A COMPARATIVE STUDY OF THE LE CONTE'S AND SHARP-TAILED SPARROWS

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MANY ecologists believe that interspecific competition will result in the elimination of one of the competing species or in the evolution of differences that will let the two species coexist without competing (Lack, 1954, 1966; Mayr, 1963). This has stimulated considerable study of the ecology of sympatric species. Ecologists studying avian populations seem convinced that food is the limiting resource of many populations, and they have focused attention on differences in morphological and behavioral adaptations associated with foraging. Sympatric species usually occupy different habitats or, if not, differ in overall size, in shape or size of bill, or in foraging habits (Lack, 1944, 1954). Many recent studies seem to support the original generalizations.

The subjects of the present study are the Le Conte's Sparrow (*Ammospiza leconteii*) and the Sharp-tailed Sparrow (*Ammospiza caudacuta*). The latter is not only sympatric with the Le Conte's Sparrow in interior North America but also with the Seaside Sparrow (*Ammospiza maritima*) along the Atlantic coast. A comparison of the relationships between the Seaside and Sharp-tailed Sparrows (Woolfenden, 1956) with those between the Le Conte's and Sharp-tailed Sparrows might show how its sympatric relatives have influenced selection in the wide-ranging Sharp-tailed Sparrow.

MATERIALS AND METHODS

The Le Conte's and Sharp-tailed Sparrows were compared both in the field and in the museum. I studied the living birds at the Lower Souris National Wildlife Refuge in North Dakota. In 1965 I arrived at the refuge 7 May and left 30 July; in 1966 I arrived 29 April and left 26 July. I studied specimens at the American Museum of Natural History, the Museum of Comparative Zoology at Harvard University, the National Museum of Canada, the Royal Ontario Museum, The University of Michigan Museum of Zoology, and the United States National Museum. Details of the methods used in gathering and analyzing data are included at the beginning of each section.

Elsewhere (Murray, 1968) I have presented evidence and arguments for placing the Le Conte's Sparrow (*Passerherbulus caudacutus* of the A.O.U. Check-list, 1957) in the genus *Ammospiza*, which requires a change in the specific trivial name to *leconteii*, and the Henslow's Sparrow (*Passerherbulus henslowii* of the A.O.U. Check-list, 1957) in the genus *Ammodramus*. In this paper I refer to the Le Conte's Sparrow as *leconteii* and to the Sharp-tailed Sparrow as *caudacuta*.

DISTRIBUTION

The limits of the breeding range were determined by plotting June, July, and August records of adult specimens on a map; December, January, and February specimen records were plotted for the winter range.

Figure 1. Breeding and winter ranges of the Sharp-tailed Sparrow. Solid circles indicate specimen records, open circles additional localities reported in the literature. A solid line delimits the areas in which specimens were collected in June, July, and August, whereas the dashed line delimits the areas in which specimens were collected in December, January, and February. The southern Ontario bird collected 12 June and the Iowa specimen collected 29 June were probably stragglers.

The Sharp-tailed Sparrow breeds in three disjunct areas (Figure 1). The race *nelsoni* inhabits freshwater marshes in glaciated portions of the Interior Plains Region from southeastern North Dakota and northwestern Minnesota northwestward to Great Slave Lake and westward into eastern British Columbia. Reports that *A. c. nelsoni* bred as far south as Chicago are unsubstantiated (*fide* Peters, 1942), and the significance of the single, late June specimen from Iowa (Figure 1) is conjectural. A second race (*altera*) inhabits coastal marshes of southern Hudson Bay and James Bay. Three races (*subvirgata, caudacuta,* and *diversa*) breed in marshes along the Atlantic coast from the Maritime Provinces to Virginia. Sharp-tailed

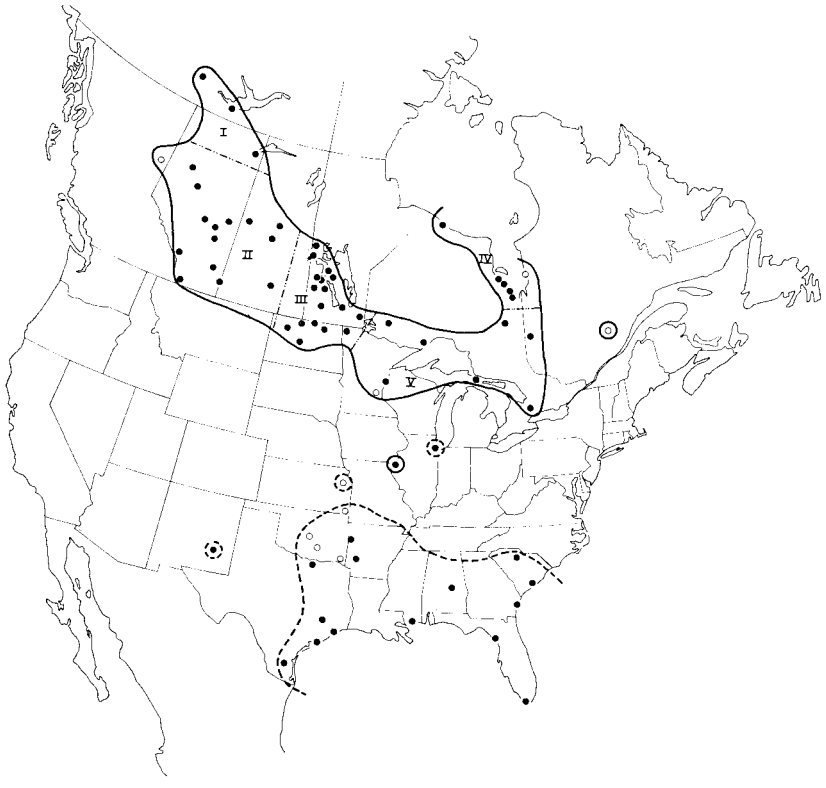

Figure 2. Breeding and winter ranges of the Le Conte's Sparrow. The symbols are the same as in Figure 1.

Sparrows do not nest on the Canadian Shield, which keeps the three breeding areas separate.

The breeding range of *leconteii* overlaps those of *c. nelsoni* and *c. altera* (cf. Figures 1 and 2). Le Conte's Sparrows inhabit freshwater marshes and low wet prairie in glaciated portions of the Interior Plains Region, extending into British Columbia. A nearly disjunct population occurs along the shores of James Bay, where Todd (1943) found it common in suitable habitat, and Hudson Bay. Le Conte's Sparrows are rare on the Canadian Shield, but a few have been taken as far east as eastern Quebec (Figure 2 and Godfrey, 1966).

The range boundaries of *c. nelsoni* and *leconteii* correspond closely with the eastern and western boundaries of the Interior Plains Region and the southern extent of glaciation (Figure 3), but no such correspondence exists between the ranges and vegetation types (Figure 4). No doubt the

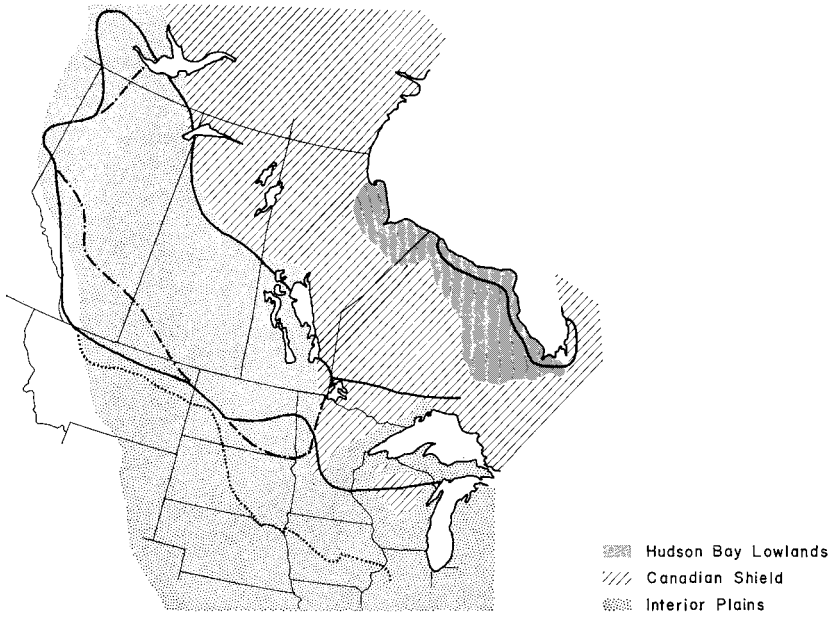

Figure 3. Ranges of the Le Conte's and Sharp-tailed Sparrows in relation to physiography. The range of *leconteii* is bounded by a solid line, and where the range of *caudacuta* differs from that of *leconteii* it is bounded by a line of dots and dashes. The dotted line represents the southern extent of Wisconsin glaciation.

substrate of the glaciated Interior Plains Region permits the growth of the lakeside and marsh vegetation that these sparrows inhabit.

In winter *caudacuta* is restricted to the Atlantic and Gulf coasts from New England to Texas (Figure 1). Most of the records west of Florida refer to *c. nelsoni*. Le Conte's Sparrows winter regularly in the southeastern United States from Oklahoma (Sutton, 1967), Missouri (Audubon Field Notes, Christmas counts, various years), and South Carolina southward to the Gulf coast and southern Florida (Figure 2). Most winter specimens were taken at the same coastal localities where many *caudacuta* specimens have been taken. Le Conte's Sparrows may winter northward locally to Kansas (Johnston, 1965) and Kentucky (Mengel, 1965) and rarely to northern Illinois (Figure 2).

HABITAT

Both *leconteii* and *c. nelsoni* breed commonly in an extensive marshy area in the floodplain of the Souris River, about 3 miles east of Upham, McHenry County, North Dakota, on the Lower Souris National Wild-

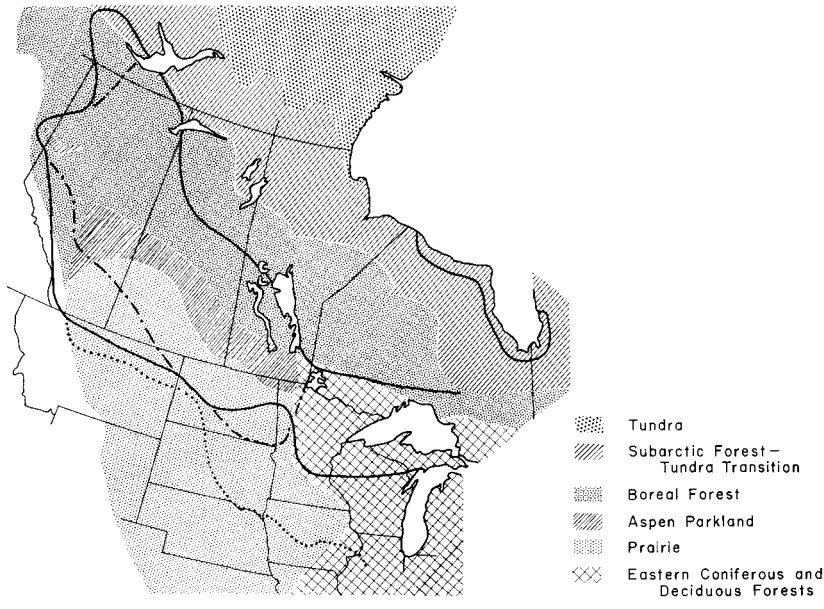

Figure 4. Ranges of the Le Conte's and Sharp-tailed Sparrows in relation to vegetation types. Symbols not indicated in the key are the same as in Figure 3.

life Refuge. In the area selected for study (Figures 5 and 6), cordgrass (*Spartina pectinata*) was the predominant plant. Other grasses forming extensive stands in the vicinity were squirreltail (*Hordeum jubatum*), whitetop (*Scolochloa festucacea*), and phragmites (*Phragmites communis*). Cattail (*Typha latifolia*) was common in nearby sloughs and ditches. Sedges were not common in the primary study area. Sourdock (*Rumex acetosa*), the only stiff-stemmed plant present, provided song perches for several bird species.

In 1965 *leconteii* occurred throughout the floodplain shown in Figure 5 except in the wettest parts. The species was most dense in *Spartina*, less dense in the sparser *Hordeum*, and rare in *Bromus* on the dry upland. In 1966 bird populations were low, and *leconteii* was rare outside the *Spartina* study area. In 1965 *c. nelsoni* was scattered throughout the area in the wetter habitats, being common in *Spartina*, frequent in *Scolochloa* and at the edges of *Phragmites* stands, but never seen or heard on the upland. In 1966 *c. nelsoni* was rare outside the *Spartina* study area, where it seemed to be almost as common as in 1965. Thus both species are most numerous in the *Spartina* habitat, while some *leconteii* are in drier habitats and some *c. nelsoni* are in wetter habitats. In some places only one species

Figure 5. Oblique aerial photograph of the study area and vicinity near the Souris River east of Upham, McHenry County, North Dakota. The study area is outlined in white. View towards northwest. (Courtesy of John W. Winship and Bureau of Sport Fisheries and Wildlife.)

occurs. Nero (1963) found only *leconteii* in the Lake Athabaska region of Saskatchewan, but both species occur at the western end of the lake in Alberta (Figures 1 and 2). In Alberta Godfrey (1952: 171–172) found *leconteii* in "drier edges of moist meadows and marshes where rank growth of sedges and grasses are interspersed with willow and alder," and *c. nelsoni* in "wetter parts of marshy areas . . . often frequenting the cattails or bulrushes at the water edge." Near Kenmare, Ward County, North Dakota, I saw *c. nelsoni* but not *leconteii* in a large dry slough in which the predominant plant was *Scolochloa*. Despite these differences the range of *leconteii* is nearly identical to the ranges of the interior races of *caudacuta*.

An advantage of *Spartina* and *Scolochloa* to these birds seems to be the thick cover they give for nest sites. *Spartina* and *Scolochloa* are tall and grow in dense stands. Most dead stems fall and form a thick mat. *Hordeum* is sparser and shorter. When it dies stems remain standing, and those that fall form, at best, a thin mat. The aerial photographs show this difference clearly. The large, dark patches in the upper part of Figure 6 are essentially pure stands of *Hordeum* that appear dark because they are open enough to expose the moist ground, while the lighter areas are

denser stands of *Spartina* or *Spartina* mixed with *Hordeum*. In oblique view (Figure 5) *Spartina* appears darker than *Hordeum*, as it is naturally. The largest *Hordeum* patch was actually the driest spot in the study area and was not occupied by either *leconteii* (cf. Figures 6 and 12) or *c. nelsoni*. Actually, two pairs of Savannah Sparrows (*Passerculus sandwichensis*) bred there.

The northern third of the study area (Figure 6) was hayed in 1964, and in 1965 *leconteii* was never seen there, even after the stubble was replaced by a lush growth of *Hordeum*. This growth occurred long after *leconteii* had established territories. However, as indicated in another area studied in 1965, *leconteii* can breed in a 2-year-old *Hordeum* field (patches of *Spartina* were present), although it was scarce there. Annual haying of *leconteii's* habitat would extirpate the species. The Sharp-tailed Sparrow can survive in habitats too wet for haying.

Birds of the Marsh

In North Dakota the passerine fauna in the Souris River floodplain where *leconteii* and *caudacuta* breed includes the Long-billed Marsh Wren (*Telmatodytes palustris*), Short-billed Marsh Wren (*Cistothorus platensis*), Yellowthroat (*Geothlypis trichas*), Western Meadowlark (*Sturnella neglecta*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), Red-winged Blackbird (*Agelaius phoeniceus*), Brown-headed Cowbird (*Molothrus ater*), Savannah Sparrow, and Song Sparrow (*Melospiza melodia*). Nonpasserines include a variety of ducks, Wilson's Phalarope (*Steganopus tricolor*), Marsh Hawk (*Circus cyaneus*), and Short-eared Owl (*Asio flammeus*).

Udvardy (1963) tentatively grouped the North American species of passerines into 27 ecogeographical faunal groups on the basis of their geographic (primarily) and ecological (when known) similarities. He included *leconteii* and *caudacuta* in the Prairie Fauna with the Sprague's Pipit (*Anthus spragueii*), Lark Bunting (*Calamospiza melanocorys*), Baird's Sparrow (*Ammodramus bairdii*), McCown's Longspur (*Rhynchophanes mccownii*), and Chestnut-collared Longspur (*Calcarius ornatus*), all of which occupy the drier grasslands. On the basis of the present evidence it seems best to remove *leconteii* and *caudacuta* from the Prairie Fauna, even though they do not appear to belong to any of Udvardy's other ecogeographic faunal groups.

Geographic Variation

Three kinds of measurement were taken from museum specimens: (1) wing chord measured to nearest 0.5 mm with dividers, (2) bill length from nostril measured to nearest 0.1 mm with dial calipers, and (3) weight

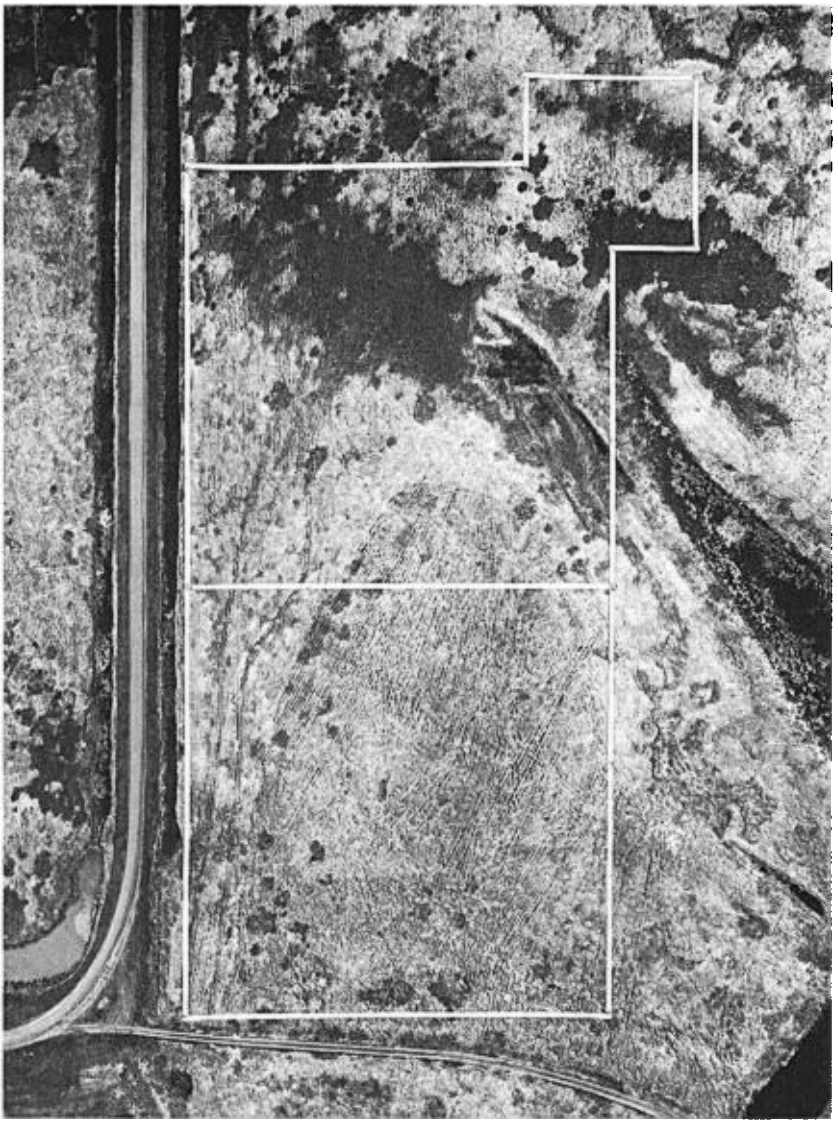

Figure 6. Vertical aerial photograph of the study area, approximate boundaries indicated by white lines. The southern (bottom) square was used in 1965, the entire area in 1966. The vegetation in the lower square is predominantly *Spartina pectinata*. The dark patch in the upper square is predominantly *Hordeum jubatum*. The lighter triangle of vegetation on the west side is *Spartina* mixed with *Hordeum*. Most of the upper square was hayed in 1964 and was stubble at the beginning of 1965. (Courtesy of John W. Winship and Bureau of Sport Fisheries and Wildlife.)

TABLE 1
MEASUREMENTS OF LE CONTE'S SPARROW POPULATIONS

Region	Sex	N	Mean (± 2 SE)	Range	SD
WING LENGTH					
I	M	10	52.6 (± 0.66)	51.0–55.0	1.05
	F	4	49.5	49.0–51.5	—
II	M	28	52.1 (± 0.43)	49.5–55.0	1.15
	F	8	49.9	48.0–51.5	—
III	M	32	52.1 (± 0.44)	50.5–56.0	1.26
	F	13	51.2	49.5–54.5	—
IV	M	22	52.0 (± 0.51)	50.0–54.0	1.19
	F	5	51.0	49.5–55.0	—
Total	M	92	52.1 (± 0.25)	49.5–56.0	1.19
	F	30	50.6 (± 0.60)	48.0–55.0	1.65
BILL LENGTH					
I	M	10	6.8 (± 0.20)	6.4–7.3	0.32
	F	4	6.8	6.4–7.4	—
II	M	24	7.0 (± 0.15)	6.2–8.0	0.36
	F	8	6.9	6.6–7.2	—
III	M	31	7.0 (± 0.09)	6.2–7.5	0.26
	F	12	7.0	6.5–7.4	—
IV	M	22	6.8 (± 0.12)	6.3–7.5	0.32
	F	5	6.9	6.4–7.2	—
Total	M	87	6.9 (± 0.07)	6.2–8.0	0.32
	F	29	6.9 (± 0.11)	6.4–7.4	0.30

to nearest 0.1 gram as indicated on the label. Damaged and distorted specimens were not measured. Additional weights were obtained from mist-netted birds. Only data from June and July specimens are used.

To determine whether *leconteii* varies geographically I divided its range into five regions (Figure 2): (I) northern Alberta and Northwest Territories, (II) southern Alberta and Saskatchewan, (III) southern Manitoba, North Dakota, and Minnesota, (IV) shores of Hudson and James Bays, and (V) southern Ontario and Michigan. Le Conte's Sparrow is rare in region V (eight specimens), so that population is not considered in the statistical comparisons.

In these populations only males may be compared statistically because sample sizes of females are too small. The variations in the means of wing length and bill length of male *leconteii* from the various regions are not statistically significant (Table 1). This is probably the case for females also. Therefore the data have been combined for each sex for comparison with other species.

I divided the range of *c. nelsoni* into three regions that correspond to regions I, II, and III, respectively, of *leconteii*. Within the same limitations of statistical treatment, no significant differences are apparent be-

TABLE 2
MEASUREMENTS OF NELSON'S SHARP-TAILED SPARROW POPULATIONS

Region	Sex	N	Mean (± 2 SE)	Range	SD
WING LENGTH					
I	M	10	56.4 (± 0.83)	54.5–58.6	1.31
	F	2	53.0	52.5–53.5	—
II	M	18	56.1 (± 0.46)	54.5–58.0	0.97
	F	5	53.6	53.5–54.0	—
III	M	40	56.4 (± 0.44)	53.0–59.0	1.41
	F	17	53.6	52.0–56.0	—
Total	M	68	56.3 (± 0.31)	53.0–59.0	1.28
	F	24	53.5 (± 0.36)	52.0–56.0	0.88
BILL LENGTH					
I	M	10	8.1 (± 0.19)	7.6–8.6	0.30
	F	2	7.8	7.7–8.0	—
II	M	17	8.1 (± 0.12)	7.7–8.7	0.25
	F	4	8.2	7.8–8.7	—
III	M	40	8.2 (± 0.08)	7.8–8.8	0.27
	F	18	8.2	7.8–8.6	—
Total	M	67	8.1 (± 0.07)	7.6–8.8	0.27
	F	24	8.1 (± 0.11)	7.7–8.7	0.29

tween mean measurements within the range of *c. nelsoni* (Table 2). Therefore, data for *c. nelsoni* also have been combined.

The data for *leconteii* and *c. nelsoni* are compared with each other and with those for *maritima* and other populations of *caudacuta*, namely: (a) *altera* from James Bay, (b) *subvirgata* from the Maritime Provinces, (c) *caudacuta* from Massachusetts to New York, (d) *caudacuta* and *diversa* from New Jersey, and (e) *diversa* from Delaware, Maryland, and Virginia (Del-Mar-Va). Figures 7 and 8 show the variation in wing length and bill length, respectively. The shortest-winged *caudacuta* is *nelsoni*, the longest-winged are *altera* and *subvirgata*, and a cline toward shorter wings extends from the Maritimes to Virginia. The ratio between the means of wing lengths in male *c. nelsoni* and *leconteii* is 1.08. The ratio between *c. caudacuta* and *c. diversa* populations and *m. maritima* is 1.08. The shortest-billed *caudacuta* is *nelsoni*, and the longest-billed are populations from New England south to Virginia, where no cline exists. The populations from James Bay and the Maritimes are intermediate. Thus the shortest-billed *caudacuta* race is sympatric with the short-billed *leconteii*, and the longest-billed *caudacuta* races are sympatric with the long-billed *m. maritima*. The ratio between the bills of *c. nelsoni* and *leconteii* is 1.19, and that between *c. caudacuta* and *c. diversa* populations and *m. maritima* is 1.21.

Weight data are available for only four populations of *caudacuta* and two of *leconteii* (Table 3). Mean weights of *leconteii* from North Dakota and James Bay are similar. However within *caudacuta*, *nelsoni* from North

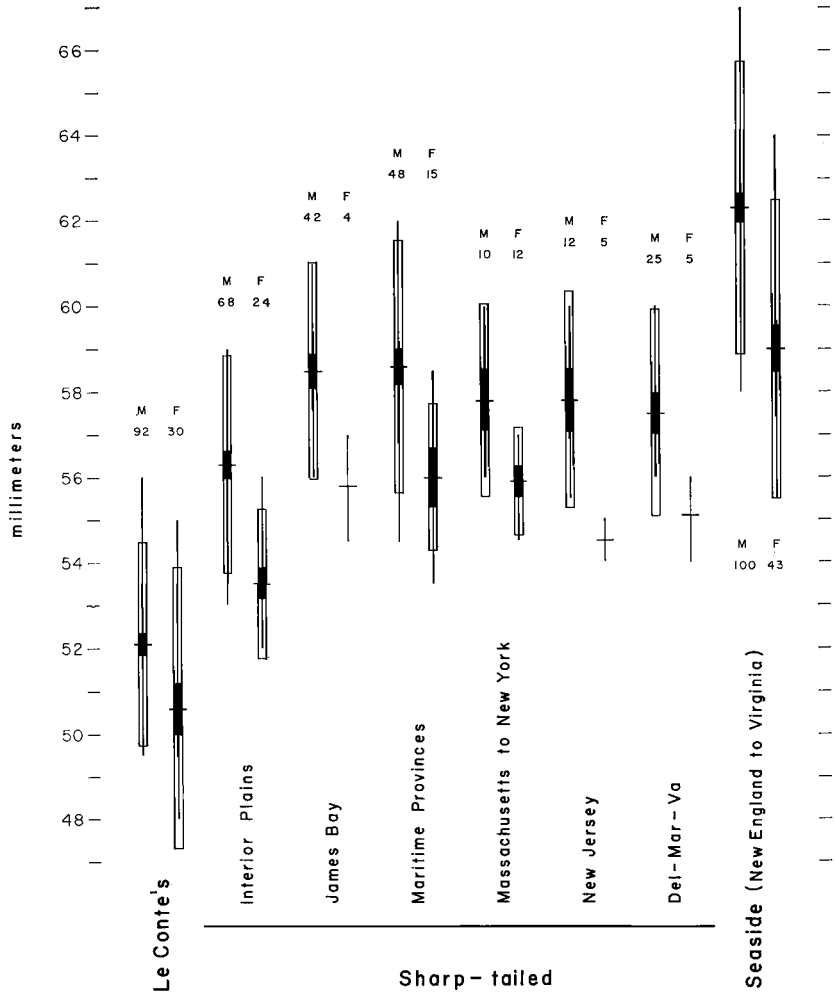

Figure 7. Comparison of wing lengths of the Le Conte's Sparrow, six populations of the Sharp-tailed Sparrow, and the Seaside Sparrow. The observed range and mean $\pm$ 2 standard deviations and $\pm$ 2 standard errors of the mean are given for males (M) and females (F). The number of specimens in each sample is also given.

Dakota averages lighter than *altera* from James Bay, and the latter averages lighter than either Atlantic coast population. The southernmost population that was measured (from New Jersey) has the greatest mean weight.

Migration

To determine the times of migration of *leconteii* and *c. nelsoni*, I com-

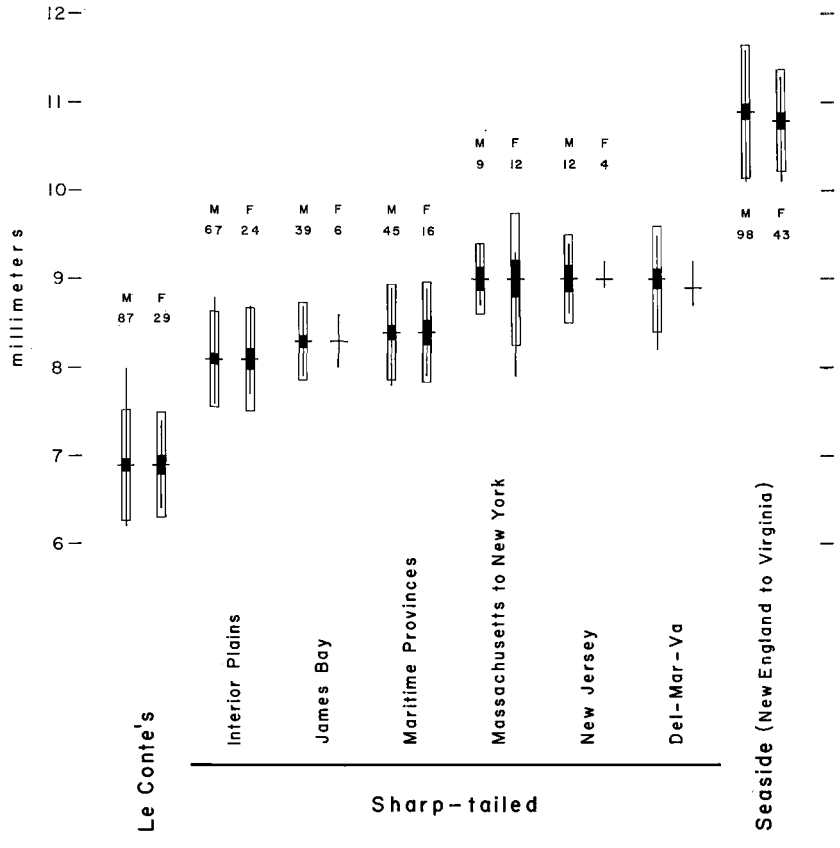

Figure 8. Comparison of bill lengths of the Le Conte's Sparrow, six populations of the Sharp-tailed Sparrow, and the Seaside Sparrow. The symbols are the same as in Figure 7.

pared specimen records for March, April, and May and for September, October, and November by date and by location (breeding range, winter range, and the area in between).

Prebreeding migration.—Le Conte's Sparrows arrive on the breeding range in late April and early May after a drawn-out migration. Most *leconteii* leave the winter range before 15 April but do not reach the breeding range until after 5 May (Figure 9). The five specimens in the migration area after 5 May were taken at Warsaw, Illinois, in 1883 and 1884. They and the adult taken at Warsaw on 2 August 1894 (Figure 2) may represent a breeding population from a formerly larger range. March records may represent wintering birds rather than migrants; only more

TABLE 3
WEIGHTS AND WING LENGTHS OF SOME LE CONTE'S AND SHARP-TAILED SPARROW POPULATIONS (MALES ONLY)

	N	Mean Wing Length	Weight		
			Mean (± 2 SE)	Range	SD
Le Conte's Sparrow					
North Dakota	26	52.0	13.4 (± 0.25)	12.4–15.2	0.63
James Bay	10	52.5	13.4 (± 0.43)	12.5–14.4	0.68
Sharp-tailed Sparrow					
North Dakota	12	55.5	15.2 (± 0.45)	14.0–16.3	0.78
James Bay	30	58.6	16.3 (± 0.28)	14.6–17.3	0.77
Maine[1]	21	59.4	18.3 —	17.4–20.9	—
New Jersey	10	57.8	19.8 (± 0.63)	18.2–21.0	1.01

[1] From Montagna (1940).

field work in the winter range and along the migration route can resolve these alternatives.

By contrast *c. nelsoni* leaves the winter range in mid-May and migrates rapidly to the breeding range, few transients being taken in between, and arrives after 15 May (Figure 9). The more rapid migration may reflect the lack of suitable habitat in the intervening area. As already noted, *leconteii* occupies somewhat drier habitats than does *c. nelsoni,* which may permit *leconteii* to migrate more slowly.

In North Dakota in 1965 *leconteii* was present the morning of 8 May. I first visited the area the previous evening and heard nothing, but the birds may have been there. The number of *leconteii* increased rapidly and reached a peak by mid-May. The first *c. nelsoni* appeared 21 May; the first day I saw more than one was 28 May. The period 21 to 28 May was cold with some snow, which may have inhibited singing and other activity and reduced my chance of finding the birds. The first *c. nelsoni* in the area west of the road appeared on 2 June. The number of *c. nelsoni* increased during the week following 28 May.

In 1966 I arrived in North Dakota on 29 April. Le Conte's Sparrows first appeared 4 May and *c. nelsoni,* 22 May. This spring the birds were quiet and numbers were difficult to estimate. As it turned out 1966 was a poor year for both *leconteii* and *c. nelsoni,* and few breeding birds appeared.

In conclusion, Le Conte's Sparrows arrive during the first week of May and reach a peak by mid-May. Sharp-tailed Sparrows arrive 2 to 3 weeks later and reach a peak in early June. On the Atlantic coast in the New York City region the Sharp-tailed Sparrow arrives on the breeding range at the same time the Seaside Sparrow does in late April (Bull, 1964).

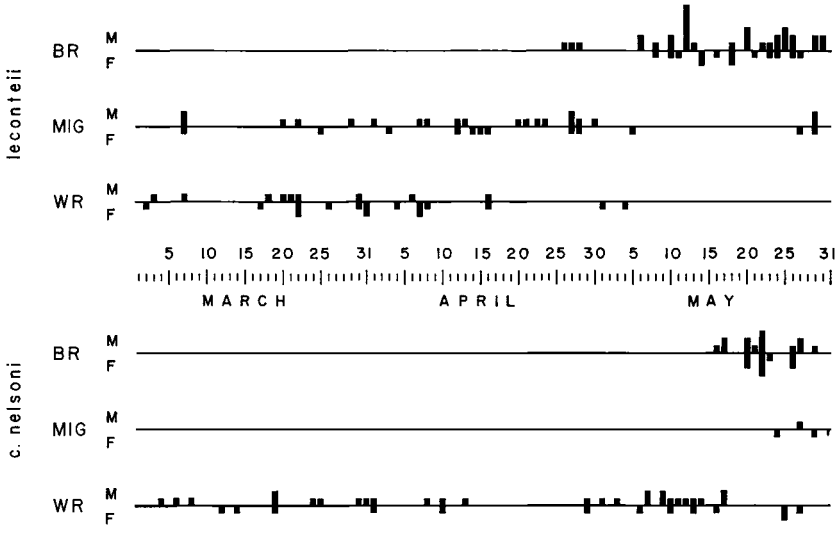

Figure 9. Prebreeding migration of the Le Conte's and Sharp-tailed (race *nelsoni*) Sparrows. Individual specimens, represented by black squares, are plotted by date according to where they were collected: on the breeding range (BR), on the winter range (WR), or in the area in between (MIG). Males (M) are plotted above the line, and females (F) below the line.

In 1955 at the central New Jersey coast both species arrived on 5 May and were most numerous during the second and third weeks of May (Woolfenden, 1956).

Postbreeding migration.—Both *leconteii* and *c. nelsoni* leave the breeding range in September, but *leconteii* does not reach the winter range before early November, long after the first *c. nelsoni* appear in late September (Figure 10). Thus, as in the spring migration, the fall migration of *c. nelsoni* is more rapid than that of *leconteii.*

VOICE

Song.—By observing marked birds I determined that only the males sing in both *leconteii* and *c. nelsoni* (see next section for method of sex determination). Breckenridge (in Roberts, 1932) thus describes the song of *leconteii,* "The Leconte's song begins with one short, barely audible, squeaky note, followed by a fine, high, insect-like buzz similar to the Grasshopper Sparrow and about one second in duration. A tiny, hardly audible, high *chip* terminates the effort," and the song of *c. nelsoni,* "a low initial note slurs immediately into a high, wheezy, nasal buzz, which terminates in a low, short, grating *ur.*" Borror (1961), using sonagrams, found

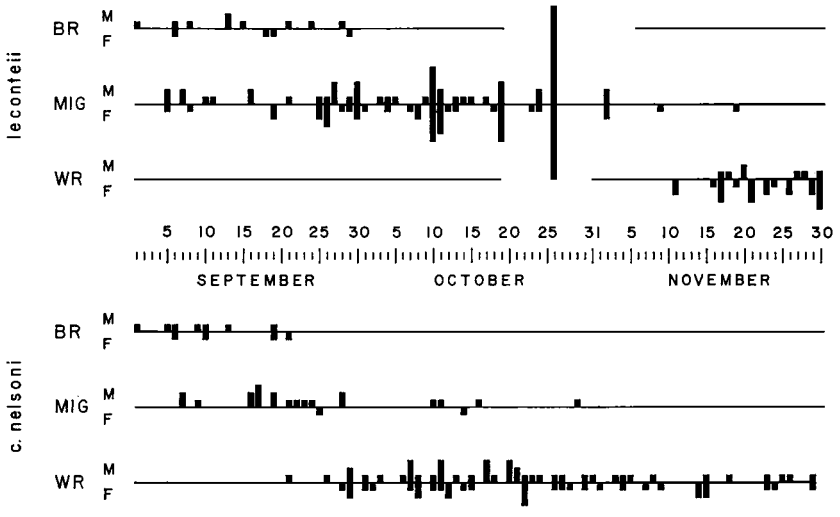

Figure 10. Postbreeding migration of the Le Conte's and Sharp-tailed (race *nelsoni*) Sparrows. Specimens are plotted in the same way as in Figure 9.

less variation between the songs of *leconteii* than between the songs of *caudacuta*. The song of *c. nelsoni* is louder than that of *leconteii*, and I could hear it as far away as 500 feet. Sonagrams show a close similarity in the songs of the two species (Murray, 1968).

Flight song.—In addition to their more typical songs, both *leconteii* and *caudacuta* have slightly different songs that are usually given in flight. The flight song of *c. nelsoni* is much like the typical song, except that it is almost always preceded by one, two, or three loud "tic" notes, spaced about a second apart. The flight song may be given one to three times in horizontal flight. Typically, *c. nelsoni* climbs to about 50 feet, levels off, flies from 200 to 500 feet and sings, drops to just above the grass, and continues flying another 100 feet or so before landing.

The flight song of *leconteii* is more complex and variable than that of *c. nelsoni*. The song is usually introduced by several "chip" notes, which are followed by an up-slurred note and a longer down-slurred note as the bird climbs to about 20 feet. As the bird is dropping into the grass on fluttering wings it gives the typical buzz. The landing is usually within a few feet of the takeoff point. Sometimes the introductory notes or the buzz is omitted. I have heard "flight songs" given from the ground.

Other notes.—Male *leconteii* give a series of high-pitched "chip" notes as an intruder enters a territory. Peabody (1901) and Walkinshaw (1937) state that the chips are given when an intruder is near the nest, but I have

heard them from the time the birds arrived in the marsh. The notes are ventriloquial and are often given at close range (ca. 15 feet). They are indistinguishable to my ear from the chip notes of *c. nelsoni.*

While in the blind I heard female *leconteii* on rare occasions give a somewhat loud, grating note. This is probably the note Walkinshaw (1937) refers to as "chit-chit-t-t-t-t." I never heard the notes "eélree-eélree-eélree-eélree," heard and described by Peabody (1901) and also heard by Walkinshaw (1937).

Singing behavior.—The singing behavior of *leconteii* in my study area differs somewhat from that reported for the species elsewhere. In Minnesota, "While . . . it occasionally sings from concealment in the dense vegetation, it is more inclined to mount to the top of a little willow or tall weed and there, over and over again, deliver its amusingly squeaky little ditty" (Roberts, 1932). Walkinshaw (1937), while stating that he rarely saw it sing more that a foot above the ground, writes, "The song, both in Michigan and Alberta, was [given] from the top or near the top of some dead rush." In North Dakota *leconteii* typically sang from the concealment of clumps of *Spartina.* Even when on the top of a mass of horizontal, dead *Spartina* stems, they were difficult to see. On occasion a particular bird would become conspicuous and sing from the top of a *Rumex* stem. Of all the birds I watched, only three used the meter-high stakes that were placed throughout the study area, and then not until mid-July. This behavior is different from other grassland species that use any tall perch within their territories. For instance, as taller stakes were placed in the territories of Grasshopper Sparrows (*Ammodramus savannarum*) on consecutive days, the tallest stakes were used immediately (Smith, 1963). Also, I heard flight songs throughout the day and the season, whereas Walkinshaw (1937) reports hearing only one flight song, and Peabody (1901) and Roberts (1932) do not mention them at all.

In 1965 I heard *leconteii* commonly give both songs and flight songs at night, but with diminishing frequency after mid-July. In 1966 I rarely heard *leconteii* sing at night.

The intensity of singing varies through the day, season, and between seasons. While *leconteii* can be heard throughout the day or night, more birds are singing in the early morning and evening than at midday or in the middle of the night. I could not relate silent periods with time of day or with weather. The difference in the intensity of singing between 1965 and 1966 was striking. In 1965 birds sang frequently from the time I arrived until I left. In 1966 singing was infrequent and did not become common until late May, although I regularly flushed silent birds. This

may have resulted from the lower population in 1966 and the consequent reduction of mutual stimulation.

In North Dakota *c. nelsoni* sings loudly and frequently from the top or the stem of sour dock, other tall plants (e.g. *Phragmites*), and the meter-high stakes, which were not used until after mid-June. Flight songs are common throughout the day and season. In 1965 I did not hear *c. nelsoni* sing at night until 21 July, when 5 or 6 were singing with only 2 or 3 *leconteii*. In 1966 *leconteii* sang infrequently at night, while I heard *c. nelsoni* almost every night I visited the study area. It seems possible that *leconteii's* nocturnal singing activity inhibits *c. nelsoni's*.

The singing of *c. subvirgata* seems to resemble that of *c. nelsoni* in that the birds sing frequently and loudly from a perch or in flight (Dwight, 1887; Lewis, 1920; Norton, 1927; Montagna, 1940, 1942). However Stone (1937), Montagna (1942), and Woolfenden (1956) remark on the weakness and infrequency of song of *caudacuta* in New Jersey. The last author reports that *caudacuta* sings a song that lasts "for almost 20 seconds and consists of a variable number of phrases." One wonders whether this difference in singing behavior of New Jersey *caudacuta* is not an effect of the presence of *m. maritima*.

Territoriality

In the past half century numerous definitions for the term "territory" have been proposed (see Nice, 1941; Hinde, 1956; and Carpenter, 1958). The most widely used definition seems to be Noble's (1939) "territory is any defended area." Emlen (1957) criticized this view, and I prefer his definition that territory is "an area or space in which a particular bird is aggressive and largely if not supremely dominant with respect to certain categories of intruders." Because aggressiveness or "defense" is often difficult to observe, Weeden (1965) suggested that "activity space" be used to refer to areas that enclose the activities of a particular individual and that "territory" be reserved for those areas in which aggression is observed.

The study area in North Dakota (Figure 6) was marked off into quadrats 100 feet square. In 1965 the study area was 500 feet square, and in 1966 this area was extended northward another 500 feet. Birds were captured with Japanese mist nets, and each was marked with a Fish and Wildlife Service numbered, aluminum band and three plastic, colored bands. At this time I measured the wing and weight, and I determined the sex by examining the cloacal protuberance as described by Salt (1954). I watched the birds with binoculars or telescope in the field or from a blind, and I marked the location and type of activity of each individual on a grid map several times a week. In order to determine the activity spaces of the males in the study area, only activity of identified males or un-

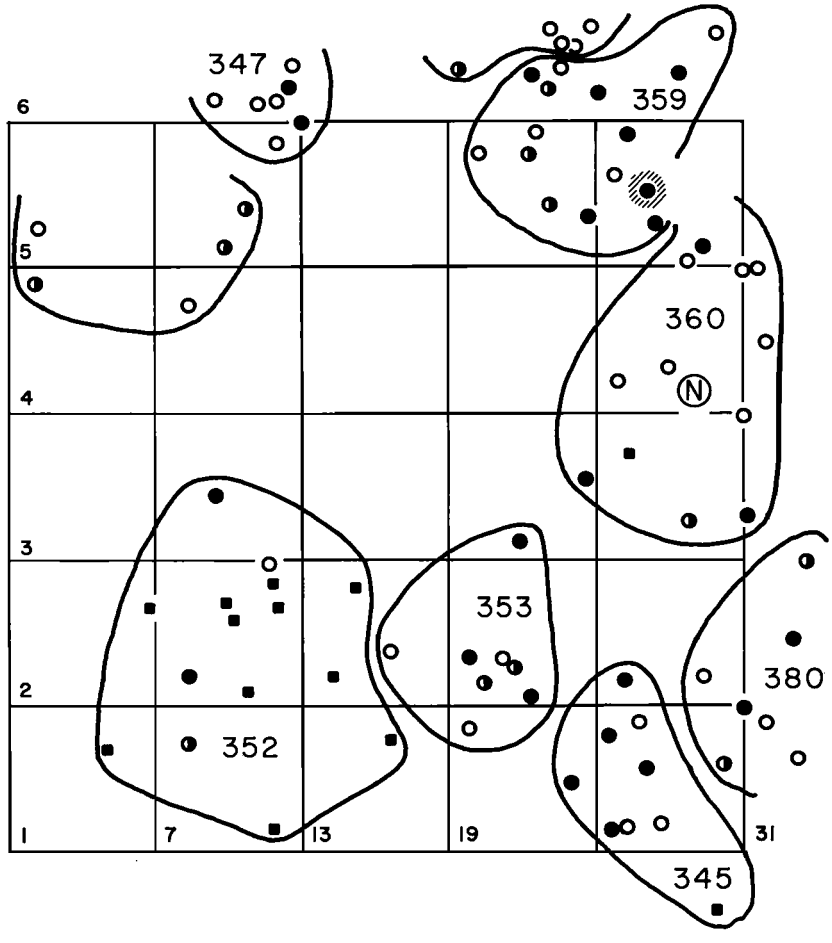

Figure 11. Le Conte's Sparrow territories in 1965. The quadrats are 100 feet square and take the number of the lowest numbered stake. Solid circles denote identified (color-marked) singing individuals, and solid squares denote identified, nonsinging individuals; open circles denote unidentified singing birds; half-open circles denote flight songs; and N denotes a nest site. Heavy lines delimit territories, and the numbers within them refer to the last three digits of the band number of the resident male. The broken territorial boundaries of 359 and 360 indicate where either a seasonal change in boundary or an overlap of territories occurred. The dot circumscribed by diagonal lines represents a single observation of 360.

identified singers was plotted on composite maps. Many observations at the same spot appear on the maps as a single dot, and thus Figures 11 and 12 do not present a quantitative picture of territory utilization. Females were seen only when they were feeding young or accidentally flushed.

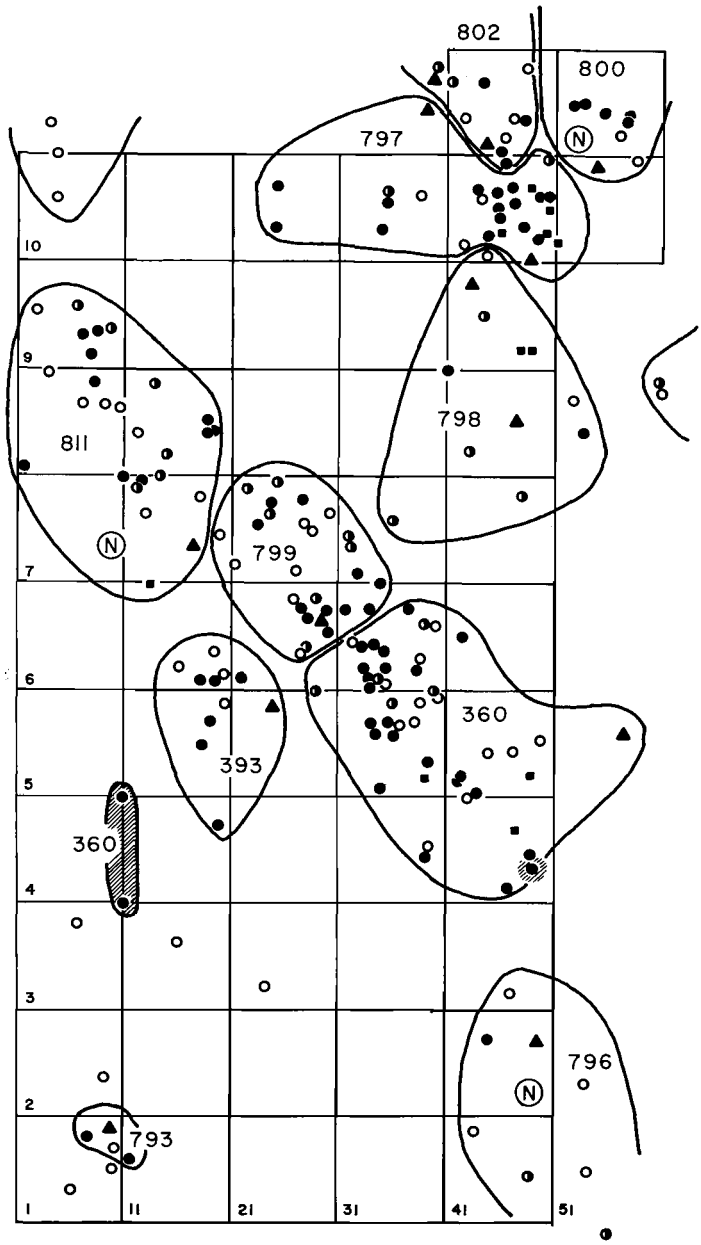

Figure 12. Le Conte's Sparrow territories in 1966. In addition to the symbols used in Figure 11, the triangles indicate where the birds were mist-netted. Stakes and quadrats were renumbered in 1966, but stakes 1 to 6 are the same for both years. Changes in territories, indicated by hatching, are described in the text.

LE CONTE'S SPARROW

Male Le Conte's Sparrows maintain activity spaces that appear to overlap only rarely and, then, at different times (Figures 11 and 12). That these activity spaces are territories is indicated by their stability, by observations of flights that resulted in supplanting an intruder, and singing, the songs being alternated with those of another individual or the songs occurring sequentially between three individuals. Territorial encounters are difficult to observe because they are brief, rarely occur near a human, and are frequently obscured by grass. They may be so subtle that an observer is not aware that two birds are doing anything more than singing. The following instances were observed well:

(1) 26 May 1966. In the evening *leconteii* 797 sang almost constantly from within a small area. Suddenly he flew about 75 feet toward the east and landed in the grass. Two other birds immediately flew up and away in different directions. Within a minute 797 returned to his original position.

(2) 29 May 1966. I watched at close range from a blind an unusually subtle instance of territorial behavior, which undoubtedly would have been missed if the blind had not been less than 50 feet from both birds. At 14:00 *leconteii* 797 and 802 were singing about 65 feet from each other. Between 14:15 and 14:30, 802 slowly moved 30 feet toward the territory of 797, singing constantly. By 14:30, 797 had moved toward 802 a few feet. The birds remained in this position, singing alternately (actually sequentially with *leconteii* 800) until 14:46. Then, 797 moved another 5 feet toward 802, who immediately moved about 10 feet away from 797 toward the center of his own territory. This encounter was not further pursued by 797, but all birds continued to sing.

(3) 30 June 1966. At 19:28 *leconteii* 360 was singing near the north edge of his territory. When he flew about 20 feet toward 799's territory, 799 immediately flew toward 360, who almost immediately flew 100 feet southward toward the center of his territory, where he began singing at 19:31. At 19:35 an unbanded *c. nelsoni* landed about 50 feet away but did not sing. Immediately, 360 flew at the *c. nelsoni*, who flew away, and 360 began singing from the spot where the *c. nelsoni* had been.

Permanence of territories.—Stenger and Falls (1959) and Weeden (1965) showed that territories of the Ovenbird (*Seiurus aurocapillus*) and the Tree Sparrow (*Spizella arborea*), respectively, are fluctuating areas without fixed boundaries, which change from day to day or even from hour to hour. This results in the seasonal composite maps showing overlapping territories. In contrast, *leconteii* territories rarely overlap (Figures 11 and 12), indicating that boundary fluctuations are small. In 1965 only one territorial boundary may have changed, but in 1966 several changes occurred. (a) Number 793 was banded on 20 May but had disappeared on 26 May when I saw an unbanded *leconteii* singing in his territory. (b)

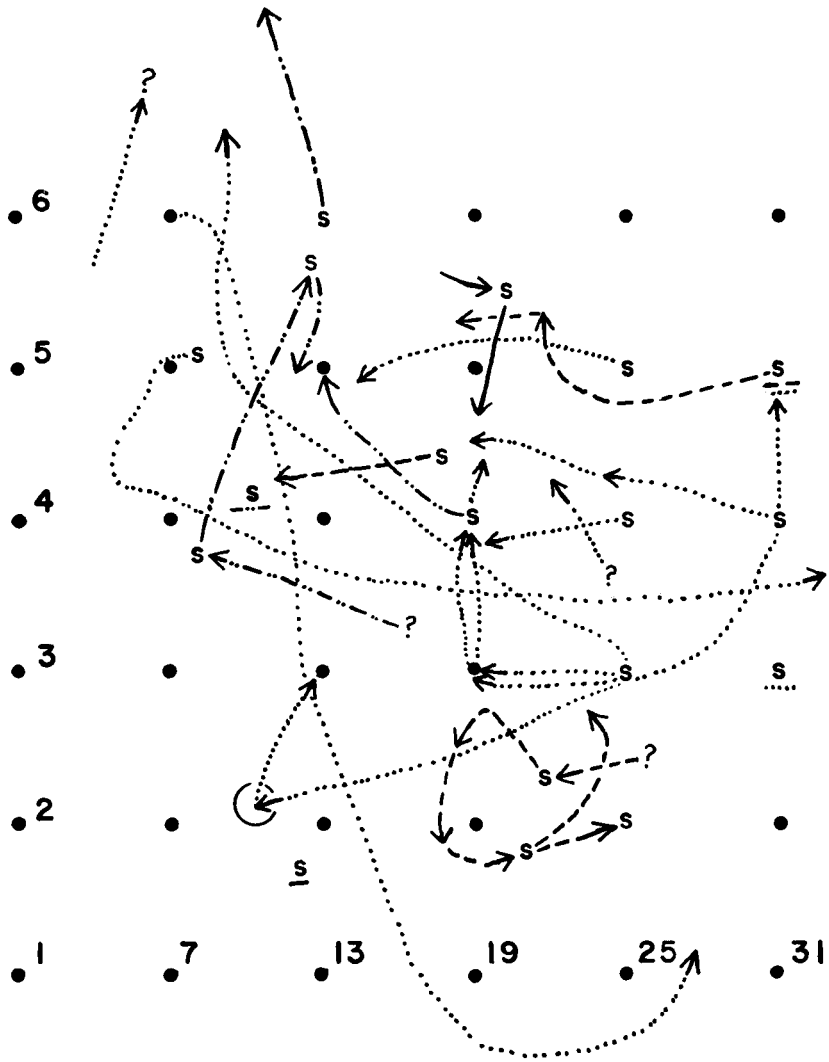

Figure 13. Activity of male Sharp-tailed Sparrows between 08:00 and 11:30 on 2 July 1965. Flight paths of three marked birds are indicated by the solid line, dashed line, and the line of alternating dashes and double dots. The flight paths of two or three unmarked birds are represented by dotted lines. The arrow shows flight from perch to perch, unless the beginning or end was not seen (indicated by a question mark). The "s" indicates a singing perch; where the singer cannot be identified by an arrow leading to or from the perch, the "s" is underlined appropriately. The circle in quadrat 8 indicates where the Sharp-tailed Sparrow was chased by a Le Conte's Sparrow.

Number 393 was banded on 1 July and was last seen on 6 July. I think his territory included the whole of the southwest corner of the study area. On 13 July, 360 was first seen outside his territory in what was probably 393's territory. He remained at this spot at least until I ended observations. (c) A single sighting of 796 on 19 July within the edge of 360's former territory was my last observation of a change or overlapping of territories.

In conclusion it appears that once territories are established in the spring, boundaries are relatively fixed, compared with those of the Ovenbird and Tree Sparrow. In middle or late July some individuals may take over sites vacated by others. Because of known stability (e.g. 797, 798, and 799), I am confident that certain individuals (e.g. 811) that were hard to catch were the unbanded birds I observed preceding capture.

Returns from 1965.—Of the seven banded males that occupied the study area in 1965 (Figure 11) only one, 360, returned in 1966 (Figure 12). None of the six banded females was known to have returned. Part of 360's 1965 territory was included in his 1966 territory. The low return of banded birds probably reflects the lower *leconteii* population throughout the floodplain in 1966.

SHARP-TAILED SPARROW

Sharp-tailed Sparrows of the race *nelsoni* have no territorial behavior. Males fly from song perch to song perch, crisscross each other's paths, and use common song perches. They often fly as much as 500 feet at a time. This behavior was evident from the time of their arrival until I left in late July. One morning's records (Figure 13) give some indication of *c. nelsoni* activity. Although no territories are maintained, the males do affect one another's behavior, as the following instances illustrate.

(4) 14 June 1966. At 09:19 an unbanded *c. nelsoni* was singing near stake 47 and *c. nelsoni* 806 was singing on stake 37. Unbanded *c. nelsoni* flew to within 5 feet of the base of stake 37. Then 806 stopped singing and flew to near stake 45. Unbanded *c. nelsoni* flew up to stake 37 and sang.

(5) 14 June 1966. At 11:02 an unbanded *c. nelsoni* flew to stake 40, after chasing or following a Savannah Sparrow that went to stake 59. Both started singing. A few minutes later another *c. nelsoni* appeared in the grass near the base of stake 40. The singing bird stopped and dropped to the ground, and almost immediately both flew westward about 100 feet before separating. Sex of the second bird is unknown.

(6) 8 July 1966. A *c. nelsoni* chipping in the grass at 15:35 dropped to the ground at 15:40. Another *c. nelsoni* flew in, landed on a grass stem, and dropped to the ground. At 15:41 both flew about 80 feet together, landed on the ground, and took off again, flying a long curving course. Sexes unknown.

(7) 11 July 1966. At 19:14 *c. nelsoni* 806 was singing on stake 16. Another *c. nelsoni* came in from the north and landed near the base of the stake. Number 806

stopped singing but remained on the stake about a half-minute before flying northeastward to stake 28. The second *c. nelsoni* flew southward, landed, and began singing.

(8) 11 July 1966. At 19:50 a *c. nelsoni* landed in the center of quadrat 15. Number 806, which had been singing at stake 26, flew to the spot. Shortly afterward a bird flew to the vicinity of stake 7 and began singing. Then 806 flew to stake 15 and sang.

(9) 12 July 1966. At 19:13, 806 was singing on stake 36, when *c. nelsoni* 384 sang in flight over stake 26 and landed in the grass near stake 16. Two minutes later 384 flew to stake 18, where he sang until 19:20. He may have flown because he had seen 806 flying toward stake 16, where 806 landed at 19:15. At 19:16, 806 flew to stake 26 without singing; then to stake 27; and then into the grass about 40 feet from stake 28 at 19:17. A minute later he was singing on stake 37.

Coloniality.—In 1965 *c. nelsoni* occurred in wet spots throughout the floodplain but seemed most common in the study area. In 1966 I rarely saw or heard a *c. nelsoni* outside the study area, where it appeared to be as common as in 1965. The concentration of *c. nelsoni* in the study area in 1966 when other locations appeared to be as suitable as in 1965 suggests that *c. nelsoni* is colonial, as are Atlantic coast *caudacuta* populations (Townsend in Forbush, 1929; Montagna, 1942; Griscom and Snyder, 1955; Woolfenden, 1956; Tufts, 1961).

Returns from 1965.—One of the three males and the only female banded in the study area in 1965 returned in 1966.

Interspecific Aggression

On occasion Le Conte's Sparrows are aggressive toward singing or nonsinging Sharp-tailed Sparrows, but I never saw *c. nelsoni* act aggressively toward *leconteii*. The following encounters are in addition to (3) above:

(10) 14 June 1966. At 09:46 *c. nelsoni* 806 was in the grass between stakes 17 and 27. He was not singing and allowed me a close approach, which is unusual. I withdrew a few feet and waited. He dropped out of sight. At 09:58 an unbanded *c. nelsoni* landed on stake 27 and sang. Almost immediately an unbanded, male *leconteii* (later banded as 811) flew to a point just over 100 feet away near stake 18. This Le Conte's Sparrow was not a persistent singer, but now he sang continuously. The two birds sang alternately until 10:02 when *c. nelsoni* flew 150 feet away. The Le Conte's Sparrow continued singing until 10:08 when he flew to where he had come from. All was quiet so I got up to leave. As I did, two *c. nelsoni* flew up. This was undoubtedly 806 and another, neither of which apparently responded to the singing that was going on around them.

(11) 17 June 1966. At 11:16 an unbanded *c. nelsoni* that had been singing halfway between stakes 17 and 18 flew to about halfway between stakes 9 and 19. He did not sing until 11:20, and after a minute a *leconteii* (later banded 811) flew directly toward the unbanded *c. nelsoni*. The latter flew off, and *leconteii* landed where *c. nelsoni* had been and chipped but did not sing. At 11:26 it dropped to the ground.

(12) 27 June 1966. At 10:13 *leconteii* 811 flew to the spot where an unbanded *c. nelsoni* was sitting quietly. The *c. nelsoni* flew off, and 811 started singing. This occurred at the same spot as encounter 11. At 10:22 the same or another *c. nelsoni* flew to this spot and sang until 10:30. It perched quietly until 10:34, when it flew away without apparent provocation. The same or another *c. nelsoni* was there at 11:18; it sang briefly before flying off, again without apparent provocation.

(13) 30 June 1966. At 18:04 a *leconteii* was singing near stake 36. At 18:05 a *c. nelsoni* flew in from the south, landed about 10 feet from the singing *leconteii*, and sang for about a minute before flying off. The *leconteii* appeared to take no interest in the *c. nelsoni*.

(14) 30 June 1966. At 19:02 a *c. nelsoni* was singing in the center of quadrat 26. When a bird flew in from the north the *c. nelsoni* stopped singing and peered around. He presently departed, and the second bird gave a brief chase before landing. The second bird (probably *leconteii* 799) then gave an incomplete *leconteii* flight song.

NESTING

The rank growth of the breeding habitat made finding nests difficult. I found three *leconteii* nests and one *c. nelsoni* nest by locating feeding parents, one *leconteii* nest by flushing the female, and one *leconteii* nest being built near my blind.

The *leconteii* nest has been well described by Peabody (1901: 132), "where dead and fallen grass is thickest, the bird interweaves dead grasses [stems and leaves] among the standing stems, thus forming a rude nest. Within this is placed the nest proper; this is an exquisitely neat, well-rounded and deeply cupped structure, composed uniformly of the very finest grasses." In the nests I found in North Dakota the inner and outer nests were not distinct entities and the open cup is almost always covered by a thick thatch of dead grasses. All five nests I found were made of *Spartina*. Peabody (1901) found that the base of the nests averaged about 8 inches above the ground. The nests I found ranged from resting on the ground to 5 centimeters (2 inches) above the ground.

The *c. nelsoni* nest I found in a small stand of *Scolochloa* near a small slough (lower center of Figure 5). Peabody's description of *leconteii's* nest fits just as well for *c. nelsoni's*, which, however, was constructed of *Scolochloa*. It was entirely above the ground, as were the *c. nelsoni* nest described by Breckenridge and Kilgore (1929), the *c. subvirgata* nests described by Lewis (1920) and Norton (1927), and the nests of *c. caudacuta* described by Woolfenden (1956). Two unusual nests reported by Rolfe (1899) and Bownan (1904) and perhaps misidentified were sunk into the ground in open stands of short grass, as are Savannah Sparrow nests.

Brood parasitism.—All *leconteii* nests were parasitized by the Brown-headed Cowbird. These large young no doubt account for the high feeding rate I observed at nests 1, 4, and 5. Both male and female were bringing

food, and feeding trips averaged one per minute. In contrast Walkinshaw (1937) reported that a female fed three 1-day-old *leconteii* nine times in 3.5 hours.

The dates on which found, the contents, and the fates of the *leconteii* nests are:

1. 20 July 1965	2 cowbirds (fledged)
2. 16 June 1966	2 cowbird eggs (deserted)
3. 19 June 1966	4 *leconteii* eggs and one cowbird egg (destroyed)
4. 7 July 1966	3 cowbirds (fledged) and one cowbird egg (unhatched)
5. 20 July 1966	1 cowbird (fledged) and 3 cowbird eggs (unhatched).

I located a *c. nelsoni* carrying food on 25 July 1966, but I could not find the well-concealed nest until the next day. The young had left, and thus their identity is unknown.

Discussion

Geographic Variation

Wing length and weight.—Snow (1954), Hamilton (1958, 1961), and others have shown that wing length is influenced by many factors. They studied species or genera of continent-wide distribution that encounter a variety of environmental conditions. My study concerns two species of relatively limited distribution and relatively uniform habitat.

No direct relationship between wing length and weight in *caudacuta* is evident (Figure 14). The shortest-winged (*c. nelsoni*) is the lightest, but the next shortest-winged (*c. caudacuta* and *diversa* from New Jersey) is the heaviest. By including data from populations of close relatives for which comparable information exists, a direct relationship between wing length and weight appears when comparing *leconteii, henslowii, c. nelsoni, c. altera, savannarum,* and *bairdii* (Figure 14). Diverging from this relationship in increasing order of magnitude are *c. subvirgata, c. caudacuta* and *diversa,* and *m. maritima.* These populations inhabit Atlantic coastal marshes. Of these, *c. subvirgata* migrates the farthest, while some individuals of the last two populations winter within the breeding range (Bull, 1964; Griscom and Snyder, 1955; Stewart and Robbins, 1958). Wing length in this group of sparrows probably has been strongly influenced by the migratory habits of the populations.

Bill length.—Differences in bill length between sympatric populations are generally assumed to be a result of divergence in allopatry because of differences in available food or a result of divergence in sympatry through

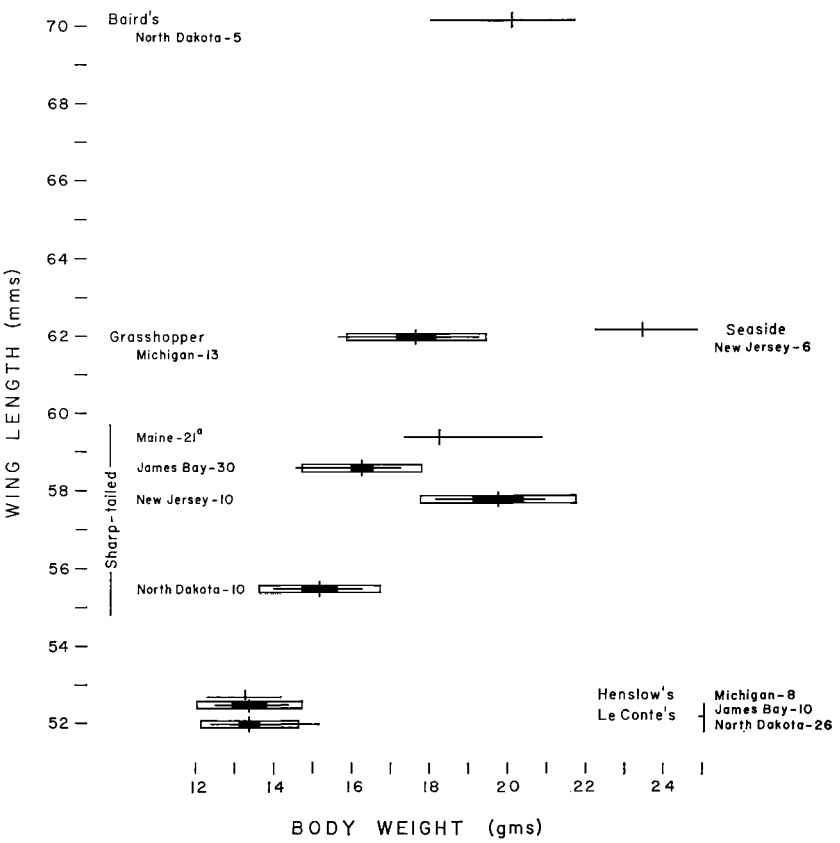

Figure 14. The relationship between body weight and wing length among several populations of sparrows. Symbols same as in Figure 7; [a] from Montagna, 1940.

interspecific competition for food. Differences in bill length may also arise in sympatric populations through selection for specific recognition marks, from differences in habitat and consequently in diet, or both.

If average differences in bill length reflect average differences in diet and if different habitats provide different diets, average differences in bill length between races of *caudacuta*, between *c. nelsoni* and *leconteii*, and between *c. caudacuta* and *m. maritima* may be explained by average differences in the food available in their habitats. Differences between the habitats of these populations are known (if only qualitatively). The three races of the Atlantic coast inhabit salt marshes that, progressing southward, lose their "meadowy appearance and [become] coarse, tall, and sparse" (Montagna, 1942: 116). While *c. caudacuta* and *c. diversa* inhabit

TABLE 4
MEASUREMENTS OF SOME SEASIDE SPARROW POPULATIONS (MALES ONLY)

Race	N	Mean (± 2 SE)	Range	SD
WING LENGTH				
maritima	100	62.3 (± 0.34)	57.0–67.0	1.72
macgillivraii	22	61.7 (± 0.54)	59.0–63.5	1.27
pelonota	16	60.6 (± 0.66)	58.5–63.0	1.33
peninsulae	17	60.4 (± 0.81)	58.5–64.0	1.66
fisheri	23	60.1 (± 0.48)	58.0–62.0	1.15
BILL LENGTH				
maritima	98	10.9 (± 0.08)	9.2–11.6	0.38
macgillivraii	27	10.8 (± 0.13)	10.2–11.4	0.34
pelonota	14	11.1 (± 0.20)	10.6–11.9	0.37
peninsulae	21	10.6 (± 0.18)	10.0–11.3	0.40
fisheri	24	11.2 (± 0.15)	10.6–12.0	0.38

only salt marshes, some populations of *c. subvirgata* live in brackish and fresh-water marshes (Dwight, 1887; Norton, 1897; Montagna, 1942). Todd (1963: 678) states, "The James Bay race of the Sharp-tailed Sparrow is virtually a salt marsh bird; its occurrence at Moose Factory is in a brackish marsh," but arctic, eastern American, and western American species of obligate halophytes, as well as more widespread species, make up the James Bay marsh flora (Schofield, 1959), which no doubt gives the James Bay marshes a different character from Atlantic coastal marshes. As noted above, *c. nelsoni* inhabits freshwater marshes. Le Conte's Sparrow tends to occupy drier habitats than does *c. nelsoni* (Godfrey, 1952; and above), and *c. caudacuta* tends to occupy drier habitats than does *m. maritima* (Stone, 1937; Montagna, 1942; Woolfenden, 1956). Because neither the foods available in these habitats nor the diets of the birds are known, the validity of the two widely accepted assumptions regarding the evolution of bill size cannot be evaluated. Nevertheless, differences in foods available in different habitats are not unexpected, and I suggest that differences in bill length result from differences in diet between the populations. The small differences in bill length of sympatric populations probably reflect slight habitat differences rather than interspecific competition for food.

Within the Seaside Sparrow the bill of *m. maritima*, the race whose breeding range overlaps *caudacuta*'s, is not significantly longer than the bill of *m. macgillivraii* and is shorter than the bill of *m. pelonota*, two Atlantic coast races whose breeding ranges do not overlap *caudacuta*'s (Table 4). Therefore, character displacement has not occurred in the bill length of *maritima*.

Conclusion.—The smallest-billed, shortest-winged, and lightest race of

caudacuta (*c. nelsoni*) lives with its smaller-billed, shorter-winged, and lighter congener (*leconteii*), whereas the longest-billed and heaviest *caudacuta* population (*c. caudacuta* and *diversa*) lives with its longer-billed and heavier congener (*m. martima*). Thus the races of *caudacuta* and their sympatric relatives show convergence rather than character displacement.

TERRITORIAL BEHAVIOR

Differences in territorial behavior and interspecific aggression between *leconteii* and *c. nelsoni* are striking. Male Le Conte's Sparrows maintain typical Type A (Nice, 1943) territories in which each pair nests and feeds, whereas male Sharp-tailed Sparrows are not territorial at all. Le Conte's Sparrows are aggressive towards Sharp-tailed Sparrows, but Sharp-tailed Sparrows are not aggressive towards Le Conte's Sparrows. Most reports indicate that emberizines are territorial. An exception is Tomkins (1941), who stated that an unmarked *m. macgillivraii* population showed no territorial behavior. A marked population should be studied because Woolfenden (1956) showed that marked *m. maritima* maintained Type A territories in which, however, the nesting area and feeding area are sometimes separated. The nonterritoriality of *caudacuta*, previously noted by Woolfenden (1956), may be unique among emberizines, and it is undoubtedly derived from more typical territorial behavior.

Birds with established territories are usually dominant over conspecific intruders (Hinde, 1956) and sometimes dominant over intruders of other species. The latter behavior is called "interspecific territoriality," which has been defined as occurring when "A territory holder of one species exhibits persistent aggressive behavior to an intruding bird of a second species, showing to it some, if not all, of the reactions usually forthcoming in intraspecific encounters" (Simmons, 1951: 407). This behavior should result in the exclusion of the second species from the territories of the first. The *leconteii*'s aggression toward *c. nelsoni* is not interspecific territoriality because it is not persistent and because *c. nelsoni* is not excluded from the territories. Nevertheless, I think interspecific territoriality may have occurred in the past and may account for the behavioral differences observed today.

Because the Le Conte's and Sharp-tailed Sparrows are more similar to each other in molt, plumage, and voice than to any other species (Murray, 1968), I think they had a common ancestor. Their evolution could have occurred in the following way: As ancestral *leconteii* and ancestral *caudacuta* diverged from their territorial ancestor, each population was territorial and occupied similar habitats. When they became sympatric they tended to occupy the same habitat, and because of their similarity in plumage and voice interspecific territoriality developed. If ancestral

caudacuta were a late migrant, as *c. nelsoni* is today, it would have the disadvantage in establishing territories because it would arrive in habitat already occupied by territorial, ancestral *leconteii*. Ancestral *caudacuta* was forced into marginal habitat, although some individuals may have occupied spaces unoccupied by ancestral *leconteii* in the optimal habitat. Any change in the behavior of ancestral *caudacuta* that enabled it to breed in space occupied by ancestral *leconteii* in the optimal habitat would be selected for, if ancestral *caudacuta* were more successful in the optimal habitat than in the marginal habitat. I hypothesize that by becoming nonterritorial and nonaggressive, ancestral *caudacuta* was able to breed more successfully in habitat occupied by ancestral *leconteii*, and that it is this difference in territorial behavior that permits *leconteii* and *c. nelsoni* to occupy the same habitat today.

Woolfenden (1956) reported that *maritima* sometimes chases *caudacuta* out of its territories, and thus nonaggression may permit *caudacuta* to live with *maritima*. Indeed, interaction with ancestral *maritima* rather than with ancestral *leconteii* may be responsible for *caudacuta's* behavior, but I prefer the *caudacuta-leconteii* interaction because of the difference in their migratory behavior.

Mating System of the Sharp-tailed Sparrow

The Sharp-tailed Sparrow is apparently promiscuous. Woolfenden (1956) observed both marked males and females copulating with several birds of the opposite sex. Male *caudacuta* may attempt copulation with any bird. Montagna (1942) collected a male *c. caudacuta* copulating with a female *m. maritima*, and in North Dakota I saw Sharp-tailed Sparrows fly after passing Savannah and Song Sparrows. As mentioned above, *caudacuta* appears to be colonial, or at least to occur in groups rather than be dispersed over the marsh. It seems possible that with the loss of territoriality there has been selection for aggregations, these groups of singing birds attracting females, and for the males to "court" any bird that appears receptive. Strong supporting evidence is difficult to gather because of the nature of the habitat (in North Dakota), the secretiveness of females, and the large activity spaces of males. The situation in *c. caudacuta* and *c. diversa* is of interest because the males sing considerably less than do males of *c. subvirgata* (Montagna, 1942) and *c. nelsoni*.

The hypothesis that promiscuous or polygynous mating systems have evolved in marsh inhabiting species because certain males obtain better territories than other males (Verner and Willson, 1966) is not applicable to *caudacuta*, which is not territorial.

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SUMMARY

The geographic range of *leconteii* overlaps and is nearly identical with the geographic range of the two inland races of *caudacuta*.

Although *leconteii* occupies habitats that are on the average drier than those occupied by *c. nelsoni*, individuals of both species occupy identical habitat where both are most common in North Dakota.

The shortest-billed population of *caudacuta* (*c. nelsoni*) occurs with shorter-billed *leconteii* and the longest-billed *caudacuta* (*c. caudacuta* and *c. diversa*) occur with longer-billed *m. maritima*. The similarity in bill lengths between the races of *caudacuta* and their sympatric relatives is attributed to convergence.

Wing length in *caudacuta* does not correlate with body weight. The short-winged but heaviest population migrates the shortest distance. The same results obtain when comparing the related species with each other.

Le Conte's Sparrow is an earlier prebreeding migrant and a later post-breeding migrant than *c. nelsoni*. The migration of *leconteii* is drawn out, whereas that of *c. nelsoni* is rapid.

Le Conte's Sparrow is territorial, *caudacuta* nonterritorial. Le Conte's Sparrow is aggressive toward *c. nelsoni* at times. The nonterritorial behavior of *caudacuta* is considered an adaptation that permits it to use habitats in which its territorial relatives have already established territories.

Nests are difficult to find, and all those found with eggs or young were parasitized by the Brown-headed Cowbird.

The singing and display of male *caudacuta* in colonies seems to be an adaptation that enables females to find males.

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