations of Sharp-tailed Sparrow: (A) *A. c. subvirgatus* phenotype, Popham Beach, Maine, recorded 17 June 1983, cut 8; (B) *A. c. subvirgatus*, Sackville, New Brunswick, Canada, recorded 2 July 1977, cut 12 (=cut 11 on tape); (C) *A. c. nelsoni*, Delta, Manitoba, Canada, recorded 10 July 1954, cut 2 (CLO no. 15032); (D) *A. c. alterus*, near Moosonee, James Bay, Ontario, Canada, recorded 27 June 1963, cut 3 (CLO no. 15035). Cut numbers refer to voucher tape in FMNH sound archives.

ulated trills. The first and longer trill contains frequencies concentrated in the 4 to 6 kHz range. Sometimes this trill exhibits two relatively distinct bands of frequencies in an audiospectrogram, one averaging about 4 kHz and the other about 6 kHz (Fig. 1A, D). Songs typically end with a second, shorter (about 200 ms), lower-pitched trill and one or several discrete, moderately high-pitched notes. Some birds start their songs with a brief, preliminary (third) trill (40 to 80 ms duration) that is lower-pitched than the main trill (Fig. 1C). Overall, frequencies in different songs lie between 2.5 and 7.5 kHz, but there may be weak overtone frequencies in the 8 to 9 kHz, and 13 to 14 kHz ranges as well.

In the field, the song has good carrying power, and may be heard from a considerable dis-

tance in still air (100 m or more). It is given repetitively, with successive renditions separated by a distinct pause of several seconds, during discrete bouts of singing from conspicuous (often favored) perches. Some perches may be used by different males at different times during the same observation period (see also Murray 1969). Bout lengths vary from less than a minute to about 30 min in one case. To a human listener, the song has a hushed, "gasping" quality, with a typical version transliterated as "pshhhh'-ipt."

Flight song and display.—The flight song is a complex vocalization that begins with a rapid series of twitters and chatters and ends with the population-specific primary song. This vocalization is considered a single functional unit.
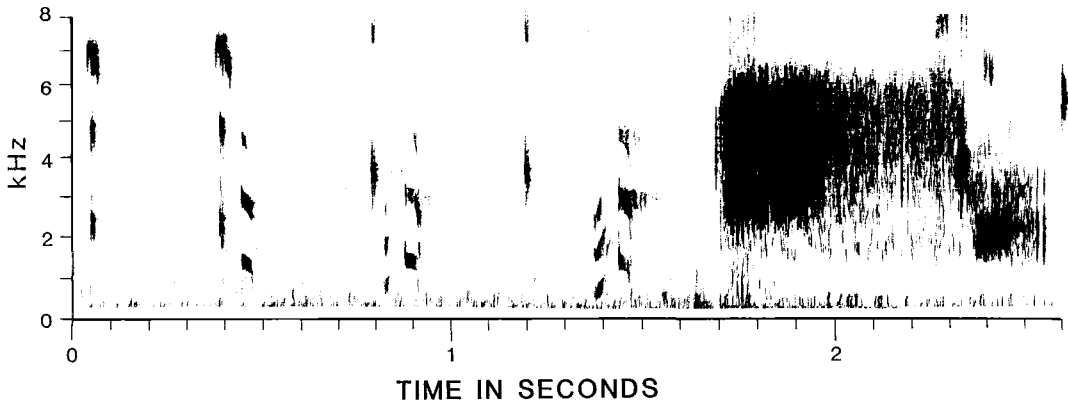
Fig. 2. Representative sonagram of flight song by *subvirgatus*-like male at Popham Beach, Maine. Recorded 28 June 1989. Cut 11 on voucher tape.

It is uttered only by the male in its breeding habitat.

An example of this song (2.42 s in duration) is illustrated in Figure 2. A complete vocalization begins with a rapid repetition of abrupt, piercing, clicklike notes ("tic twitter"). In Figure 2 this twitter is atypically abbreviated to two notes, or it was incompletely recorded. The twitter is followed by one to several lower-pitched, more complex syllables ("chatter") and then by one to three primary-song phrases in a terminal flourish. The displayer sets its spread wings a little above the level of the back, and lifts its head slightly, as the first (or only) primary-song phrase is uttered. This song phrase is indistinguishable from regular primary song given from a perch, but a repeated song phrase during the display is often abbreviated or "hurried." A typical, complete flight song can be transliterated as "tictictictictictictektektek pshhhh'-ipt."

Flight song is associated with a towering visual display in which the singer emerges from the vegetation in a steep ascent (usually varying from 50° to 80° above the horizontal) on rapidly beating wings. The twitter is uttered during ascent, usually starting 3 to 4 m above the ground (rarely beginning in grass just before ascent). The song is completed at and just beyond the apogee (4 to 20 m above ground) of the flight path, whereupon the bird descends steeply in a controlled glide to the marsh and directly enters the grass, or the bird levels off just above the vegetation and flies a short distance before landing out of view. Immediately following this display, the male may rarely sing one or two primary songs from a hidden position, but usu-

ally it will remain silent, not singing again for a considerable length of time. This visual display may vary somewhat within and between populations (e.g. Murray 1967).

Complex whisper song.—This vocalization complex consists of a variable mix of notes, syllables, and phrases. Many phrases are evidently homologous to primary song in northern sparrows and in other emberizines. The whole is presented as a continuous "sound stream." For this reason, and because the song phrases in the complex are not uttered as a separate, discrete display by southern sparrows, I have chosen to identify this as a single vocal display.

As noted, this vocalization is restricted to populations from extreme southwestern Maine southwards along the coast. It is characterized by: (1) a hushed, whispery, wheezy quality (trills are weak and almost cricketlike; see Fig. 3); (2) a complex and variable composition; (3) a prolonged, continuous delivery; and (4) the absence of repetitive presentation of the vocalization during a discrete bout of singing. The song typically is given once by a male at a particular spot and then not again for an unpredictable length of time later at another location. It has little carrying power. The sound may be so soft and weak that a naive listener may overlook it altogether, or may conclude that the singer is a distant bird when actually it is close by. The song may be uttered from a hidden or an exposed perch, or from horizontal (traveling) flight. A singing bird on a perch often continues its song uninterrupted as it flies to another perch nearby. Also, a singing bird in flight frequently continues to sing without interruption when it lands. In some cases, a single song
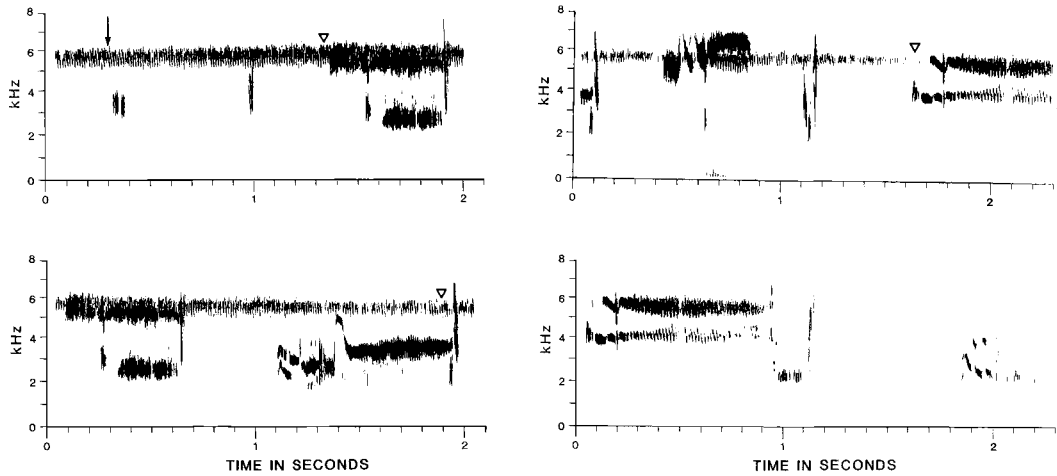
Fig. 3. Sonagram of a representative segment of complex whisper song showing successive notes and phrases. Open triangles indicate beginning of phrase sequence in next panel, reading top to bottom, left to right. Continuous background trill (arrow) was produced by a cricket (Gryllidae). Song recorded at Dividing Creek, New Jersey, from a perched male *A. c. diversus*, 24 July 1960. Cut 1 on voucher tape (CLO no. 15034).

performance may last over a minute as the bird flies between successive perches, with pauses on each.

Audiospectrograms of representative segments of two different songs are shown in Figures 3 and 4. Each segment is part of a longer delivery. Generally, frequencies fall between 2.0 and 7.5 kHz, and the intervals between notes and phrases (end of one to start of next) vary from 260 to 700 ms ($n = 7$). Phrases are present in this vocal display that resemble primary song in related emberizines. Usually they contain an "introduction" of abrupt notes, complex syllables, or short trills and other vibrato elements, followed by a trill of variable duration. Trill phrases also may occur without an introductory phrase. Abrupt, clicklike notes are present in the song as well, often interspersed between song phrases or associated with them.

I am unable to distinguish by ear the songs given from a perch versus those uttered in horizontal flight between perches. Also, both occur in similar functional contexts. Thus, singing in flight in this case does not constitute a true, distinctive flight song in the sense described earlier for northern populations. Rather, it is a continuation of perched song during traveling flight to another perch. The tempo of wingbeats is modified during song production, however, evidently as an artifact of the mechanics of song delivery while flying.

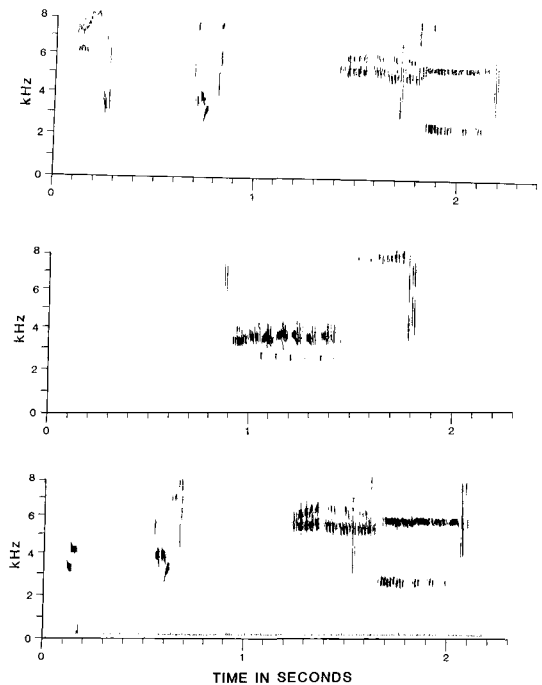*Vocal behavior in contact zone.*—Males in the

Fig. 4. Sonagram of a representative segment of complex whisper song showing successive notes and phrases beginning in top panel. Interphrase intervals portrayed as recorded within panels only. Song recorded at Oak Beach, Suffolk County, New York, from a perched male *A. c. caudacutus*, 20 July 1977. Cut 4 on voucher tape.

TABLE 1. Mean and standard error for measurements (mm) of *Ammodramus caudacutus* in five geographic populations along northeastern Atlantic coast. Number in parentheses indicates number of different individuals measured in sample. Statistical comparison involved southern populations in New York and Massachusetts combined[a] versus Canadian Maritime population.[b]

Character	Long Island	Massachusetts	Scarborough Marsh	Popham Beach	Canadian Maritimes
Bill length (nares)	9.4 ± 0.06 (27)	9.3 ± 0.07 (17)	8.5 ± 0.05 (19)	8.7 ± 0.08 (16)	8.6 ± 0.04 (36)**
Bill depth (base)	5.8 ± 0.05 (26)	6.0 ± 0.06 (16)	6.0 ± 0.06 (18)	6.0 ± 0.04 (16)	5.9 ± 0.03 (36)
Wing chord (males)	58.4 ± 0.23 (17)	59.0 ± 0.30 (14)	58.6 ± 0.24 (12)	59.1 ± 0.30 (11)	57.9 ± 0.25 (24)*
Wing chord (females)	54.4 ± 0.30 (9)	—	54.9 ± 0.45 (6)	54.7 ± 0.47 (5)	55.3 ± 0.49 (11)
Tarsus length	19.8 ± 0.11 (23)	19.8 ± 0.15 (14)	19.5 ± 0.14 (19)	19.8 ± 0.10 (16)	20.0 ± 0.13 (36)

[a] No statistical differences found between New York and Massachusetts populations; therefore, these samples pooled for further comparisons with northern populations.

[b] ANOVA model I analyses with *a priori* hypotheses based on information from literature on differentiation between populations (*, $P < 0.05$; **, $P < 0.01$).

Scarborough Marsh population sang only the complex whisper song. The song and associated singing behavior was similar to that performed by birds farther south. On one occasion, I thought I heard a distant primary song on the marsh typical of a northern (*subvirgatus*) male, but I was unable to confirm this tentative observation. All birds that I saw were quite brown dorsally, and had a strong ochraceous tone on the face and dark, moderately distinct breast streaks (*caudacutus*-like).

Most birds at Popham Beach sang primary (Fig. 1A) and flight songs, and performed the flight display typical of *subvirgatus* farther north. But, during both visits to the population, at least one (1989) or two (1983) relatively brown and distinctly streaked males were observed that sang complex whisper songs like those sung by southern birds.

For 61 visual sightings using a spotting scope or binoculars during the two visits, primary songs as well as typical flight songs and displays were performed consistently only by birds whose color and pattern most closely resembled that present in *subvirgatus* (relatively pale, "washed out" appearance overall, and blurred, indistinct ventral streaking). Likewise, typical complex whisper songs were sung only by *caudacutus*-like birds. However, on one occasion in 1983, I witnessed a flight display by a *caudacutus*-like male that I thought might be intermediate in form between that found in northern birds and complex whisper song given by a bird in horizontal flight. The display involved an ascent path of about 50° above the horizontal to a height of 10 to 12 m. There was a brief "tic"

twitter during the short ascent, but at the apogee the bird leveled off and flew about 25 m in a slow fluttery flight as it sang typical complex whisper song. This observation may have no special significance with regard to putative gene flow between northern and southern birds in this population. In late June 1989, I observed a similar display by a breeding *caudacutus* male in New York. These observations suggest that a true flight song and display may persist in southern birds but are rarely expressed.

EXTERNAL MORPHOLOGY

Measurement error.—Percent measurement errors of mensural characteristics were low to moderate (0.0 to 8.9%) in 14 of 20 data sets (four characters in five geographic areas). Measurement error of narial bill length varied in the five geographic samples as follows: 15.4% (New York/Connecticut), 1.6% (Massachusetts), 2.9% (Scarborough Marsh), 0.3% (Popham Beach), and 3.4% (Canadian Maritimes). The mean within-bird difference between two independent measurements of this character in all samples combined was 0.09 mm (SD = 0.016). In other variables, %ME varied as follows: (1) tarsus length, from 0.0 to 12.7% ($\bar{x} = 3.9\%$); (2) wing chord, from 0.6 to 18.0% ($\bar{x} = 7.2\%$); and (3) basal bill depth, from 1.0 to 19.2% ($\bar{x} = 15.2\%$). Overall, these errors are in line with those reported by others (Boag 1983, Lougheed et al. 1991).

Morphometric characteristics.—The mean values of four morphometric characters in five populations between New York and Nova Scotia are summarized in Table 1. In evaluating the

Maine populations, the first concerns were to identify characters that distinguish the southern populations in New York and Massachusetts from northern ones along the Atlantic coast in Canada, and to determine whether the populations south of Maine exhibited a clinal pattern of mensural variation in these parameters.

Mean tarsus length and mean bill depth did not differ among populations along the Atlantic coast. Thus, northern and southern Atlantic coastal populations are separable only by measurements of bill length and possibly by wing length (Table 1). Canadian Maritime birds are shorter-billed than birds from New York and southern New England (Table 1; but see Murray 1967). The difference in male wing chord between New York/Massachusetts birds and those in the Canadian Maritimes was barely significant at the 95% level, with northern sparrows exhibiting shorter wings than southern ones (Table 1). However, male wing length between these populations was not significantly different when only the New York sample was compared with the Maritime sample (ANOVA, F = 2.73, df = 1 and 86, P > 0.05).

Neither bill length nor wing chord exhibited a significant difference between New York and Massachusetts populations (Table 1, Fig. 5). Thus, in comparisons with Maine and Canadian populations, samples of birds from the central Atlantic coast (New York to Massachusetts) were pooled.

Variation in narial bill length and wing chord between the two Maine populations and between Maine birds and those to the north and south along the coast is evaluated in Tables 1 and 2, and in Figure 5. Mean narial bill length of sparrows in Scarborough Marsh is significantly shorter than that of birds in more southern populations. It does not differ from that of Popham Beach or Canadian Maritime birds. Thus, relatively small-billed sparrows typical of *subvirgatus* are found in both Maine populations, including one commonly assigned to *A. c. caudacutus* (Montagna 1942). There is a southward "step-increase" in bill size from extreme southwestern Maine to Massachusetts populations within the range of the nominate race (Fig. 5). Regressions of narial bill length on latitude (Fig. 5) for populations along the coast from Maine north and from Massachusetts south to New York have slopes indistinguishable from zero (b = −0.01 and −0.05, respectively). The respective mean bill lengths of birds in the two
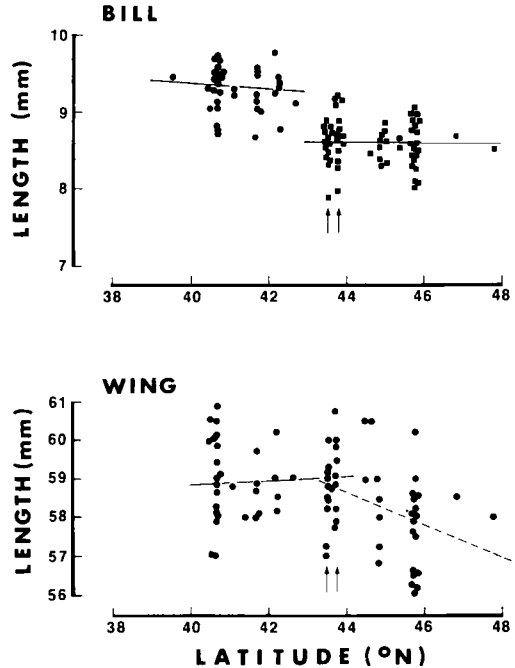

Fig. 5. Linear regressions of narial bill length and wing chord versus latitude. In each panel, regression on left covers latitudes from Long Island, New York, to northeastern Massachusetts, while one on right covers latitudes from Scarborough, Maine, north to Gulf of St. Lawrence. Two arrows identify data sets from Scarborough Marsh and Popham Beach, Maine, left and right, respectively.

sets of populations (8.6 ± 0.06 mm vs. 9.4 ± 0.06 mm) are significantly different (ANOVA, P < 0.01).

In a regression analysis of male wing chord on latitude, there was no significant change in wing length across the geographic gradient between Long Island, New York, and Popham Beach, Maine (b = 0.17; r = 0.21, P > 0.05). However, Canadian males averaged shorter wings (P < 0.05) than Maine males, but this difference was not evident in the females (Table 1). Since Murray (1967) reported a mean wing chord for males in his Canadian Maritime sample (58.6 ± 0.22 mm) that was larger than the mean reported here (57.9 ± 0.25 mm), I suspect a Type 1 error (rejection of a true null hypothesis) in my analysis. In my sample of Canadian birds, 6 of 24 males had wing chords of 56.0 to 56.5 mm. These chords are unusually short and within the range of variation in female wing chords. One expects some overlap between sexes in this morphometric variable, but the fre-

TABLE 2. Comparisons of bill length (mm) and male wing chord (mm) in two coastal Maine populations of *Ammodramus caudacutus* with one another, and with other coastal populations using single-classification ANOVA (model I). All hypotheses *a priori*.

Character	Within-group MS (df)	Between-group MS	Ratio	P^a
Popham Beach vs. Scarborough Marsh[b]				
Bill length (nares)	0.083 (125)	0.190	2.3	ns
Wing chord (male)	1.198 (86)	1.746	1.4	ns
Scarborough Marsh vs. New York/Massachusetts[c,d]				
Bill length (nares)	0.083 (125)	8.362	100.7	<0.001
Wing chord (male)	1.198 (86)	1.406	1.2	ns
Popham Beach vs. New York/Massachusetts[b,d]				
Bill length (nares)	0.083 (125)	4.896	58.9	<0.001
Wing chord (male)	1.198 (86)	0.743	0.6	ns
Scarborough Marsh vs. Canadian Maritimes[b]				
Bill length (nares)	0.083 (125)	0.069	0.8	ns
Wing chord (male)	1.198 (86)	4.109	3.4	ns
Popham Beach vs. Canadian Maritimes[b]				
Bill length (nares)	0.083 (125)	0.060	0.7	ns
Wing chord (male)	1.198 (86)	12.131	10.1	<0.05

[a] ns = not significant ($P > 0.05$).
[b] One-tailed test.
[c] Two-tailed test.
[d] New York and Massachusetts samples pooled to represent southern populations (see Table 1).

quency of 25% of male wing chords in the range 56.0 to 56.5 mm is high (Greenlaw unpubl. data).

Plumage characteristics.—Relative error based on two independent assessments of plumage characteristics in all specimens (average difference between corresponding assessments/total range of assessment scale × 100) was least for breast streaking (6.0%) and about double that (11.7%) for midback hue.

No differences in plumage characters were evident between birds in New York and Massachusetts. However, the Maine populations dif-

TABLE 3. Significance[a] of interpopulation variation in midback hue and breast streaking for Sharp-tailed Sparrows of the Atlantic coast.

Comparisons	Midback hue	Breast streaking
New York vs. Massachusetts (2)[b]	ns (20, 12)[c]	ns (21, 13)
New York/Massachusetts vs. Scarborough Marsh (2)	*** (32, 18)	*** (34, 18)
New York/Massachusetts vs. Popham Beach (1)	*** (32, 15)	*** (34, 16)
Scarborough Marsh vs. Popham Beach (1)	* (18, 15)	ns (18, 16)
Scarborough Marsh vs. Canadian Maritimes (1)	*** (18, 19)	* (18, 19)
Popham Beach vs. Canadian Maritimes (2)	* (15, 19)	ns (16, 19)

[a] Mann-Whitney *U*-test corrected for ties.
[b] One- or two-tailed comparison as indicated in parentheses.
[c] Sample sizes, respectively.
*, $P < 0.05$; ***, $P < 0.001$; ns, not significant ($P > 0.05$).
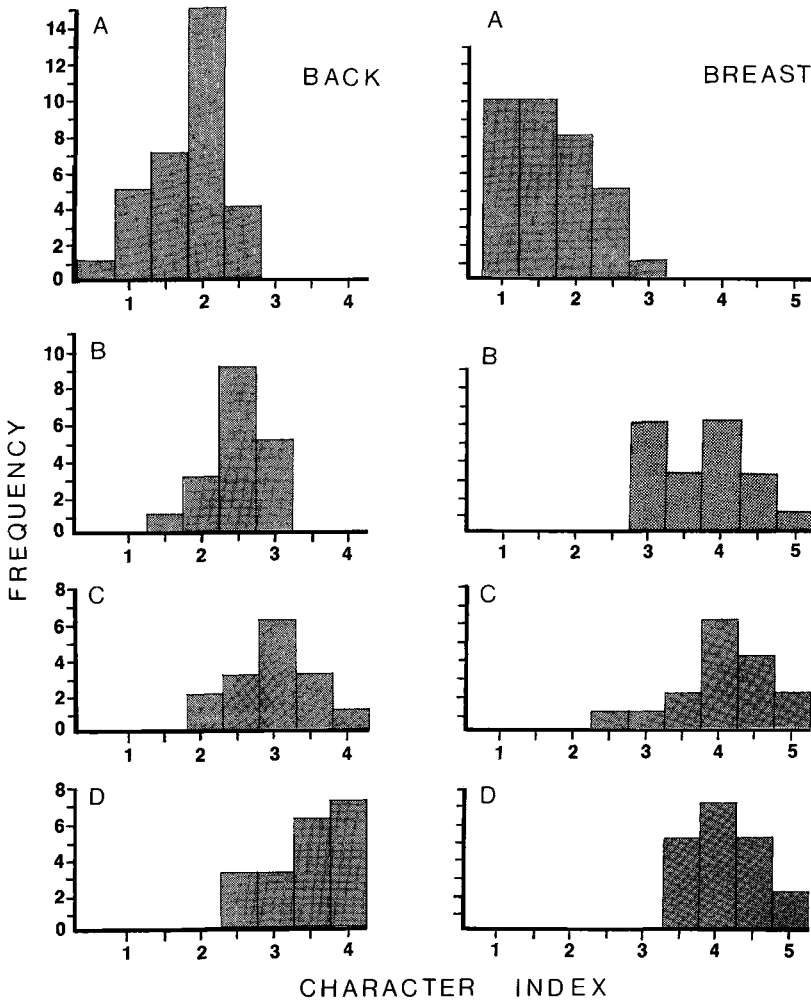
Fig. 6.   Frequency (number of specimens) distribution of mid-back hue and breast streaking in four Atlantic coastal populations of Sharp-tailed Sparrows: (A) New York to Massachusetts; (B) Scarborough Marsh, Maine; (C) Popham Beach, Maine; and (D) Canadian Maritimes.

fered significantly from those to the south in both ventral streakiness and back hue (Table 3). There appears to be an abrupt change from dark, broad, distinct streaking in birds from northern Massachusetts to more dusky, narrow streaking in birds from Scarborough, Maine. Still, although overall variation in ventral streakiness in the Scarborough population is strongly skewed toward the northern, coastal pattern, streaks remain moderately distinct on the breasts of many specimens (index value 3.0; Fig. 6). The pattern of variation in midback hue is more gradual across the Maine populations (Fig. 6). Birds in both Maine populations are interme-

diate in this characteristic between those in northern and southern populations, but Scarborough sparrows are darker-backed on average than Popham Beach birds (Table 3).

DISCUSSION

Songlike vocalizations.—A full discussion of songlike vocalizations in this species must await a more thorough analysis of display repertoires in relation to social organization. However, some observations are appropriate here.

Emberizines have an abbreviated, ritualized primary song that is broadcast by the male loud-

ly and repetitively during discrete bouts of singing from conspicuous perches (Andrew 1956, Borror 1961). In contrast, adult southern male Sharp-tailed Sparrows employ a variable, prolonged whisper song as their only songlike vocalization. Some adult male emberizines of other species also sing long, variable songs that contain stereotyped elements (J. D. Rising pers. comm., Greenlaw pers. observ.), but such songs are heard only occasionally and in none of the species do they replace the species-specific primary song.

Understanding the evolution of the complex whisper song is problematic. The view that this song type represents a retention of a primitive song trait in a part of the Sharp-tailed Sparrow complex is unsupported by outgroup comparisons with its closest living relatives in *Ammodramus* (e.g. Post and Greenlaw 1975). Perhaps it should be viewed as being a song bout in which muted primary songs are rendered repetitively in a continuous "sound stream" by dropping the usual intersong intervals. However, the matter is more complicated, since the primary songlike phrases used in the song complex vary among themselves, they are often incomplete, and call-like notes frequently are interspersed. A more likely possibility is that the complex whisper song, representing an ontogenetic stage of primary song development normally expressed during song crystallization (Marler 1981, Irwin 1988), has been retained into adulthood as a primary vocalization. This hypothesis is supported by clustering of whisper song traits in adult sparrows, such as continuous, muted delivery, low stereotypy, and a large repertoire of syllable types, which correlates with the same traits during development of primary song in other emberizines (Irwin 1988). Under this view, the adult whisper song must be regarded as derived (apomorphic) in southern Sharp-tailed Sparrows in the sense that the paedomorphic developmental trajectory that produces it is derived from an ancestral trajectory, which normally terminates in stereotyped primary song in northern Sharp-tailed Sparrows and other emberizines (see Irwin 1988).

The almost complete suppression of a classic emberizine flight song uttered during a high, parabolic flight in southern populations, and the importance of such a display in northern birds, are notable as well. This suppression also must be viewed as an autapomorphic condition in the southern birds, while the plesiomorphic state persists in northern populations.

Nature of racial contact in Maine.—Contact between the southern Sharp-tailed Sparrows and the more northern birds along the Atlantic coast occurs in southwestern Maine. This contact was identified by Norton (1897), who pointed out that *caudacutus* was the breeding population at Scarborough, while *subvirgatus* occurred only 48 km to the northeast at Small Point (near Popham Beach). The recently published breeding-bird survey in Maine (Adamus 1987) documented the next-nearest sparrow populations north of Scarborough to be south of Bath on the Phippsburg Peninsula (where Popham Beach is located) and nearby in the Brunswick area.

However, contact in Maine between northern and southern populations of this species must not be viewed simply as a subspecies problem. Rather, geographic variation of behavioral and morphological characteristics in this contact has an important bearing on the history of the populations involved. There is no evidence of gradual clinal changes with distance along the mid- and north Atlantic coast in any of the characteristics measured. Instead, a "step cline" evidently exists in bill size, ventral streaking, and back hue in southwestern Maine (Figs. 5 and 6). Small-billed birds statistically indistinguishable from northern birds in the Canadian Maritimes are found at least as far south as Scarborough Marsh. In contrast, bill lengths characteristic of southern birds occur as far north as northeastern Massachusetts. Bill size in New Hampshire populations needs to be examined. A similar pattern of change occurs in ventral streaking and back hue, although the geographic transitions in these variables are more evident across the two Maine populations. Breast and flank streaking in Scarborough birds is strongly skewed towards the condition in northern birds, yet a vestige of the southern pattern is sufficiently strong to have caused earlier workers to rank this population with the nominate race (Norton 1897, Montagna 1942). The transition in back hue in Scarborough sparrows and those in nearby Popham Beach essentially spans most of the gradient between northern and southern populations in this character. Finally, and most interestingly, there is no evidence for a clinal shift in song and singing behavior across the two Maine populations. The

"transition" not only is discrete, but the two qualitatively different patterns of song-related behaviors represented in northern and southern populations coexist side by side in the marsh at Popham Beach.

The step-clinal transitions in plumage and morphometric characteristics correspond geographically to a habitat discontinuity along the coast of Maine. Southern sparrows mostly inhabit intertidal areas on salt marshes that are expansive and strongly influenced by tides (Montagna 1942, pers. observ.). Coastal relief tends to be low and historically such marshes were widespread in the mid-Atlantic area (Reimold 1977). Northern populations in contrast commonly live in localized, often isolated, brackish marshes along the Atlantic coast that have a meadowy aspect and are less tidal (Montagna 1940, pers. observ.). Some birds may even occupy suitable subcoastal freshwater wetlands (Woodruff 1960, J. D. Rising pers. comm.). These habitat tendencies are reflected as well in habitat selection expressed in James Bay (brackish to freshwater) and interior (freshwater meadows) populations (Hill 1968, Murray 1969).

Dwight (1896) and Norton (1897) were the first to note the ecological differences between northern and southern Atlantic coastal sparrow populations. Norton (1897) and Montagna (1942) also pointed out that Scarborough Marsh was the northernmost marsh of the southern type in Maine, while nearby Popham Beach marsh exhibited the features of the northern type. Between these two disparate marshes, there is little or no habitat suitable for Sharp-tailed Sparrows.

The interpretation of step-clinal geographic patterns is inherently difficult. Stepped transitions are often treated as evidence of secondary contacts and hybridization, while gradual transitions are viewed as areas of primary intergradation in which isolation by distance promotes differentiation across environmental gradients. However, from the standpoint of cline theory (Endler 1977), unless a zone of secondary contact is observed shortly after being formed, it may not be possible to distinguish secondary and primary intergradations. Both kinds of contact can produce similar geographic patterns (stepped or gradual clines). Since only these patterns are observable, knowledge of the processes that produce and distinguish them may not be directly recoverable.
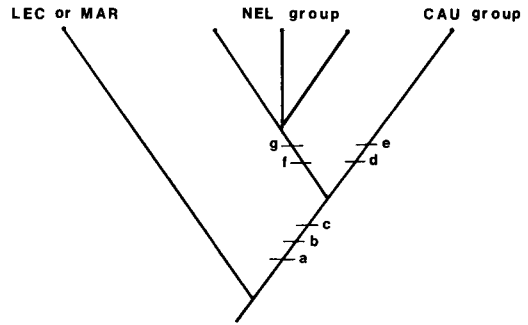

Fig. 7. Cladistic hypothesis of relationships in part of marshland sparrow clade based on postulated apomorphies: (a) loss of territoriality; (b) no male parental care; (c) "Sharp-tail" plumage color pattern; (d) group-specific primary song; (e) reduced or indistinct ventral streaking; (f) complex whisper song; (g) suppression of parabolic flight display and flight song. See Figure 8 for explanation of abbreviations.

Still, as a working hypothesis, the proposition that the Popham Beach and Scarborough Marsh sparrow populations represent an established secondary contact that stabilized across a narrow-fronted, discontinuous habitat bottleneck seems to have merit. The strongest evidence for this view relates to a phylogenetic argument. Both northern and southern populations of sparrows share the synapomorphic conditions of no male parental care, loss of territoriality, and similar plumage patterning (Greenlaw and Post unpubl. manuscript). These characters supply concrete support for the traditional and undisputed view that the two groups are sister members of a single clade. However, the presence of distinctive (autapomorphic) song-related characters within each of these groups (see Fig. 7 and below) provides a persuasive reason to believe that northern versus southern populations of Sharp-tailed Sparrows have diverged genetically from one another relatively recently (see also Rising and Avise 1993). The fact that the different northern populations also are more similar ecologically to one another than any are to southern birds, even though they are distributed partly across a continent, further suggests that the two groups have had a history of vicariance.

Evolution in Sharp-tailed Sparrows.—Apart from an analysis by Beecher (1955), little attention has been devoted to understanding the evolutionary history of the Sharp-tailed Sparrow complex until now (also Rising and Avise 1993).

Beecher proposed a late Pleistocene/Holocene model that involved dispersal (and subsequent isolation) of maritime *caudacutus* northwards along the Atlantic coast and then inland (perhaps after transforming to *subvirgatus*) following marine shorelines south of the receding ice front. Inland populations adjusted to freshwater habitats secondarily. A simplified (ignoring *A. c. diversus*) phylogenetic tree that reflects this viewpoint is shown in Figure 8A. The polytomy in this tree indicates probable contemporaneous diversification of the northern races.

There are problems with this proposal. Beecher (1955) sought to explain morphological diversification in Atlantic coastal Sharp-tailed Sparrows as consequences of population isolation by drowned river valleys during glacial melting. However, such isolation is microgeographic in scale and relatively temporary, since marshes quickly develop in estuarine environments as river currents deposit loads of alluvial sediments. Indeed, contrary to Beecher's (1955) assertion, the northern and southern limits of the modern ranges of *diversus* and *caudacutus*, respectively, are not delimited by Delaware Bay (Montagna 1942). Moreover, since no major river systems are present in southwestern Maine where *subvirgatus* and *caudacutus* are in contact, Beecher (1955) accepted by default an ad hoc hypothesis of primary differentiation across a habitat (marshtype) discontinuity (Montagna 1942). Most seriously, however, Beecher's model of a single cycle of late Pleistocene dispersal followed by post-Pleistocene primary differentiation in pockets of isolation or semi-isolation cannot easily explain the distribution of different autapomorphic behavioral characters between northern and southern populations that have been identified here.

A cladistic hypothesis of relationships within the Sharp-tailed Sparrow complex based on behavioral autapomorphies and synapomorphies within and between northern and southern

populations is presented in Figure 7. This cladogram accepts the monophyletic status of the group containing the Sharp-tailed Sparrow, Seaside Sparrow (*A. maritimus*), and LeConte's Sparrow (*A. leconteii*) as well corroborated (Murray 1968, Robins and Schnell 1971, Zink and Avise 1990) without specifying the clade's uniquely derived characters. The precise relationships among the three species within the clade remains uncertain (Zink and Avise 1990). The particular primary song and complex flight vocalization (flight song) present in all northern populations of Sharp-tailed Sparrows are considered apomorphic in that group, even though the generalized occurrence of primary song and flight display is plesiomorphic in grassland sparrows. As noted earlier, the complex whisper song also is believed to be autapomorphic in southern sparrows, perhaps derived by a paedomorphic event. Further, I postulate that indistinct or reduced ventral streaking is derived in the Sharp-tailed Sparrow complex, and is another autapomorphy present in the northern group. Distinct, well-developed streaks on breast and sides are widespread in grassland sparrows (outgroup criterion), and occur as well in the Seaside Sparrow and to a lesser degree in the LeConte's Sparrow. In addition, two putative molecular apomorphies recently were discovered in Sharp-tailed Sparrows by Rising and Avise (1993). These new characters also identified clades within the species that corresponded to the northern and southern groups recognized independently by Rising and Avise (1993), and by me.

This cladogram suggests a more complex history than that implied in Beecher's (1955) model. Specifically, there may have been two episodes of isolation and allopatric differentiation within the complex, namely that leading to species formation (*caudacutus* sensu lato), and that producing the divergence between northern and southern groups. Considering the northerly

→

Fig. 8.   Three proposed models representing possible geographic and phylogenetic events in evolution of Sharp-tailed Sparrows: (**A**) Beecher's (1955) late Pleistocene/Holocene model showing dispersal of maritime *caudacutus* sensu stricto inland following Wisconsin ice recession. (**B**) Pleistocene model of vicariance involving two separate episodes of range expansion (t_1, t_2) during mild periods, each followed by isolation and differentiation. Most recent cycle of expansion and differentiation produced northern races and secondary contact with coastal *caudacutus*. This model assumes *A. maritimus* to be sister species of *A. caudacutus*. (**C**) Alternate Pleistocene model of vicariance with two episodes of range expansion and differentiation, under assumption
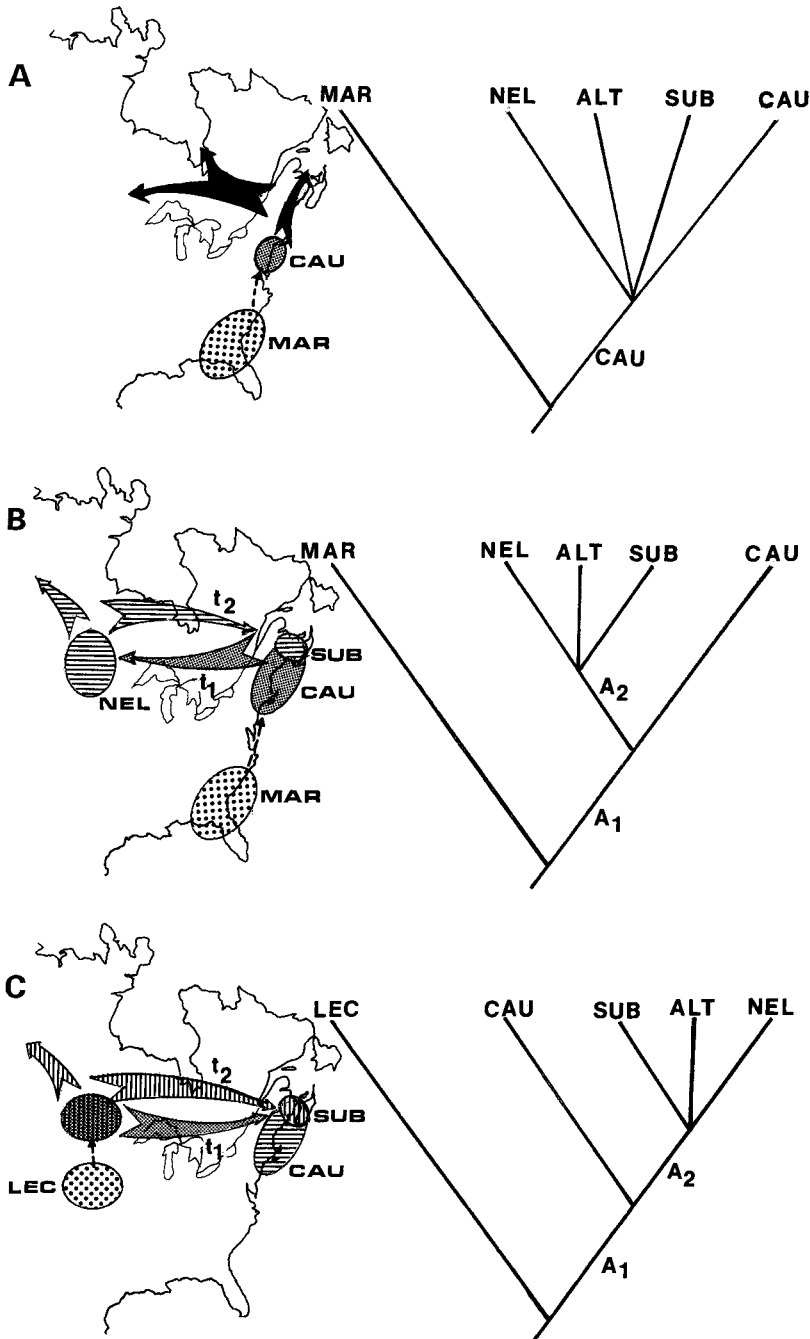
that *A. leconteii* is sister species of *A. caudacutus*. Ellipses diagrammatically indicate relative geographic locations of some modern populations of *A. caudacutus* (NEL, *nelsoni*; SUB, *subvirgatus*; CAU, *caudacutus*; ALT, *alterus* in James Bay area), and related species (MAR, *A. maritimus*; LEC, *A. leconteii*), and postulated locations (interior versus coastal) of ancestral vicariates (A_1, A_2). Shading distinguishes events of dispersal (arrows) and proposed areas of subsequent differentiation: stippling, hypothesized sister-species of *caudacutus* sensu lato; gray shading, initial dispersal event (t_1, Pleistocene interglacial) involving A_1; horizontal hatching, location of A_1 and its racial derivative (NEL or CAU), and second dispersal event (t_2, early Holocene) in model B; vertical hatching, location of A_2 (*nelsoni* or pro-*nelsoni*) and second dispersal event in model C.

distribution of the species, and the east-west pattern of continental differentiation, it is reasonable to propose a vicariant history that has been fundamentally influenced by at least two cycles of Pleistocene continental glaciation. Following initial differentiation as a new species, possibly during a glacial maximum, a coastal or inland population of sparrows (depending on locus of isolation) may well have occupied newly developing grassy wetlands either westward or eastward as the ice mass receded, perhaps spreading along a "corridor" through south-central and eastern Canada corresponding roughly to that proposed by LaRocque (1949) and Beecher (1955). This view of a dispersal route open to marshland sparrows gains some support (see Croizat et al. 1974) from the concordant distributions of a few other monophyletic groups of wetland taxa that are maritime and occur only in northern areas, notably those of certain plants that have halophytic affinities (e.g. *Eleocharis halophila, Juncus balticus,* and *Scirpus rufua;* Schofield 1959). These halophytes provide evidence for an Atlantic coast to interior range expansion, but the reverse pattern can be expected as well. For example, two species of northern Great Plains birds, the LeConte's Sparrow and the Marbled Godwit (*Limosa fedoa*), also have established James Bay populations. Indeed, LeConte's Sparrow has a continental interior distribution that is remarkably cordordant with that of the Sharp-tailed Sparrow in the same region (Murray 1969). Such a dispersal track along an east-west axis between the north Atlantic coast and interior plains, north of the Appalachian uplands, may also have existed in previous postglacial periods during the Pleistocene.

Two possible Pleistocene scenarios for such an evolutionary history are shown from geographic and phylogenetic perspectives in Figure 8. In one case (Fig. 8B), *caudacutus* (sensu lato) evolved from *A. maritimus,* or the two shared pro-*maritimus* as an ancestor, along the Atlantic coast. This population subsequently dispersed inland and later became isolated from Atlantic populations by continental glaciation. Following diffentiation, the interior isolate spread eastward to the Atlantic coast after recession of the Wisconsin ice mass, thus establishing the modern range and differentiates. The second case (Fig. 8C) presents the logical alternative involving *leconteii* or pro-*leconteii* as ancestor of

caudacutus sensu lato. This scenario also postulates two cycles of dispersal and an east-west vicariance. In this model, the two dispersals originated from the continental interior, the first leading to establishment of coastal populations now recognized as *caudacutus* sensu stricto, and the second producing the modern contact in Maine. Other models, or variations on those presented here, may be possible.

Unfortunately, although one of the two models of vicariance (models B and C; Fig. 8) may adequately represent actual events in the evolutionary history of Sharp-tailed Sparrows, it is not possible to test the models directly using Hennigian methods. Since the events expressed in these scenarios were chosen to faithfully represent relationships among modern populations (Fig. 7), the topologies of the phylogenetic trees derived from them are the same. However, other lines of evidence may help to evaluate the models. For example, any evidence that establishes the sister species to the Sharp-tailed Sparrows in principle could eliminate one or the other of the vicariant hypotheses.

Regarding the Beecher model (Fig. 8A), the cladistic pattern of relationships in the sparrow complex (Fig. 7) fails to support this view. Moreover, the proposed timing of the model is unsupported by the apomorphic character complexity exhibited in the species. Also, the genetic studies by Rising and Avise (1993) suggested that divergence between northern and southern clades is considerably older than the post-Pleistocene timing postulated by Beecher (1955).

Taxonomic considerations.—For nearly a century, following Dwight's (1896) influential revision, the taxonomic status of the Sharp-tailed Sparrow has remained largely uncontroversial (Ridgway 1901, Montagna 1942, Peters 1942, AOU 1957, 1983). Although Dwight's (1896) treatment was conservative, he hinted at a potential problem. He noted that *subvirgatus* seemed to have closer affinities to interior *nelsoni* than to its nearest neighbor on the Atlantic coast, *caudacutus,* and that this raised an interesting distributional problem which has been a focus of this paper. He further remarked that, should *subvirgatus* and *caudacutus* ever be found to regularly co-occur in the same breeding habitat, the question of the species status of *nelsoni* (with *subvirgatus* an eastern representative) would need to be reconsidered. In 1897, Norton

expressed the view, based on an evaluation of specimens collected in southwestern Maine marshes, that *subvirgatus* and *caudacutus* were specifically distinct; nevertheless, he followed Dwight's (1896) conservative lead.

My study and that of Rising and Avise (1993) have merely reopened the question of species limits in what I call the Sharp-tailed Sparrow complex. Clearly, the northern and southern groups in this complex each represent a phylogenetic species (Cracraft 1983, McKitrick and Zink 1988). They are monophyletically related in a larger clade (marshland sparrows; Zink and Avise 1990), and they are the smallest diagnosable units definable by unique, qualitative, apomorphic characters. Each evidently has had a distinctive recent geographic history. On the whole, members of the northern group are readily separable in the field by song and plumage traits from members of the southern group.

The morphological characters considered here provide some evidence of intermediacy between *caudacutus* and *subvirgatus* in the contact area, particularly in the Scarborough population. This suggests a certain level of genetic exchange across the contact. However, the birds at Scarborough exhibit the typical song-related behaviors of *caudacutus*. At Popham Beach, just a few kilometers away, and essentially the first neighboring population north of Scarborough, sparrows are mostly indistinguishable in morphology from *subvirgatus*. Also, at this site, both Montagna (1940) and I found a few *caudacutus*-like individuals (resembling modal, "intermediate" phenotypes at Scarborough) co-occurring in a mixed population with *subvirgatus*-like birds. Each individual bird observed in the field sang only the distinctive song types that corresponded to expectation based on phenotype. There was no evidence of behavioral intermediacy in the song performances of individual birds. Moreover, in June 1989 I discovered a nest of a *caudacutus*-like female (identifiable by behavior; Greenlaw and Post unpubl. manuscript) that contained young. I watched one or more *caudacutus*-like males (also identifiable by behavior in the field) following and harassing this female on her trips away from the nest, but *subvirgatus*-like birds in the neighborhood seemed to ignore her.

Under the circumstances, the taxonomic status of northern versus southern groups of Sharp-tailed Sparrows is a matter of some subjectivity.

This species complex represents a case of evolutionary intermediacy between full biological species and traditional subspecies levels of differentiation. Little is known currently about reproductive isolating mechanisms in this species. However, the genetic distance between recognized species in *Ammodramus* is substantially larger than that found between the two groups of Sharp-tailed Sparrows (Zink and Avise 1990, Rising and Avise 1993). Recognizing the groups as separate subspecies (Rising and Avise 1993) may have some merit (Avise and Ball 1990), but that approach ignores intragroup variation that traditionally has been associated with subspecific rank in the complex. It also seems to place too little emphasis on the observation by Rising and Avise (1993) that about 60% of their specimens from Popham Beach assayed genetically and morphologically as "pure" forms. As noted above, my study and that of Montagna (1940) also found northern and southern phenotypes co-occurring in this population. Finally, the two distinctive groups of sparrows are mostly allopatric, with only limited parapatry in Maine. I suggest that the best taxonomic resolution of this case at the moment is to recognize the two groups as allospecies within a superspecies. The southern allospecies should be known as *A.* [*caudacutus*] *caudacutus* (Sharp-tailed Sparrow, or Salt-marsh Sparrow if a new name is desired) and the northern one as *A.* [*caudacutus*] *nelsoni* (Nelson's Sparrow).

JON S. GREENLAW [Auk, Vol. 110]

and an anonymous reviewer. R. S. Palmer kindly answered questions about his experience with the sparrows at Popham Beach, and A. D. Smith (Canadian Wildlife Service) encouraged and facilitated my work in the Maritimes. This work was supported by National Science Foundation grant BNS 77-07314 and by funds from the C. W. Post Campus Research Committee of Long Island University.

LITERATURE CITED

ADAMUS, P. R. 1987. Atlas of breeding birds in Maine, 1978–1983. Maine Department of Inland Fisheries and Wildlife, Augusta.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, 5th ed. Am. Ornithol. Union, Washington, D.C.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Am. Ornithol. Union, Washington, D.C.

ANDREW, R. J. 1956. The aggressive and courtship behaviour of certain emberizines. Behaviour 10: 255–308.

AVISE, J. C., AND R. M. BALL. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surv. Evol. Biol. 7:45–67.

BAPTISTA, L. F. 1977. Geographic variation in song dialects of the Puget Sound White-crowned Sparrow. Condor 79:356–370.

BEECHER, W. J. 1955. Late-Pleistocene isolation in salt-marsh sparrows. Ecology 36:23–28.

BOAG, P. T. 1983. The heritability of external morphology in Darwin's ground finches (Geospiza) on Isla Daphne Major, Galapágos. Evolution 37: 877–894.

BORROR, D. J. 1961. Songs of finches (Fringillidae) of eastern North America. Ohio J. Sci. 61:161–174.

CRACRAFT, J. 1983. Species concepts and speciation analysis. Curr. Ornithol. 1:159–187.

CROIZAT, L., G. NELSON, AND D. E. ROSEN. 1974. Centers of origin and related concepts. Syst. Zool. 23: 265–287.

DWIGHT, J., JR. 1896. The Sharp-tailed Sparrow (Ammodramus caudacutus) and its geographical races. Auk 13:270–278.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton.

HILL, N. P. 1968. James Bay and Nelson's Sharp-tailed Sparrows. Pages 814–819 in Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237, part 2.

IRWIN, R. E. 1988. The evolutionary importance of behavioral development: The ontogeny and phylogeny of bird song. Anim. Behav. 36:814–824.

LAROCQUE, A. 1949. Post-Pleistocene connection be-

tween James Bay and the Gulf of Saint Lawrence. Bull. Geol. Soc. Am. 60:363–380.

LOUGHEED, S. C., T. W. ARNOLD, AND R. C. BAILEY. 1991. Measurement error of external and skeletal variables in birds and its effect on principal components. Auk 108:432–436.

MARLER, P. 1981. Birdsong: The acquisition of a learned motor skill. Trends Neurosci. 4:88–94.

MCKITRICK, M. C., AND R. M. ZINK. 1988. Species concepts in ornithology. Condor 90:1–14.

MONTAGNA, W. 1940. The Acadian Sharp-tailed Sparrows of Popham Beach, Maine. Wilson Bull. 52:191–197.

MONTAGNA, W. 1942. The Sharp-tailed Sparrows of the Atlantic coast. Wilson Bull. 54:107–120.

MURRAY, B. G., JR. 1967. A comparative study of the LeConte's and Sharp-tailed sparrows with comments on the ecology of sympatric species. Ph.D. dissertation, Univ. Michigan, Ann Arbor.

MURRAY, B. G., JR. 1968. The relationships of sparrows in the genera Ammodramus, Passerherbulus, and Ammospiza with a description of a hybrid LeConte's × Sharp-tailed Sparrow. Auk 85:586–593.

MURRAY, B. G., JR. 1969. A comparative study of the LeConte's and Sharp-tailed sparrows. Auk 86:199–231.

NATIONAL GEOGRAPHIC SOCIETY. 1987. Field guide to the birds of North America, 2nd ed. National Geographic Society, Washington, D.C.

NORTON, A. H. 1897. The Sharptailed Sparrows of Maine. Proc. Portland Soc. Nat. Hist. 2:97–102.

PETERS, J. L. 1942. The Canadian forms of the Sharp-tailed Sparrow, Ammospiza caudacuta. Ann. Carnegie Mus. 29:201–210.

POST, W., AND J. S. GREENLAW. 1975. Seaside Sparrow displays: Their function in social organization and habitat. Auk 92:461–492.

REIMOLD, R. J. 1977. Mangals and salt marshes of eastern United States. Pages 157–166 in Ecosystems of the world: Wet coastal ecosystems (V. J. Chapman, Ed.). Elsevier Scientific Publishing Co., New York.

RIDGWAY, R. 1901. The birds of North and Middle America, pt. 1. U.S. Natl. Mus. Bull. 50:1–715.

RISING, J. D., AND J. C. AVISE. 1993. Application of genealogical-concordance principles to the taxonomy and evolutionary history of the Sharp-tailed Sparrow (Ammodramus caudacutus). Auk. In press.

ROBINS, J. D., AND G. D. SCHNELL. 1971. Skeletal analysis of the Ammodramus-Ammospiza grassland sparrow complex: A numerical taxonomic study. Auk 88:567–590.

SCHOFIELD, W. B. 1959. The salt marsh vegetation of Churchill, Manitoba, and its phytogeographic implications. Natl. Mus. Canada, Bull. 160:107–132.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

THORPE, W. H. 1961. Bird-song: The biology of vocal communication and expression in birds. Cambridge Univ. Press, Cambridge.

WOODRUFF, R. E. 1960. Bird notes from the Calais area. Maine Field Nat. 16:66–67.

WOOLFENDEN, G. E. 1956. Comparative breeding behavior of *Ammospiza caudacuta* and *A. maritima*. Univ. Kansas Publ., Mus. Nat. Hist. 10:45–75.

ZINK, R. M., AND J. C. AVISE. 1990. Patterns of mitochondrial DNA and allozyme evolution in the avian genus *Ammodramus*. Syst. Zool. 39:148–161.