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A COMPARATIVE STUDY OF THE LE CONTE'S AND SHARP-TAILED SPARROWS WITH COMMENTS ON THE ECOLOGY OF SYMPATRIC SPECIES

by
Bertram George Murray, Jr.

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Doctoral Committee:

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A COMPARATIVE STUDY OF THE LE CONTE'S AND SHARP-TAILED SPARROWS WITH COMMENTS ON THE ECOLOGY OF SYMPATRIC SPECIES

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The Le Conte's Sparrow (Passerherbulus caudacutus) and the Sharp-tailed Sparrow (Ammospiza caudacuta) occupy nearly identical ranges in the interior of North America, and they are most common in the same habitat. As sympatric avian species usually differ in habitat, bill size, or foraging behavior, the purpose of this study is to determine the differences between the Le Conte's and Sharp-tailed sparrows that permit them to coexist.

The problem is approached by (1) determining mensural differences from museum specimens, (2) studying the behavior and ecology of color-marked birds in North Dakota, and (3) comparing the inland race of the Sharp-tailed Sparrow (nelsoni) with other races, especially with caudacuta, which lives with another relative, the Seaside Sparrow (Ammospiza maritima), in salt-marshes along the Atlantic coast.

The Sharp-tailed Sparrow differs from its sympatric relatives in length of wing, length of bill, body weight, habitat, song, and territorial behavior, and it is a later migrant in spring than the Le Conte's Sparrow. Le Conte's and Seaside sparrows are territorial while the Sharp-tailed Sparrow is not territorial. I hypothesize that the Sharp-tailed Sparrow lost its territorial behavior as a result of interspecific territorial behavior of the Le Conte's Sparrow. The Le Conte's Sparrow is dominant in its territorial behavior because it arrives in the

breeding habitat several weeks earlier than does the Sharp-tailed Sparrow and is able to establish territories before the Sharp-tailed Sparrow arrives. The lack of territorial behavior in the Sharp-tailed Sparrow is considered to be the adaptation that permits the Sharp-tailed Sparrow to live with its relatives. Other differences between the species are slight and are not considered to be adaptations that permit sympatry. The colonial nature of Sharp-tailed Sparrows is an adaptation that aids the females in finding non-territorial males.

Other instances of interspecific territoriality are examined. In two of the three other cases where two related species live in the same habitat, one of the pair is non-aggressive and it comes into breeding condition later than its interspecifically aggressive relative. In the third case the later-arriving species is dominant by virtue of its larger size. In all other cases the two species maintain mutually exclusive territories and are normally separated ecologically, geographically, or both. From this survey interspecific territoriality appears to be an inadaptive character in at least one species whenever it occurs. One of the species must change its territorial behavior if it is to coexist with its dominant relative indefinitely. Thus, territorial species seem to be competing for space rather than food.

Differences in habitat, bill size, and foraging behavior, which are usually considered adaptations that permit sympatry and which result from interspecific competition for food or some resource other than space can be as well explained as a result of interspecific territoriality or aggression.

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INTRODUCTION

The conviction of most ecologists that interspecific competition will result in the elimination of one of the competing species or in the evolution of differences that will permit the two species to coexist without competing 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). Differences in habitat seem to be the rule in sympatric species of Vireo (Hamilton, 1962); differences in bill size or shape in drepaniids (Amadon, 1947), geospizines (Lack, 1947), Sitta (Vaurie, 1950, 1951), and numerous pairs of species (Schoener, 1965); differences in foraging behavior in Parus (Hartley, 1953; Gibb, 1954) and Dendroica (MacArthur, 1958); and differences in food items eaten by cormorants (Lack, 1945), birds of prey (Lack, 1946; Storer, 1966), and Parus (Betts, 1955). In spite of apparent exceptions in Pipilo (Marshall, 1960) and Thryothorus (Grant, 1966), these examples support the original generalizations but do not preclude further study of other sympatric species.

The subjects of the present study are the Le Conte's Sparrow (Passerherbulus caudacutus) and the Sharp-tailed Sparrow (Ammospiza caudacuta). I chose this pair for study because the latter is not only sympatric with the Le Conte's

Sparrow in interior North America but is sympatric with the Seaside Sparrow (Ammospiza maritima) along the Atlantic coast. A comparison of the relationship of the Seaside and Sharp-tailed sparrows, studied by Woolfenden (1956), with the relationship of the Le Conte's and Sharp-tailed sparrows might show how selection on the wide-ranging Sharp-tailed Sparrow was influenced by its sympatric relatives.

In the first part of this paper I describe what I have learned about the Le Conte's and Sharp-tailed sparrows and interpret their ecologic and taxonomic relationships, as well as compare Sharp-tailed Sparrow populations with each other and with their sympatric relatives. The results of this study have led me to reconsider interpretations of the ecologic relationships of other groups of species, and in the second part of this paper I present alternative explanations for interspecific territoriality and differences in habitat, bill size, and foraging behavior between sympatric species.

NOMENCLATURE

The Le Conte's Sparrow and the Sharp-tailed Sparrow are currently placed in different genera by the American Ornithologists' Union (1957). Only briefly were they ever considered congeneric. The first (A.O.U., 1886) and second (A.O.U., 1895) editions of the "Check-list" listed both species in Ammodramus but in different subgenera (Coturniculus and Ammodramus, respectively). Ridgway (1901) gave generic rank to these subgenera and transferred Le Conte's Sparrow and Henslow's Sparrow (then Coturniculus henslowii, now Passerherbulus henslowii) to Ammodramus, a treatment later followed by the A.O.U. (1903). The group remained intact despite rapid nomenclatural changes, which saw Coturniculus become Ammodramus and the former Ammodramus become first Ammospiza (Oberholser, 1905) and, then, Passerherbulus (Stone, 1907), until 1917 when Oberholser split the five species he recognized in 1905 as Ammospiza into four genera. The Sharp-tailed Sparrow became Ammospiza caudacuta, and the Le Conte's Sparrow became Passerherbulus leconteii, later to become Passerherbulus caudacutus (Oberholser, 1919). Not all of the changes proposed by Oberholser (1905, 1917, 1919) were accepted by the A.O.U. (1931), but the generic distinction between Le Conte's Sparrow and Sharp-tailed Sparrow was accepted. No changes have been made since. As yet, no diagnoses exist for these genera as presently constituted. For reasons discussed later, I think the Le Conte's Sparrow is more closely related to the Sharp-tailed Sparrow than to the Henslow's Sparrow, and I propose that the Le Conte's Sparrow be placed in the genus Ammospiza and the Henslow's Sparrow in Ammodramus. The specific name

Fringilla caudacuta Latham 1790, for the Le Conte's Sparrow becomes a secondary homonym of the specific name for the Sharp-tailed Sparrow (Oriolus caudacutus Gmelin 1788). The earliest available name for the Le Conte's Sparrow is Emberiza Le conteii Audubon 1844. The Le Conte's Sparrow becomes Ammospiza leconteii (Audubon) and the Henslow's Sparrow becomes Ammodramus henslowii (Audubon).

In this paper when the common name is not used, the Le Conte's Sparrow is referred to as leconteii and the Sharp-tailed Sparrow as caudacuta. Subspecific names of the races of caudacuta are preceded by "c." After being introduced with complete common and scientific names, other species are often referred to by use of the specific name, and the names of their races are preceded by the initial of the specific name.

METHODS AND MATERIALS

Field work on leconteii and caudacuta was carried out at the Lower Souris National Wildlife Refuge near Upham, McHenry County, North Dakota, in the summers of 1965 and 1966. In 1965 I arrived at the refuge on 7 May and departed on 30 July; in 1966 I arrived on 29 April and departed 26 July. The primary study area was in the floodplain of the Souris River, about three miles east of Upham.

In addition, I examined and measured specimens of leconteii, caudacuta, and other species in six museums: The University of Michigan Museum of Zoology, The American Museum of Natural History, United States National Museum, Museum of Comparative Zoology at Harvard University, National Museum of Canada, and Royal Ontario Museum.

Details of the methods used in analyzing the data are included at the beginning of the topical sections of the first part of this paper.

DISTRIBUTION AND HABITAT

Distribution

In order to determine the limits of the breeding range, June, July, and August records of adult specimens were plotted on a map. December, January, and February specimen records were plotted for the winter range.

The Sharp-tailed Sparrow occupies three disjunct areas (Figure 1). The race *nelsoni* inhabits fresh-water marshes in glaciated portions of the Interior Plains Region from southeastern North Dakota and northwestern Minnesota northwestward to Great Slave Lake. Its range extends into eastern British Columbia (Munro and Cowan, 1947). Reports that *c. nelsoni* bred as far south as Chicago are unsubstantiated (*fide* Peters, 1942), and the significance of the single 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*) occur in marshes along the Atlantic coast from the Maritime Provinces to Virginia. Breeding Sharp-tailed Sparrows do not occur on the Canadian Shield, which keeps the three breeding areas separated.

The range of *leconteii* overlaps those of *c. nelsoni* and *c. altera* (cf. Figures 1 and 2). Le Conte's Sparrows inhabit fresh-water marshes and low wet prairie in glaciated portions of the Interior Plains Region, extending into British Columbia (Munro and Cowan, 1947). A nearly disjunct population occurs along the shores of Hudson and James bays. Todd (1943) found it common in suitable habitat in southern James Bay. Le Conte's Sparrows are rare on the Canadian

Shield, but a few have been taken as far east as eastern Quebec. The ranges of c. nelsoni, c. altera, and leconteii in relation to physiographic regions and vegetation types are shown in Figures 3 and 4, respectively.

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, letter, 27 October 1966), Missouri (Audubon Field Notes, Christmas counts, various years), and South Carolina southward to the Gulf coast (Figure 2). Most winter specimens were taken at coastal localities, where many caudacuta specimens also 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 occur commonly in an extensive marshy area in the floodplain of the Souris River, about three miles east of Upham, McHenry County, North Dakota. In the area selected for study (foreground Figure 5 and Figure 6), cordgrass (Spartina pectinata) was the predominant plant. Other grasses forming extensive stands in the vicinity were squirrel-tail (Hordeum jubatum), white-top (Scolochloa festucacea), and phragmites (Phragmites communis). Cat-tail (Typha latifolia) was common in nearby sloughs and ditches. Sedges were not common near the study area. The common stiff-stemmed plant that served as song perches was sour dock (Rumex Acetosa).

In 1965 leconteii was found throughout the floodplain shown in Figure 5, except in the wettest parts. It was most dense in Spartina, less dense in the sparser Hordeum, and rare in Bromus on the dry upland. In 1966

when bird populations were very low, leconteii was rare outside the Spartina study area. In 1965 c. nelsoni was found scattered throughout the area but in wetter habitats. It was common in Spartina, frequent in Scolochloa and at the edges of Phragmites stands, and was never seen or heard on the upland. In 1966 c. nelsoni was rarely observed away from the vicinity of the Spartina study area, where it appeared to be almost as common as in 1965. Although there is an average difference between habitats utilized by leconteii and c. nelsoni, both occupy the Spartina habitat, where both seem to be most common. However, only leconteii is found in some habitats and only c. nelsoni in others. Nero (1963) found leconteii but not c. nelsoni in the Lake Athabaska region of Saskatchewan, while both species occur at the western end of the lake in Alberta (Figures 1 and 2). In Alberta leconteii occupies "drier edges of moist meadows and marshes where rank growths of sedges and grasses are interspersed with willow and alder," and c. nelsoni occupies "wetter parts of marshy areas ... often frequenting the cat-tails or bulrushes at the water edge" (Godfrey, 1952: 171-172). 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 that of the interior races of caudacuta.

An advantage of Spartina and Scolochloa 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 may remain standing and those that fall form, at best, a thin mat. This difference is illustrated particularly well in the vertical photograph (Figure 6). The large dark patch in the upper center is an essentially pure stand of Hordeum that appears dark because it is 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 is darker than Hordeum. The large Hordeum patch is actually the driest spot in the study area and was not occupied by leconteii (cf. Figures 7 and 16) or c. nelsoni. Instead, two pairs of Savannah Sparrows (Passerculus sandwichensis) bred there.

The upper third of the study area (Figure 7) was hayed in 1964, and in 1965 leconteii was never seen there, even after the stubble was replaced by 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 two-year-old Hordeum field, although they are scarce there. If an area is hayed year after year, leconteii would become scarce or absent. The Sharp-tailed Sparrow could survive in areas that are too wet for haying.

Zoogeography

Udvardy (1963) tentatively grouped the North American species of passerines into 27 Ecogeographic Faunal Groups on the basis of their geographic (primarily) and ecological (when known) similarities. He included leconteii and caudacuta in the Prairie Fauna with 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). Although the ranges of leconteii and caudacuta overlap these five prairie species, leconteii and caudacuta are not found in the prairie community, and I think they should be removed from the Prairie Fauna. In North Dakota, the passerine fauna in the Souris River floodplain where leconteii and caudacuta are found includes 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). According to Udvardy, the Short-billed Marsh Wren is in the Eastern Ecotone Fauna, the Western Meadowlark and Yellow-headed Blackbird are in the Western Woodland-edge Fauna, and the rest have widespread distributions. Another indication that leconteii and caudacuta do not belong to the Prairie Fauna is that their ranges extend far north of the northern limit of prairie and eastward to coastal Hudson and James bays (Figure 4).

GEOGRAPHIC VARIATION

Methods

Three kinds of measurement were recorded from museum specimens. They are (1) wing chord, measured to nearest 0.5 mm with dividers, (2) bill from nostril, measured to nearest 0.1 mm with dial calipers, and (3) weight to nearest 0.1 gram (taken from label). Damaged and distorted specimens were not measured. Additional weights were obtained from mist-netted birds. Only data from specimens taken in June and July are used.

Results

To determine whether *leconteii* varies geographically its range has been divided into five areas (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 the last area, and that population is not considered in the statistical comparisons.

In these populations only males can 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 areas are not statistically significant (Table 1). Variations in the means of females are probably not significant. Therefore, the data have been combined for each sex for comparison with other species.

The range of *c. nelsoni* has been divided into three

areas, which correspond to areas I, II, and III, respectively, of leconteii. Within the same limitations of statistical treatment, there is no significant variation in mean measurements within the range of c. nelsoni (Table 2). The data on c. nelsoni have been combined for comparison with leconteii, maritima, and other populations of caudacuta. These populations are (a) altera, (b) subvirgata, (c) caudacuta of New England and New York, (d) caudacuta-diversa of New Jersey, and (e) diversa of Delaware, Maryland, and Virginia.

Figures 8 and 9 show the variation in wing length and bill length, respectively, in populations of caudacuta, leconteii, and m. maritima. The shortest-winged caudacuta is nelsoni; the longest-winged are c. altera and c. subvirgata; and there is a cline toward shorter wings 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 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, in which there is no cline as there is in wing length. The populations from James Bay and the Maritimes are intermediate. Thus, the shortest-beaked caudacuta is sympatric with shorter-beaked leconteii and the longest-beaked are sympatric with longer-beaked m. maritima. The ratio between the bills of c. nelsoni and leconteii is 1.19, and that between c. caudacuta and diversa populations and m. maritima is 1.21.

Weight data are available for only four populations of caudacuta and two of leconteii (Figure 10; Table 4). There is no difference between the weights of leconteii from James Bay and those from North Dakota. However, c. nelsoni averages lighter than c. altera, which averages lighter than either Atlantic coast population. The southernmost population that was measured (c. caudacuta - diversa) has the greatest mean weight.

Discussion

Differences in bill length between sympatric populations are generally assumed to be a result of divergence in allopatry resulting from differences in available food or a result of divergence in sympatry through interspecific competition for food. Differences in bill length may also arise in sympatry as a result of selection for specific recognition marks, as a result of differences in habitat and, consequently, differences in diet, or both. Differences in habitat may result from competition between species, but such competition does not have to be for food. Full treatment of this point is postponed until page 58.

If (1) average differences in bill length reflect average differences in diet and (2) different habitats provide different diets, average differences in bill length between races of caudacuta, between c. nelsoni and leconteii, and between c. caudacuta (and presumably c. diversa) and m. maritima may be explained by average differences in available food in utilized habitat. 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 only salt marshes, some populations of c. subvirgata inhabit 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). As noted above, c. nelsoni inhabits fresh-water marshes. The Le Conte's Sparrow utilizes on the average drier habitats than does c. nelsoni (Godfrey, 1952; and above), and c. caudacuta utilizes on the average

drier habitats than does m. maritma (Stone, 1937; Montagna, 1942; Woolfenden, 1956). Because neither the available food 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. However, differences in available food between habitats is not unexpected, and I suggest that differences in bill length result from average differences in the available food in the habitats utilized by the populations. The ratios of bill-size difference between leconteii and c. nelsoni (1.19) and between m. maritima and c. caudacuta (1.21) are lower than the value (1.3) suggested by Hutchinson (1959), who is followed by others, as being necessary to permit coexistence of two species. The bill differences between caudacuta and its sympatric relatives are probably not necessary to permit the coexistence of the species. There is no indication that bill length in m. maritima has been affected by the presence of caudacuta (Table 3). A full discussion on the evolution of bill size and the ecological significance of bill differences is presented later (59 ff.).

Studies on geographic variation in wing length, weight and wing length relationships, and their ecological significance conclude that wing length is influenced by many factors (Snow, 1954; Hamilton, 1958, 1961; Rand, 1961). These studies have been on species or genera of continent-wide distribution that encounter a variety of environmental conditions. The present study concerns two species of relatively limited distribution and relatively uniform habitat. Within caudacuta there is no direct relationship between increasing wing length and increasing weight (Figure 10). The shortest-winged (c. nelsoni) is the lightest, but the next shortest-winged (c. caudacuta-diversa from New Jersey) is the heaviest. Data from populations of close relatives for which there is comparable information show a straight-line relationship between wing

length and weight of leconteii, henslowii, c. nelsoni, c. altera, Grasshopper Sparrow (Ammodramus savannarum), and bairdii (Figure 10). Diverging from this relationship in increasing order of magnitude are c. subvirgata, c. caudacuta-diversa, and m. maritima. The last two populations migrate the shortest distances, and, indeed, some individuals winter within the breeding range. That the more migratory populations are longer-winged is consistent with studies in other groups (Averill, 1920; Chapman, 1940; and others). The reason c. subvirgata is so heavy in relation to its wing length is not clear.

The Sharp-tailed Sparrow race (c. nelsoni) living with leconteii is smaller-billed, shorter-winged, and lighter in weight than is the population (c. caudacuta-diversa) living with m. maritima in New Jersey. I think the difference between the two caudacuta populations results from convergence toward their sympatric relatives. Differences between the sympatric populations result from their inhabiting slightly different parts of the habitat. Too little is known about the ecology of the James Bay populations of leconteii and c. altera to permit discussion of the greater differences in the measurements between these populations than exist between leconteii and c. nelsoni. The direct relationship between bill length and body weight in the group leconteii, caudacuta races, and m. maritima I attribute to coincidence because in another group of relatives (henslowii, savannarum, and bairdii), to which Ammospiza is related, there is no such relationship (Figure 11). The relationship between bill length and body weight in other groups of passerines cannot be determined because comparable data are lacking, and generalizations regarding the relation of bill length and weight cannot be made.

MIGRATION

Methods

To determine the timing of the pre-breeding migration, March, April, and May specimen records are compared by date and by area of occurrence: (1) those on the breeding range; (2) those on the winter range; and (3) those in the area between the breeding and winter ranges. September, October, and November specimen records are treated in the same way for the post-breeding migration.

Pre-breeding Migration

Le Conte's Sparrows arrive on the breeding range in late April and early May, after a drawn-out migration. Most leconteii have departed the winter range before 15 April but do not reach the breeding range until after 5 May (Figure 12). The five specimens in the migration area after 5 May were taken at Warsaw, Illinois, in 1883 and 1884 and may represent with the adult taken at Warsaw on 2 August 1894 (Figure 2) a breeding population from a formerly larger range. March records may represent wintering birds rather than migrants. Only more field work in the winter range and in the migration area can resolve these alternatives.

By contrast, c. nelsoni departs 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 12). The more rapid migration may be a result of the lack of suitable habitat in the intervening area.

In North Dakota in 1965 leconteii was present on the morning of 8 May. I first visited the area in the early evening of 7 May 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 on 21 May. The first day on which 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 activity and reduced my chance of finding them. 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 arrived on 4 May and c. nelsoni first arrived on 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 arrived.

In conclusion, Le Conte's Sparrows arrive during the first week of May and reach a peak by mid-May. Sharp-tailed Sparrows arrive two to three weeks later and reach a peak in early June.

Post-breeding Migration

The post-breeding migration is nearly the reverse of the pre-breeding migration. Both leconteii and c. nelsoni depart from the breeding range early in September, but leconteii does not reach the winter range before early November, long after the first c. nelsoni appear in late September (Figure 13).

VOICE

Song

The song of leconteii has been described best by Breckenridge (in Roberts, 1932), "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." According to Borror (1961), who studied sonograms, there is little variation between songs of individuals or between songs of different individuals. The song of c. nelsoni is buzzy like that of leconteii but is lower in pitch and more variable (Borror, 1961). Breckenridge (in Roberts, 1932) describes the song, "a low initial note slurs immediately into a high, wheezy, nasal buzz, which terminates in a low, short, grating ur." The song of c. nelsoni is louder than that of leconteii, and I could hear it as far away as 500 feet. Sonograms show a close similarity in the structure of the songs of these two species.

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 before the bird lands. The song flights of c. nelsoni are longer

and at a higher altitude than those of leconteii (Figure 14).

The flight-song of leconteii is more complex and variable than that of c. nelsoni. The song is introduced by several "chip" notes, which are followed by an up-slurred note and a longer down-slurred note, as the bird ascends. The typical buzz is given as the bird is dropping into the grass on fluttering wings. The introductory chips and the final buzz are not always given. 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 the intruder is near the nest, but I have heard them before nesting is underway. The notes are ventriloquial and are often given at close range (ca. 15 feet). These notes are indistinguishable, to my ear, from notes given by c. nelsoni.

While in the blind, I heard on rare occasions a somewhat loud, grating note given by a female leconteii. This is probably the note Walkinshaw (1937) refers to as "chit-chit-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 seems to differ somewhat from leconteii in other areas. 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 (1937:316), while stating that he rarely saw it sing more than 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." Le Conte's Sparrows in North Dakota 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 was watching only three used the meter-high stakes that were placed throughout the study area, and they did not use them until mid-July. This behavior is different from other grassland species that utilize any tall perch within their territories. For instance, as taller stakes were placed in the territories of Grasshopper Sparrows on consecutive days, the tallest stakes were immediately used (Smith, 1963). On the other hand, I heard flight songs throughout the day and throughout the season, whereas Walkinshaw (1937) reports hearing only one flight-song, and Peabody (1901) and Roberts (1932) do not mention flight-songs.

In 1965 Le Conte's Sparrows could always be heard at night, although in diminished numbers from about mid-July on, but in 1966 they were rarely heard 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 in mid-day 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 singing birds were common, and singing was frequent 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 loss of mutual stimulation.

In North Dakota, c. nelsoni is a loud and frequent singer. Flight-songs are common. Songs were delivered from the top or the stems of sour dock, other tall plants (Phragmites), and the meter-high stakes. The stakes were regularly used after mid-June, several weeks after the birds arrived.

In 1965 I did not hear c. nelsoni sing at night until 21 July, when 5 or 6 individuals were singing and only 2 or 3 leconteii were singing. In 1966 leconteii sang infrequently at night, while c. nelsoni was heard almost every night I visited the study area. It seems possible that leconteii's nocturnal singing activity may inhibit c. nelsoni's.

The singing of c. subvirgata seems to resemble that of c. nelsoni in that the birds are conspicuous, frequently singing 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. Woolfenden (1956) reports that caudacuta often 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 reviews by Nice (1941), Hinde (1956), and Carpenter (1958)]. The most widely accepted definition seems to be Noble's (1939) -- "territory is any defended area." Emlen (1957a) criticized this view, and I agree with him 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. The use of this term, instead of territory, seems desirable in those cases where aggressiveness between neighboring males is not detected. Activity spaces may or may not be territories.

Methods

The study area in North Dakota (Figure 6) was marked off into quadrats 100 feet by 100 feet. In 1965 the study area was 500 feet by 500 feet, 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 aluminum, numbered band and three plastic, colored bands. The location and type of activity of each individual were recorded on a grid map several times a week. Observations were made with binoculars or telescope in the field or from a blind. In 1965 when

sparrow populations were high, incidental observations were made throughout the area in Figure 5. In 1966 observations were nearly restricted to the study area. In order to determine the activity spaces of the males in the study area, only activity of identified males or unidentified singers was plotted on composite maps, and when this information was repetitious it was plotted once. Activity of females was not seen except when they were feeding young or accidentally flushed.

Territoriality in Le Conte's Sparrows

Le Conte's Sparrows maintain activity spaces that appear to overlap only rarely and, then, at different times (Figures 15 and 16). That these activity spaces are territories is indicated by observation 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. These territorial encounters are often difficult to observe because they are too far away, obscured by grass, or too brief. They may be so subtle that the observer may not even be aware that two birds are doing anything more than singing. Several instances were observed well.

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

(2) 29 May 1966. I observed 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 within about 50 feet of both birds.

At 1400 hours, 797 and leconteii 802 were singing about 65 feet from each other. Between 1415 and 1430, 802 slowly moved 30 feet toward the territory of 797, singing

constantly. By 1430, 797 had moved toward 802 a few feet. The birds remained in this position, singing alternately (actually sequentially with leconteii 800) until 1446. Then, 797 moved another five 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 singing was continued by all birds.

(3) 30 June 1966. At 1928 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 1931. At 1935 an unbanded c. nelsoni landed about 50 feet away but did not sing. Immediately, 360 flew at c. nelsoni, who flew away, and 360 began singing from the spot where c. nelsoni had been.

Permanence of Territories

Stenger and Falls (1959) and Weeden (1965) have shown that territorial boundaries in the Ovenbird (Seiurus aurocapillus) and Tree Sparrow (Spizella arborea), respectively, fluctuate during the breeding season. If boundaries of leconteii territories fluctuate, the changes are not great because activity spaces rarely overlap (Figures 15 and 16). In 1965 there was one possible case of a territorial boundary change, but in 1966 there were several instances of territorial change. (a) Number 793 was banded on 20 May but had definitely disappeared by 26 May when I saw an unbanded leconteii singing in 793's area. (b) Number 393 was banded on 1 July and was last seen on 6 July before enough observations could be made to determine if his activity space included the whole of the southwest corner of the study area. (c) On 13 July, 360 was first seen well outside his territory. He remained in this new area at least until I terminated observations. (d) A single observation of 796 on 19 July within the edge of 360's

former territory was my last observation of a change of territory.

In conclusion, it appears that once territories are established in the spring, boundaries are relatively stable, compared to those of the Ovenbird and Tree Sparrow, until middle or late July, when individuals may take over areas that have been vacated by others. Because of known stability (e.g., 797, 798, and 799), I am confident that certain other individuals (e.g., 811) that were difficult to capture were indeed the birds I observed as unbanded birds and attempted to capture during the preceding few weeks.

Returns from 1965

Of the seven banded males that occupied the study area in 1965 (Figure 15) only one, 360, returned in 1966 (Figure 16). None of the six banded females returned. Part of 360's 1965 territory was included in his 1966 territory. The low return of banded birds was not caused by banding, as the leconteii population in the whole floodplain was much lower in 1966 than in 1965 (as mentioned above).

Territoriality in the Sharp-tailed Sparrow

There is no territorial behavior in c. nelsoni. Males fly from song perch to song perch, criss-crossing each other's paths and using 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. Two maps (Figure 17 and 18) 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 0919 an unbanded c. nelsoni was singing near stake 47 and c. nelsoni 806 was singing on stake 37. Unbanded c. nelsoni flew to within five feet of the base of stake 37. Then, 806 stopped singing and flew off to near stake 45. Unbanded c. nelsoni flew up to stake 37 and sang.

(5) 14 June 1966. At 1102 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 dropped to the ground, and almost immediately both flew westward about 100 feet before separating. Sex of second bird is unknown.

(6) 8 July 1966. A c. nelsoni chipping in the grass at 1535 dropped to the ground at 1540. Another c. nelsoni flew in, landed on a grass stem, and dropped to the ground. At 1541 both flew off together about 80 feet, landed on ground, and took off again, flying a long curving course. Sexes unknown.

(7) 11 July 1966. At 1914 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 and began singing.

(8) 11 July 1966. At 1950 a c. nelsoni landed in the center of quadrat 15. Number 806, which had been singing on 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 1913, 806 was singing on stake 36, when c. nelsoni 384 sang in flight over stake 26 and landed in grass near stake 16. Two minutes later 384 flew to stake 18, where he sang until 1920. He may have flown because he had seen 806 flying toward stake 16,

where 806 landed at 1915. Without singing, 806 flew to stake 26 at 1916; then, to stake 27; and, then, into the grass about 40 feet from stake 28 at 1917. A minute later he was singing on stake 37.

Coloniality

In 1965, c. nelsoni occurred in wet areas 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, while there appeared to be almost as many in the study area as there were in 1965. The concentration of c. nelsoni in the study area in 1966 when other areas appeared as suitable as they had been in 1965 suggests that c. nelsoni may be colonial, as are Atlantic coast caudacuta populations (C. W. Townsend in Forbush, 1929; Montagna, 1942; Griscom and Snyder, 1955; Woolfenden, 1956; and Tufts, 1961).

Returns

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

Interspecific Territoriality

Interspecific territoriality occurs when "A territory holder of one species exhibits persistent aggressive behaviour 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 territory of the first. Le Conte's Sparrows are at times aggressive toward Sharp-tailed Sparrows but this is not interspecific territoriality, as defined, because the aggression is not persistent. The aggression of leconteii is, however, apparently the same as that "forthcoming in intraspecific encounters."

In addition to the instance mentioned in (3) above, the following interspecific encounters were observed well.

(10) 14 June 1966. At 0946 c. nelsoni 806 was spotted in the grass between stakes 17 and 27. He was not singing and allowed me a close approach, which is unusual in c. nelsoni, so I withdrew a few feet and waited to see what would happen. He dropped out of sight. I waited, and at 0958 an unbanded c. nelsoni landed on stake 27 and sang. Almost immediately an unbanded leconteii (later banded as 811) flew to a point just over 100 feet away near stake 18. Le Conte's Sparrow 811 was not a persistent singer, but now he sang continuously. The two birds sang alternately until 1002 when c. nelsoni flew 150 feet away. The Le Conte's Sparrow continued singing until 1008 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 responded to the singing that was going on around them.

(11) 17 June 1966. At 1116 an unbanded c. nelsoni that had been singing half-way between stakes 17 and 18 flew to about mid-way between stakes 9 and 19. He did not sing until 1120, 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 until 1126, when it dropped to the ground.

(12) 27 June 1966. At 1013 leconteii 811 flew to the spot where an unbanded c. nelsoni was sitting quietly. The c. nelsoni flew off and leconteii started singing. This occurred at the same spot as the encounter described in (11). At 1022 the same or another c. nelsoni flew to this spot and sang until 1030, when it stopped singing. It remained there until 1034, when it flew away without apparent provocation. The same or another c. nelsoni was there at 1118 when it sang briefly before flying off, again without apparent provocation.

(13) 30 June 1966. At 1804 a leconteii was singing near stake 36. At 1805 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 c. nelsoni.

(14) 30 June 1966. A c. nelsoni was singing at 1902 in the center of quadrat 26. When a bird flew in from the north, c. nelsoni stopped singing and peered around. He presently departed, and the second bird gave a brief chase before landing. The second bird (probably 799) then gave an incomplete leconteii flight-song.

Discussion

The difference in territorial behavior is perhaps the greatest difference between leconteii and c. nelsoni. Le Conte's Sparrows maintain typical Type A (Nice, 1943) territories in which each pair nests and feeds. Most reports indicate that emberizines are territorial. Although the Seaside Sparrow has been reported to be non-territorial (Tomkins, 1941), Woolfenden (1956) found that most Seaside Sparrows maintain Type B territories on which they nest but obtain only part, if any, of their food, while a few pairs feed as well as nest on their territories. This is a result of the usual separation of breeding and feeding habitat. The non-territoriality of caudacuta, previously noted by Montagna (1942) and Woolfenden (1956), appears to be unique among emberizines, and it is undoubtedly derived from more typical territorial behavior.

It is known that birds with established territories are usually dominant to conspecific intruders (see Hinde, 1956). Birds with established territories may also be dominant to intruders of other species, and I suggest that non-territorial behavior evolved in the following way. If the ancestors of leconteii and caudacuta were both territorial and both occupied similar habitats (habitat A), when they became sympatric caudacuta would be

at a distinct disadvantage in establishing territories because, being a later migrant than leconteii (Figure 12), it arrived in a habitat in which leconteii had already established territories. As a result of interspecific territoriality caudacuta would be found in marginal habitat (habitat B) or rarely in spaces unoccupied by leconteii in habitat A. Any change in the behavior of caudacuta that permitted it to breed in the space in habitat A occupied by leconteii would be selected for, if caudacuta were more successful in habitat A than in habitat B. By becoming non-aggressive and non-territorial, caudacuta was able to utilize space used by leconteii. I think it is the difference in territorial behavior that permits coexistence of leconteii and caudacuta. Woolfenden (1956) reported that maritima sometimes chases caudacuta out of their territories, and, again non-aggression may permit caudacuta to live with maritima.

The hypothesis, briefly stated here, will be further developed on page 52ff. by examining other cases of interspecific aggression. Implications of the hypothesis concerning the ecology of sympatric species, will also be discussed later.

NESTING

The rank growth of the breeding habitat made nest finding difficult. I looked for nests by searching the area from which I flushed a bird thought to be a female, but the most successful method was locating parents carrying food to the young. I found three leconteii nests and one c. nelsoni nest in this way; one leconteii nest was found when the female flushed from it; and one female leconteii built the nest near the 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." The open cup is almost always covered by a thick thatch of fallen dead grasses. All five nests I found were made of Spartina. Peabody (1901) found that the base of the average nest was about eight inches above the ground. The nests I found ranged in height from resting on the ground to five cm above the ground.

The c. nelsoni nest was found in a small stand of Scolochloa near the study area. Peabody's description of leconteii's nest fits just as well for c. nelsoni, except that the latter's nest was constructed of Scolochloa. It was entirely above ground, as was the nest described by Breckenridge and Kilgore (1929). Two unusual nests, perhaps misidentified, were reported by Rolfe (1899) and Bownan (1904). Both were sunk into the ground in an open area of

short grass, as are Savannah Sparrow nests. Rolfe's report is particularly unconvincing.

Brood Parasitism

I found the c. nelsoni nest empty the day after the young fledged. All leconteii nests were parasitized by the Brown-headed Cowbird. Although Walkinshaw (1937) reported that a female fed three two-day-old young leconteii nine times in 4.5 hours, I observed both male and female leconteii bringing food to young cowbirds; feeding trips averaged one per minute at two nests where I counted the feeding flights.

The leconteii nests that I found and their contents were:

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

MOLTS AND PLUMAGES

Detailed study of the molts of leconteii, caudacuta, and their relatives has yet to be done. What is known about the molts and plumages of these species is largely the work of Dwight (1900). Additional contributions have been made by Chapman (1910, 1911), Forbush (1929), Rand (1929), Roberts (1932), Sutton (1935, 1936), Tordoff and Mengel (1951), Graber (1955), and Dickerman (1962). In the course of measuring specimens I looked for evidence of molt, and I can add some information to what is already known.

Le Conte's Sparrow. Chapman (1910) was unable to determine the extent of the first prebasic (postjuvenal) molt. Of 99 specimens labelled as juveniles or immatures I saw no indication of molting primaries. Therefore, the first prebasic molt is partial.

Sharp-tailed Sparrow. The prealternate (prenuptial) molt is not always complete, as suggested by Forbush (1929), although all subsequent references are to Dwight (1900), who stated it was complete. I found only a few specimens (all races) that appeared to have molted all primaries. Most individuals had molted from three to five outer primaries, but a few did not molt any.

Seaside Sparrow. Dwight (1900), Chapman (1910), and Forbush (1929) state that there is no prealternate molt in maritima. I saw several April specimens that were molting body feathers extensively and some spring specimens that were in fresh plumage. Most specimens, however, show little, if any, indication of molt.

Baird's Sparrow. Chapman (1910) noted that there were too

few specimens available for a description of the molts, but he mentioned that wear was responsible for the change in appearance between winter and summer. There are still too few specimens for determining the extent of the first prebasic molt, but the state of wear of the plumage of spring specimens confirms Chapman's statement, except that a few feathers on the head may be replaced.

The sequence of molts of these and other species are diagrammatically illustrated in Figure 19. There is considerable variety of molt sequences for a small group of sparrows that are sometimes considered congeneric. Striking differences occur between Le Conte's and Henslow's sparrows, currently together in Passerherbulus, and between Seaside and Sharp-tailed sparrows, currently together in Ammospiza. Le Conte's Sparrow is most similar to Sharp-tailed Sparrow, and both are similar to Savannah Sparrow. Henslow's Sparrow is apparently identical to Grasshopper Sparrow, and Baird's may be similar to them or to Savannah Sparrow.

In this group molt sequences by themselves are probably not reliable as indicators of relationships. For instance, the Seaside Sparrow would have to be placed with Grasshopper and Henslow's sparrows on the basis of molt sequence, when it is clearly related to the Sharp-tailed Sparrow on the basis of other evidence.

Juvenal Plumages

The juvenal plumages of leconteii and henslowii differ, the first having a streaked back pattern and the second having a scalloped back pattern. These patterns ally henslowii with the Grasshopper Sparrow, which also has a scalloped back pattern, and Le Conte's Sparrow with caudacuta and maritima. The Savannah Sparrow also has a streaked back pattern, and Baird's Sparrow has a scalloped back pattern. Juveniles of leconteii and caudacuta are so similar that Breckenridge (1930) and Roberts (1932) described juvenal leconteii specimens as c. nelsoni (Dickerman, 1962).

Adult Plumages

As will be described in the next section, the adult plumages of leconteii and caudacuta differ only quantitatively; that is, in the intensity of pigmentation. In general pattern they are the most similar species in the group, and the patterns of individual feathers are frequently identical.

DESCRIPTIONS OF ADULT PLUMAGES OF LE CONTE'S AND SHARP-TAILED SPARROWS AND OF A PROBABLE HYBRID

A specimen (CNM 36939) in the National Museum of Canada resembles in general appearance the Le Conte's Sparrow (Figure 20), but in several characters it resembles the Sharp-tailed Sparrow or is intermediate between the two species. Therefore, I consider the specimen to be a hybrid between Le Conte's and Sharp-tailed sparrows rather than an aberrant Le Conte's Sparrow. The specimen, a male, was collected by A. Macpherson on 18 June 1949 on Ship Sands in the mouth of the Moose River, Ontario, near James Bay. In the following description the hybrid is compared with 16 male leconteii and 22 male c. altera specimens, all taken in June along the shore of James Bay.

Head. The median crown stripe of c. altera is broad and gray with a few feathers having an olive tinge in some specimens. The feathers of the lateral crown stripes have black centers and reddish-brown edgings that produce a distinctly streaked appearance. In contrast, leconteii has a narrow median crown stripe that is tannish-white with a yellowish-buff spot at the anterior end. The lateral crown stripes have black centers and narrow buffy edges that soon wear off, giving a flecked appearance. In the hybrid the median crown stripe is narrow but brownish-gray with a trace of yellowish-buff at the anterior end. The feathers of the lateral crown stripes have broad black centers with dark brown edgings.

The auriculars of leconteii are grayish-tan, and those of c. altera are dark gray. The superciliary stripe and subauricular area is an intense buff in c. altera and a

washed-out buff in leconteii. The auriculars of the hybrid are darker than in leconteii but lighter and browner than in most c. altera. The auriculars are made conspicuous, as in c. altera, by an intense buffy coloration of the superciliary stripe and subauricular area.

Nape. The feathers of the nape of leconteii are tawny-chestnut bordered by pale tan. A blackish subterminal spot varies in size and intensity. Only one specimen (CNM 32834) has indistinct spots and grayish edgings. The nape feathers of c. altera are reddish-brown tinged with olive or gray. The subterminal spot is indistinct. In the hybrid nearly all of the feathers lack the black subterminal spot. All the feathers are reddish with gray edges. The gray edging is narrow in the medial feathers and becomes increasingly broad laterally, giving a reddish appearance to the medial portion and grayish appearance to the lateral portions of the nape.

Back. The proximal three-quarters or so of the back feathers of both species and the hybrid is dark gray. The distal portions of the back feathers are patterned with black, brown, buff, and white. All of the back feathers of leconteii have a broad, brownish-black center, bordered by a narrow band of chestnut, and edged with varying amounts of buff. The medial back feathers are nearly symmetrical with a narrow pale buff edge, whereas the lateral back feathers are asymmetrical, having a narrow buff edge on the medial side and a broad, lighter buff edge on the lateral side. The scapulars are similar to the back feathers except that both edges are broad and light buff. In addition, they are tipped with chestnut and buff. The lateral edge of the lateral back feathers and the medial edge of the scapulars produce the two broad, light-buff, dorso-lateral stripes.

On close inspection the patterns of the back and scapular feathers of c. altera are similar to those of leconteii. Sharp-tailed Sparrows differ in having subdued

coloration and a reduction in the amount and intensity of black pigmentation. The medial back feathers are brownish-olive, darkest at the center and becoming lighter toward the edges. The lateral back feathers are asymmetrical with a broad white lateral edge. The scapulars are nearly symmetrical with white edges.

In general appearance the hybrid's back feathers are similar to those of leconteii. Because of the make of the skin it is difficult to describe the different feather groups. However, the buffy edges are not so light nor so broad as they are in leconteii.

Tertials. The tertials of leconteii are like the scapulars in pattern and coloration. The longest tertial in c. altera is dull brownish-olive, lighter and buffier on the edges. The two shorter tertials are blackish-brown with narrow buffy medial edge and a broad, dull white outer edge. The tertials of the hybrid are much like those of leconteii except the black of the longest tertial is more diffuse and the buffy edges broader.

Rump and Upper Tail Coverts. The rump feathers and upper tail coverts of leconteii have a broad, dark brown central streak that is bordered by a narrow band of chestnut and edged by light buff. In c. altera the black is reduced to a narrow streak or a subterminal spot, and the general color is buffy-brown, sometimes with a slight reddish tint. Most of these feathers in the hybrid resemble those of c. altera, although a few, especially of the upper rump, that have broad, brownish-back centers are edged with the buff of c. altera rather than the light buff of leconteii.

Underparts. On the average the upper breast of c. altera is an intense buff with suffused olive-brown streaking, whereas that of leconteii is pale buff, usually without streaking. A few leconteii have faint spotting on the breast, much like the spotting in juveniles. The streaking along the sides and flanks of leconteii is more distinct than in c. altera, being sharply delineated and darker.

The bright buff upper breast of the hybrid resembles that of *C. altera* and the streaking is like that of *leconteii*.

RELATIONSHIP OF *LECONTEII* AND *CAUDACUTA*

Tordoff and Mengel (1951) suggested that the Le Conte's Sparrow and the Sharp-tailed Sparrow were more closely related than the current classification indicated. They pointed out similarities in juvenal plumage, prealternate molt, song, and habitat. On the basis of juvenal plumage, Graber (1955) suggested *leconteii* be placed in *Ammospiza*. I think *leconteii* and *caudacuta* are closely related because they are similar in (1) juvenal plumage, (2) adult plumage, (3) molt sequence, (4) song, and (5) because there is an apparent hybrid between the two species. In each of the first four items, they are more similar to each other than either is to its present congener. However, both species inhabit similar and sometimes identical habitats, and it is conceivable that some similarities result from convergence. It is also conceivable that closely related species should be found in similar habitats. There are several reasons, admittedly not ironclad, for thinking that the similarities result from relationship rather than convergence. (1) From descriptions of *henslowii* habitats (reviewed by Hyde, 1939), *henslowii* seems to occupy in the east habitats that are occupied by *leconteii* in the west. The habitats are similar enough that the species occurred together in Minnesota (Roberts, 1932) and in Ontario (specimens in ROM). Yet, the back patterns of the juveniles and molt sequences are different. (2) Seaside and Sharp-tailed sparrows occur together on the Atlantic coast and have different molt sequences. (3) The Savannah Sparrow breeds in habitats with both Baird's and Grasshopper sparrows, (as well as in habitats with Le Conte's and Sharp-tailed

sparrows) and has different juvenal and adult back patterns from them. It does not seem possible that convergence between leconteii and caudacuta could have caused such close resemblances in juvenal plumage, adult plumage, molt sequence, and song. I think the evidence shows that leconteii is more closely related to caudacuta than to henslowii. I think henslowii should be placed with savannarum. Whether all of the species considered here should be placed in Ammodramus with Savannah Sparrow, Baird's Sparrow, Xenospiza, and Myospiza awaits further study.

MATING SYSTEM OF THE SHARP-TAILED SPARROW

The Sharp-tailed Sparrow's non-territorial behavior invites speculation regarding its reproductive behavior. Several authors have suggested that territoriality enhances pair formation and maintenance of the pair bond (Lack and Lack, 1933; Mayr, 1935; Noble, 1939; Nice, 1941; Lack, 1943; Tinbergen, 1957; and others). If this is one selective advantage of territorial behavior, how does caudacuta survive without territorial behavior?

As already suggested, the selective advantage of caudacuta's losing its territorial behavior is that the individuals are able to breed in habitats in which they are best adapted but which are otherwise closed to them by the presence of leconteii (and perhaps maritima). Coincident with becoming non-territorial they have become colonial. The colonial nature of caudacuta has been remarked by C. W. Townsend (in Forbush, 1929), Montagna (1942), Griscom and Snyder (1955), Woolfenden (1956), and Tufts (1961). The distribution and behavior of c. nelsoni in North Dakota also suggest coloniality. Male caudacuta seem interested in any sparrow that flies near. I saw c. nelsoni fly after Savannah Sparrows and Song Sparrows that happened to be flying past a song perch, and Montagna (1942) collected a male c. caudacuta copulating with a female m. maritima. From these observations I think females are attracted to aggregations of singing males. The males "court" any bird that appears receptive but are rebuffed by all (almost all) but their own females. Males take no part in nesting after copulation (Woolfenden, 1956).

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* is more interesting in that the males are more secretive than are males of *c. nelsoni* and *c. subvirgata*.

The hypothesis that the promiscuous or polygynous mating systems that have evolved in marsh inhabiting species because certain males obtain better territories than other males (Verner and Willson, 1966) is not applicable because male *caudacuta* are not territorial. Although Verner and Willson (1966) listed the Sharp-tailed Sparrow as a promiscuous or polygynous species, this is not known (Woolfenden, 1956).

GENERAL DISCUSSION

Major differences between leconteii and c. nelsoni are color and width of crown stripe, overall size, length of bill, song, and territorial behavior. In interpreting these data and in attempting to understand the ecological relationship of leconteii and c. nelsoni, I have had to consider the various possible interpretations that have regularly appeared in the literature on similar differences between other pairs or groups of species. In so doing I have found that some interpretations are not necessarily the only explanations for a given set of information. Some interpretations I think are incorrect. In the following discussion I present alternative views on interspecific territoriality and on differences between species that have been suggested to be adaptations that permit sympatry.

Several words require definition. By "competition" I mean that when two or more individuals or populations utilize a resource that is in short supply, one (or more) is adversely affected. A resource is in short supply when there is an amount insufficient to permit an individual (or pair) to maintain its activities (staying alive, feeding young, pre-migratory fat deposition, etc.). For example, a sufficient available food supply depends upon the ease of gathering, and this, in turn, depends upon the total food supply. Available food supply and total food supply are not synonymous. Thus, if the total food supply has a caloric value that could sustain two individuals, the supply is short if the presence of a second individual reduces the total supply to the extent that food becomes

more difficult to gather (less available) and neither individual could maintain its activities normally. If a second individual is present, the two are competing.

By "competitive exclusion principle," sometimes referred to as "Gause's Principle," I mean that if individuals of two populations are competing, one or both populations will change or one will become extinct in the geographic area of competition. The degree of competition does not determine the outcome. If the environment is fluctuating rapidly enough such that first one population has the advantage and, then, the other, and so on, it can be said that both populations are always competing for some resource, but it is improbable that any changes, which would eliminate competition, could evolve under these conditions.

By "limitation" I mean that there is a maximum density for a population that is set by some resource or by behavior. If a potentially limiting resource, such as nest sites, remains constant, fluctuations in population density are independent of the resource, except that the maximum density cannot be exceeded. If a particular resource or behavior varies in time but always sets only the upper limit to density, fluctuations in population density may result from changes in availability of the resource or in behavior. The cause of these fluctuations is different from the cause of fluctuations in a "regulated" population.

By "regulation" I mean that there is an optimum density for a population and that if a population is above optimum density, it will decrease, and if a population is below optimum density, it will increase. In other words, a regulated population is one that is homeostatic or in a steady-state (Nicholson, 1933, 1954; Odum, 1959; Lack, 1954, 1966). Fluctuations in population density are caused by adaptations that tend to restore the optimum density. Optimum density may vary, and fluctuations in population density may be caused by changes in optimum density.

Limitation and regulation are not necessarily mutually exclusive. In the case of a population that is limited by the number of nest sites, which remains constant, population density may be regulated at a level below that set by the number of nest sites.

INTERSPECIFIC TERRITORIALITY

Introduction

Orians and Willson (1964) emphasize that interspecific territoriality appeared to be most common in species that inhabit "structurally simple vegetation such as marshes, grasslands, tundra, deserts, and shore lines" or species that have "specializations for feeding on resources concentrated at a given level of vegetation." They argue that interspecific territoriality is advantageous in those habitats that do not permit morphological or behavioral divergence in foraging adaptations because the habitat is too simple to be subdivided.

Johnson (1963) pointed out that pairs of species that maintained mutually exclusive territories had similar displays in their territorial behavior and that sympatric congeners that did not maintain mutually exclusive territories were different in their territorial behavioral displays. Species may or may not evolve differences in their displays while in allopatry. When two species that did not evolve differences in territorial displays came into contact, they evolved differences if it were advantageous or maintained their similarities if it were advantageous.

Hamilton (1962) suggested that interspecific territoriality is an adaptation that permits sympatry of congeneric species because it results in the "avoidance of both intraspecific and interspecific competition."

Each of these authors explicitly states that interspecific territoriality is adaptive when it occurs. I

propose to show that interspecific territoriality is in fact an inadaptive character in at least one species whenever it occurs.

Lanyon (1956a:489) pointed out that "The hazards of misinterpreting all interspecific interactions within a territory as interspecific territorialism are admittedly genuine. But it would seem to be equally hazardous, from the standpoint of our understanding the significance and function of territory, to establish criteria that eliminate all possibility of an interspecific aspect." It also seems hazardous to treat interspecific territoriality as a single type of interaction between species, as has been done by Johnson (1963) and Orians and Willson (1964). In fact, the nature of the interspecific relationship depends upon the distribution and ecology of the species involved. A consideration of the variation in interspecific territorial relationships may be the best approach to understanding interspecific territoriality.

In the following discussion I include only the better documented cases, rejecting many of the cases accepted by Johnson (1963), Orians and Willson (1964), and others. For the sake of completeness I have discussed in the Appendix the reasons why I have rejected these cases.

Cases of Interspecific Territoriality

Genus Centurus. Selander and Giller (1959) report that a male Red-bellied Woodpecker (C. carolinus) and a male Golden-fronted Woodpecker (C. aurifrons) maintained mutually exclusive territories. The "feeding and nesting habits are similar in the two species, as are vocalizations and displays" (op. cit., p. 122). The two species are essentially allopatric but have a narrow zone of sympatry in Texas.

Genus Empidonax. Johnson (1963) reported interspecific territoriality between the Dusky Flycatcher (E. oberholseri) and the Gray Flycatcher (E. wrightii) along the western

edge of the Great Basin, where they have recently come in contact. This case differs from most in that there is a distinct difference between foraging and nesting behavior and between the habitats used by each species. Where overlap occurs each species is found in its typical habitat, and the absence of one of them would not necessarily permit the increase of the other. Some of the habitat of the other species is included at the periphery of the territories, but the ecologic effect is unknown (Johnson, 1966).

Genus Oenanthe. One Wheatear (Oe. oenanthe) excluded from its territory two territorial Pied Wheatears (Oe. pleshanka) (Eggebrecht, 1943). Meinertzhagen (1954) observed that two species of wheatears may breed near each other but there are few places in the world where they breed within sight of each other. This implies that sympatric species may most often be ecologically separated.

Genus Acrocephalus. Interspecific territoriality between the Sedge Warbler (A. schoenobaenus) and Reed Warbler (A. scirpaceus) in England has been described by Brown and Davies (1949). The Sedge Warbler arrives before the Reed Warbler in the spring and establishes territories. When the Reed Warbler arrives, it stops in a Sedge Warbler territory and begins singing. The Sedge Warbler chases the Reed Warbler, which immediately flies away but in a circle and returns to his singing perch. This performance is repeated for several hours, after which the Sedge Warbler becomes tolerant of the Reed Warbler and the latter becomes aggressive toward the Sedge Warbler.

Genus Sturnella. Lanyon (1956a, 1957) reported that the Eastern Meadowlark (S. magnas) and the Western Meadowlark (S. neglecta) maintain mutually exclusive territories. Several behavior patterns associated with the establishment and maintenance of meadowlark territories appear identical

in both species. The narrow zone of sympatry has been expanding during the past 50 years (Lanyon, 1956b).

Genus Agelaius. The Red-winged Blackbird in California is aggressive toward the Tricolored Blackbird (A. tricolor), which is colonial (Orians, 1961; Orians and Collier, 1963). Although neither species regularly breeds earlier than the other, Red-winged Blackbirds establish and maintain territories earlier than do Tricolored Blackbirds. Breeding activity in tricolor begins abruptly, and they establish territories in the territories of Red-winged Blackbirds. Territorial phoeniceus are intensely aggressive toward tricolor but are unsuccessful because there are several tricolor males in each phoeniceus territory. The phoeniceus male chases a tricolor, who retreats but returns when phoeniceus is chasing another tricolor out of his territory. There are too many tricolors, and phoeniceus stops displaying and chasing. The phoeniceus females depart and breeding is not accomplished.

Genera Agelaius and Xanthocephalus. The Red-winged Blackbird and Yellow-headed Blackbird (X. xanthocephalus) maintain mutually exclusive territories (Linsdale, 1938; Fautin, 1940; Orians and Willson, 1964). Yellow-headed Blackbirds evict phoeniceus that have already established territories in the part of the marsh where the water is deeper but do not evict those along the edge of the marsh. When xanthocephalus finish breeding and leave the marsh, phoeniceus move in and breed. These two species differ considerably in plumage and size.

Genera Euplectes and Coliuspasser. The two genera are considered congeneric (as Euplectes) by Delacour and Edmond-Blanc (1933). The interspecific relationships of the species that have been studied are complex.

The Black-winged Red Bishop (E. hordeacea) and the Zanzibar Red Bishop (E. nigroventris) maintain mutually exclusive territories where they occur together (Fuggles-Couchman, 1943). However, throughout most of their ranges (that of nigroventris is entirely within that of hordeacea) there is little ecological overlap (Moreau and Moreau, 1938). The plumages of the male are similar, but hordeacea is larger. Lack (1935) and the Moreaus (1938) noted conflict between the Black-winged Red Bishop and the Red-collared Widow-bird (C. ardens), and Emlen (1957b) subsequently observed three C. ardens and a single E. hordeacea maintaining mutually exclusive territories. These two species do not resemble one another. Emlen (1957b) also reported that the Red-collared Widow-bird and the White-winged Widow-bird (C. albonotatus) maintain mutually exclusive territories. As a result of his studies on six species of Euplectes (including Coliuspasser), Emlen (1957b) concluded that overlapping territories occur most frequently between species whose territory sizes differ appreciably. This is consistent with Lack's (1935) observation that the territory of the Yellow Bishop (E. capensis) was six times as large as that of hordeacea and overlapped four territories of hordeacea. According to Lack hordeacea and capensis occupying the same area were tolerant of each other but were aggressive toward and successfully excluded intruding "strangers" of either species. Despite striking differences in coloration between most of the species of Euplectes and Coliuspasser, studied by Emlen, the territorial boundary displays are markedly uniform. Emlen also shows that the species are partially segregated by habitat differences.

Genus Ammospiza. The interspecific territorial relationship of leconteii and caudacuta is described above (pp. 27-30).

Summary. - Pairs of species that are essentially allopatric (Centurus, Sturnella) have similar territorial behavior and maintain mutually exclusive territories. Pairs of species that are widely sympatric either maintain mutually exclusive territories or have different territorial behavior. If they maintain mutually exclusive territories, one species is larger (Xanthocephalus) or there are differences in the habitat (Oenanthe, Empidonax, and Euplectes sensu lato). If they are found in the same habitat, their territorial behaviors are different (Acrocephalus, Agelaius, and Ammospiza).

Interspecific Territoriality and Evolution

Because non-aggressiveness must be a condition derived from aggressive territorial behavior, the cases in which the territorial behaviors are different are of most interest. Although the behaviors of the Reed Warbler, Tricolored Blackbird, and Sharp-tailed Sparrow are different and each unique (not being reported in other species), there are two aspects of their life histories that are common to all three species. Each is interspecifically non-aggressive (except that the Reed Warbler becomes aggressive after establishing his territory through non-aggression) and each migrates or comes into breeding condition later than its sympatric congener.

I propose the following general explanation to account for the evolution of non-aggressive interspecific behavior. Species A is intraspecifically territorial when it becomes split into two populations. In time the populations diverge and become species B and C, each retaining the intraspecific territoriality of its ancestor. When the two populations come into sympatry, each is still better adapted to the same habitat than to the other available habitats. Because B migrates earlier than species C, it has an advantage in obtaining territories. Thus, species

C arrives in a habitat already occupied by B. Species B, by interspecific territoriality, excludes C from the habitat, forcing it into marginal habitat. If species B is not abundant enough to fill the habitat, species C can breed in the space unoccupied by B, although it will be rare. Because C would reproduce best in B's habitat if B were not there, any change that permitted C to breed in this habitat would be favorably selected. I think this is the best hypothesis to account for the lack of interspecific aggressiveness in the Reed Warbler, Tricolored Blackbird, and Sharp-tailed Sparrow. Therefore, it is the lack of interspecific territoriality in these species that permits them to be widely sympatric with their congeners.

The significance of habitat differences in Oenanthe and Euplectes (sensu lato) cannot be evaluated with respect to this hypothesis because data are insufficient. I would guess that habitat differences are responsible for geographic sympatry in these genera. The Yellow-headed Blackbird is big enough to be dominant to established, territorial Red-winged Blackbirds, and they have not had to modify their behavior.

If the above hypothesis is true, then interspecific territoriality in the ancestors of the Reed Warbler, Tricolored Blackbird, and Sharp-tailed Sparrow was an inadaptive character. Interspecific territoriality in the Red-winged Blackbird is manifestly inadaptive in that they are unsuccessful in breeding where Tricolored and Yellow-headed blackbirds breed, even though they establish territories first. Whether interspecific territoriality is inadaptive in species that maintain mutually exclusive territories is not so apparent. However, I do not know how it can be adaptive in both species. The species are at least competing for space, and it is not inconceivable that one species would be dominant to the other and eventually force it out of the habitat. Interspecific territoriality in the last situation could be considered adaptive, if it

could be shown that species B not only excluded species C but recognized species C as C. In most, if not all cases, interspecific aggressiveness may be no more than a case of mistaken identification.

The hypothesis presented above to account for the lack of interspecific aggressiveness in one of a pair of species coexisting in a habitat is predictive and can be tested. I predict that if two related species are found to use a grassland or marshland habitat in common, one of the species will be non-aggressive and the non-aggressive species will come into breeding condition later than the territorial species.

An underlying assumption made in the hypothesis is that territorial behavior in some way determines the number of birds that may breed in an area, and I shall now take up this question.

TERRITORIALITY AS A LIMITING FACTOR

Because there is a finite amount of space in a habitat and because territories take up space, space may be a factor that sets an upper limit to the breeding density of a population. Huxley (1934) expressed such a view when he compared a territory to a partially compressible elastic disc. He concluded (p. 277), "What seems quite clear is that [territoriality] does, in conjunction with other factors, play a part in determining the actual density of a breeding population in those species in which it is manifested." Hinde (1956) cited evidence that "territory owners are forced to defend their territories from encroachment, that some attempts to settle are unsuccessful, and that some individuals are forced to breed in sub-optimal habitats." In addition, birds removed from a habitat are quickly replaced by new birds (Hensley and Cope, 1951; Stewart and Aldrich, 1951). These data indicate that territorial behavior may prevent some birds from breeding and, thus, plays a role in determining the number of pairs that do breed in an area. Lack (1954, 1966) argues against this view on the basis that there is no evidence that the minimum size limit to which a territory can be compressed is ever reached. Hinde (1956:352) points out that it is not necessary for territories to be of minimum size before they can limit density: "In practice it is a matter not of minimum size at which the defence of territory owners is sufficient to keep out all intruders, but of an optimum ultimately determined by the relative advantages, to both owners and newcomers, of persistent defence (or intrusion) or retreat." That some individuals are able

to establish territories in habitats that are apparently already totally occupied only emphasizes that the number of breeding pairs in an area depends on Huxley's "other factors" as well. Some individuals may be more aggressive than others and the strength of aggression may be affected by environmental conditions, and in years of large spring populations aggressive birds may be more numerous. Thus, even though (a) territories may never reach their minimum size limit, (b) some individuals are able to establish territories against aggressive residents in an apparently completely occupied habitat, and (c) territory does not limit the population at low densities, territoriality undoubtedly plays a role in determining breeding density, which in turn results in dispersal, breeding in marginal habitats, and non-breeding.

ADAPTATIONS THAT PERMIT SYMPATRY

Lack (1954) agrees that there is no evidence that the minimum size to which a territory can be compressed provides only the minimum quantity of food that permits successful reproduction. This is consistent with his frequent assertion that territoriality has evolved because of an advantage other than its possible food value (e.g., Lack and Lack, 1933; Lack, 1943, 1954, 1966). Hinde (1956) reviewed the evidence and concluded that territories rarely, if ever, are maintained as a food source. Although a Type A territorial bird maintains an area that contains sufficient food for successful reproduction, the size of the territory is independent of the food supply. Thus, a Type A territory contains more than enough food to ensure successful reproduction. The difference between Type A and Type B territories may be that birds whose territories contain food feed within their territories and birds whose territories are without food feed outside their territories. This difference in territory "types" is found intraspecifically in the Black-winged Red Bishop (Moreau and Moreau, 1938), in the Seaside Sparrow (Woolfenden, 1956), and in the Song Sparrow (cf. Nice, 1937, with Tompa, 1962, 1963).

The information on territorial behavior and the hypothesis proposed to explain the lack of aggressiveness in some species indicate that food is not the limiting factor and that space probably is a limiting factor, to territorial bird populations. If food is not the limiting factor, one must consider the several differences between sympatric species that have been considered adaptations that permit sympatry because they eliminate competition for food.

They are differences in habitat, in bill length, and in foraging behavior.

Habitat Differences

When two related species are sympatric they are usually found in different habitats. The prevailing view is that each species was better adapted to one of the two habitats when the species became sympatric. Even though each could occupy both habitats in allopatry, they excluded one another from the habitat in which they were better adapted through interspecific competition for some resource. There is no doubt that such situations have occurred, but I think interspecific territoriality may often be involved.

In the hypothesis developed above (pp. 52-53) I assumed that species C was invading the geographic range of species B and that, of the habitats available, it was best adapted to B's habitat. I suggested that species C was excluded from the habitat by species B's interspecific territoriality. As a result species C was restricted to marginal habitat (or rare in B's habitat). Species C adapted by becoming non-aggressive and co-occupied the habitat with B. However, species C could instead become adapted to the marginal habitat and in time appear better adapted to it (the investigator would not recognize C's habitat as being formerly marginal). Marginal habitat for species C was also marginal for species B. Why did not B also use this habitat? Probably B did, but as it was best adapted to its usual habitat it did not also become well-adapted to marginal habitat and did not become common there. Species C had to (1) adapt to the presence of B, (2) adapt to marginal habitat, or (3) become extinct in this part of the range. If species C adapted to the marginal habitat, it would become commoner there and could eventually exclude B by interspecific territoriality.

That this explanation to account for habitat differences is possible is indicated by those cases where

ecologically separated species exhibit interspecific territoriality where their habitats come together (Oenanthe, Empidonax, and Euplectes). I doubt that two species would become sympatric, eliminate each other from parts of their common habitat through competition for food or some resource other than space, and, then, later become interspecifically territorial.

Bill Size Differences

An average difference in the bill sizes of two sympatric species has often been interpreted as either an adaptation that permits two species to coexist (selection occurring through interspecific competition for food) or independently evolved adaptations that arose in allopatry but permit coexistence upon sympatry. These alternatives derive from the assumptions that (1) average differences in bills reflect average differences in diets of sympatric populations and (2) food is the factor limiting the populations. Neither of these assumptions is necessarily correct. However, how can differences in bills of sympatric populations be explained if food is not limiting?

Consider two sympatric populations of species A and B that feed on the same food in the same way and live in a habitat in which food is so abundant that competition for food does not occur. If bill size and shape is dependent only on the type of food eaten and how it is obtained, then species A and B will have identical bills. However, it is unlikely that the two species will have identical geographic ranges; therefore, they will have allopatric populations. Different selection pressures are not unexpected between allopatric populations, and in this case the food may be sufficiently different that selection would produce bills of different size or shape in the areas of allopatry. Now, if there is gene flow between sympatric and allopatric populations, bill size or shape in the area of sympatry will diverge (Figure 21). Thus, in this case,

the difference in bill size in sympatric populations results from different selection pressures in the areas of allopatry, in spite of identical selection pressures in the area of sympatry. Therefore, bill size differences in sympatric populations do not necessarily indicate that interspecific competition for food is occurring or ever has occurred.

On a microgeographic scale, average differences in bill size can result from average differences in the habitats of the species. While the individuals are adapted to average conditions of the population, those living with another species that has a different bill need not necessarily be feeding on different foods.

An obvious exception to this explanation is character displacement in bill size, which occurs in Sitta (Vaurie, 1950, 1951), the drepaniids (Amadon, 1947), the geospizines (Lack, 1947), and other groups (Brown and Wilson, 1956). Where bill size differences are greater in the zone of sympatry than in areas of allopatry, the difference may be a result of interspecific interaction. The universal interpretation is that the bill differences result from ecological competition (e.g., Lack, 1947; Vaurie, 1950, 1951; Brown and Wilson, 1956; Mayr, 1963). However, in other species of Sitta (Ripley, 1959), in Centropus (Parkes, 1965), and in other cases (Brown and Wilson, 1956) character displacement involves coloration and pattern of plumage. These differences probably have evolved as pre-mating isolating mechanisms permitting specific recognition. The question arises, can bill differences serve as specific recognition marks? Lack (1947:53-55) presents evidence that the bills of geospizines do serve as specific recognition marks but he (p. 62ff.) concludes that the beak differences are adaptations that eliminate competition for food between sympatric populations. One hypothesis seems sufficient. Because there is some indication that geospizines recognize each other by their

bills and no evidence that food was ever in short supply, I prefer the hypothesis that the bills of geospizines serve as specific recognition marks. [Bowman (1961) believes that food is not in short supply for geospizines, but as Bock (1963:206) correctly pointed out, "Bowman did not really determine the most important fact, to wit, whether there was a shortage of seeds of certain sizes," but, then, neither did Lack!]

In conclusion, I think an average difference in bill size between populations probably indicates an average difference in diets. However, other factors, such as use as specific recognition marks, may affect bill size. Difference in bill size between sympatric populations does not necessarily indicate that competition for food has ever occurred.

Foraging Differences

Sympatric species almost always differ in foraging behavior or in diet (Lack, 1944, 1945, 1946, 1947, 1954, 1966; Hartley, 1953; Gibb, 1954; Betts, 1955; MacArthur, 1958). Such differences are only average differences, there being overlap to some extent. At least one food analysis found few differences between diets of three species (Evans, 1964). While differences in foraging behavior may have evolved as a result of interspecific competition for limited food resources, it seems possible that interspecific peck orders may be the ultimate if not proximate cause of the foraging differences. It seems possible that some parts of a habitat may be better food sources than others. There are no data.

In order to discuss the possible effect of interspecific peck orders a hypothetical situation must be considered. Assume that individuals of species A live in a habitat in which the best foraging area is the lower levels. Species A is territorial and, thus, food is not limiting. Species A forages most frequently in the lower levels.

Whereas a male of A is aggressive toward other singing and displaying males and excludes them from his territory, he is not aggressive toward feeding individuals, except when they are detected feeding in the lower levels. Reported observations of such differential behavior (Mickey, 1943; Lack, 1943; Gibb, 1956) usually do not indicate whether feeding intruders were detected or were feeding in favored areas of the resident. Assume also that species B feeds at the lower levels in similar but allopatric habitats. When species B expands its range into that of species A it occupies species A's habitat. When species B sings and displays species A does not respond, but when species B is detected feeding in the lower levels, species A chases him. If individuals of species B are going to remain in the habitat and feed unmolested, they will tend to confine their feeding to the upper levels. In time they will become better adapted as upper level foragers. That interspecific aggressiveness can effect a difference in foraging behavior was shown by Willis (1966) in the Plain-brown Woodcreeper (Dendrocincla fuliginosa), which fed more frequently at greater heights when the Ocellated Ant-thrush (Phaenostictus mcleannani) was present than when it was absent. The woodcreeper was often supplanted by the antthrush when it fed or perched low.

In the studies on foraging behavior in Old World Parus species (Hartley, 1953; Gibb, 1954) and New World Dendroica species (MacArthur, 1958) information on the role of interspecific aggressiveness is lacking. It is known that there is interspecific aggression in Parus (Hinde, 1952; Gibb, 1954) and in Dendroica (Morse, 1967) associated with foraging, but whether it results in the several foraging differences between the species is unknown. The critical information required is whether there is a difference in foraging behavior when another species is present or not.

The Non-breeding Season

Discussion in this section has been concerned with competition occurring in the breeding season, which in most species is not more than a few months per year. However, selection occurs throughout the year. Differences between species that are sympatric only during the breeding season may come about through selection occurring while the species are allopatric. Interspecific competition with other species may or may not be involved. The ecology of most species outside the breeding season is poorly known, but the importance of selection during the non-breeding season has been emphasized by Salomonsen (1955). It is not the purpose of this discussion to determine why particular sympatric species are different but whether the usual hypotheses are necessarily correct.

Conclusions

Although observations of the relationships of sympatric populations in nature appear to be what one would predict from the competitive exclusion principle, these observations do not constitute proof of the principle nor can the principle be invoked as the explanation of the observations. One first has to demonstrate that some resource is (or was) in short supply, if not interspecifically at present, at least intraspecifically. I accept as a possible hypothesis that the observed differences between sympatric populations result from interspecific competition for food. However, I present alternative hypotheses for the differences, which do not require an assumption that food is a limiting factor: interspecific competition for space results in differences in habitat or behavior that, in turn, result in differences in diet, the species becoming adapted to the foods available to it. I think the evidence, reviewed by Hinde (1956), suggests that territoriality may prevent some individuals from

breeding and, thus, space is a limiting factor to territorial breeding bird populations. Lack (1954, 1966) provides no evidence that territorial bird populations are limited by food supply during the breeding season. Thus, explanations of phenomena based on the assumption that food is limiting are more tenuous than are explanations based on the assumption that space is limiting. Obtaining direct evidence for any of several hypotheses is notably difficult, but the difficulties involved do not permit unqualified acceptance of unsubstantiated hypotheses. I think the following statements can be made on the available evidence.

(1) Space is a limiting factor to territorial breeding bird populations, and, therefore, population density is limited but not regulated by territory size.

(2) The size of a territory is an "optimum ultimately determined by the relative advantages, to both owners and newcomers, of persistent defence (or intrusion) or retreat" (Hinde, 1956:352).

(3) Birds whose territories contain sufficient food feed within their territories; birds whose territories contain insufficient food feed outside their territories.

(4) Interspecific territoriality is competition for space and, thus, for at least one species it is inadaptive.

(5) The various differences between species that are often cited as adaptations that permit sympatry because they eliminate competition for food and as evidence that food is (or was) limiting, can be equally well explained in other ways.

(6) There is no question that food plays an important role in the lives of birds. Clearly, geographic variation in available food supply may determine local abundance of breeding, migrating, and wintering birds; annual variation may affect annual reproductive success; and seasonal variation is no doubt the ultimate factor in the evolution of bird migration. These effects cannot be taken as evidence that available food supply is limiting the population.

SUMMARY

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

(2) Although leconteii lives in habitats that are on the average drier than those lived in by c. nelsoni, individuals of both species occupy identical habitat, where both are most common in North Dakota.

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

(4) Wing length in caudacuta does not correlate with body weight. The relatively shorter-winged, heavier-bodied population migrates the shortest distance. The same relationship appears in comparing the related species with each other.

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

(6) Songs of leconteii and c. nelsoni are more similar to each other than they are to other species.

(7) Le Conte's Sparrow is territorial, whereas caudacuta is non-territorial. Le Conte's Sparrow is interspecifically aggressive toward c. nelsoni at times. The non-territorial behavior of caudacuta is considered an adaptation that

permits it to use habitats in which its territorial relatives have already established territories.

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

(9) Molts and juvenal and adult plumages of leconteii and caudacuta are more similar to each other than either is to its present congener.

(10) A probable hybrid between leconteii and c. altera from James Bay is described.

(11) The similarities in molt, juvenal and adult plumages, and song and the existence of a probable hybrid are considered sufficient to justify putting leconteii with caudacuta in Ammospiza. Henslow's Sparrow is put with the Grasshopper Sparrow in Ammodramus. These changes more accurately represent the relationships of Le Conte's and Henslow's sparrows.

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

(13) Interspecific territoriality is reviewed in other groups of birds. In two other sympatric but not ecologically separated pairs of species, one species is interspecifically non-aggressive and that species comes into reproductive condition later than the interspecifically aggressive species. Another species is considerably larger than its sympatric relative and has not had to modify its behavior. Mutually exclusive interspecific territories are maintained between species whose ranges overlap slightly or between species which are normally separated ecologically.

(14) Territoriality seems to be a factor limiting breeding density in some species.

(15) Food does not seem to be a factor limiting the breeding density of territorial species.

(16) Alternative explanations are presented for differences between sympatric species that are usually interpreted on the assumption that food is (or was) the limiting factor.

APPENDIX

OTHER CASES OF INTERSPECIFIC AGGRESSIVENESS

Hamilton (1962), Wynne-Edwards (1962), Johnson (1963), and Orians and Willson (1964) have cited papers that are supposed to present evidence for interspecific territoriality. While some of these cases may prove to be cases of interspecific territoriality, the present evidence is fragmentary; at least one case has definitely been shown to be between species that overlap extensively in the same habitat. I do not consider either allopatric distribution or ecological separation as evidence of interspecific territoriality. Some cases of apparent interspecific territoriality occur between migrants or in winter ranges. I did not consider these in the main text because they are apparently independent of breeding. Some cases may be no more than a general aggressiveness toward other species.

Predators. Evidence for interspecific territoriality between hawks and between owls are presence of one and absence of the other in a particular habitat (Wilson, 1938; Baumgartner, 1939; and Stewart, 1949) or fights (Dixon, 1928; and Bennett, 1938). Craighead and Craighead (1956) show overlapping ranges of Red-tailed (Buteo jamaicensis) and Red-shouldered (B. lineatus) hawks, but they suggested (p. 259) that the overlaps "are the result of encroachment, often repulsed by active defense." This occurred most frequently near Red-shouldered Hawks' nests. This aggressiveness could be no more than generalized aggression near the nest sites toward any intruder (including man).

In the case of the Screech Owl (Otus asio) and the Whiskered Owl (O. trichopsis), Marshall (1957:61, 76) stated that the territories of the two species often overlap. Orians and Willson (1964) emphasized the exceptional instance of one area that was occupied by Screech Owls in November 1951 and by Whiskered Owls in April 1953. Other than that the Screech Owls were collected, what happened in the year and a half between censuses is not known. The rarity of Whiskered Owls in the November census is difficult to evaluate because they very rarely call at this time.

Pomarine Jaegers (Stercorarius pomarinus) maintain intraspecific territories and are persistently aggressive toward Snowy Owls (Nyctea scandiaca) (Pitelka et al., 1955). While Snowy Owls defend themselves they do not attack; however, they breed successfully. The exact nature of the jaegers' aggression toward Snowy Owls is obscured by their aggressiveness toward other birds, including a Sandhill Crane (Grus canadensis).

Genus Pluvialis. Concerning Golden Plovers (P. dominica) and Black-bellied Plovers (P. squatarola), Drury (1961:211) states, "Our few observations do not allow us to say whether there were interspecies territorial struggles or not."

Genus Charadrius. The Ringed Plover (C. hiaticula), Little Ringed Plover (C. dubius), and Kentish Plover (C. alexandrinus) maintain relatively large territories in which they nest but usually do not feed, and they are aggressive toward each other (Simmons, 1953; Sluiters, 1954). Aggression in at least the Ringed Plover is not only directed toward other plovers but toward "every 'outside' bird, regardless of species" (Mason, 1947). However, some terns are tolerated by the territorial plover and breed successfully, while the plover is aggressive to other terns within its territory. Meadow Pipits (Anthus pratensis) are always chased.

Hummingbirds. Interspecific relations between Anna's (Colypte anna) and Allen's (Selasphorus sasin) hummingbirds have been reported by Pitelka (1951) and Legg and Pitelka (1956). Territoriality in hummingbirds is different from the usual types reported in passerines (Pitelka, 1942): males and females are independent during the breeding season, except when copulating; males maintain feeding and mating territories; females maintain nesting territories and, sometimes, feeding territories; males and females are aggressive toward members of both sexes; territorial boundaries are usually not observed by other hummingbirds; hummingbirds are generally aggressive, not only toward their own species but toward other hummingbirds and some passerines. Anna's and Allen's hummingbirds differ in habitat and females nest in habitats different from the male's territory. While there is definite conflict between the species, there are cases of overlap without conflict (e.g., A7 and S3 in 1943; A10 and S5 in 1944; A8 and S5 in 1945; A2 and S1 in 1946; and A4 and S6 in 1947, from Pitelka, 1951). Interpretation is complicated because the birds were unmarked and because feeding territories are temporary.

In other reports of feeding territories in hummingbirds (Moore, 1939; Fox, 1954; and Armitage, 1955), variation in habits is also apparent. While many hummingbirds are intra- and interspecifically aggressive in feeding areas, others are not, and some hummingbirds are aggressive in one part of their feeding area and not in another part. The reports of Bene (1942) and Trousdale (1954) do not clarify the understanding of hummingbird territoriality.

Genus Centurus. Selander and Giller (1963) report a possible but unstudied case between the Golden-fronted Woodpecker and the Gila Woodpecker (C. uropygialis) in Mexico, where these two essentially allopatric species meet. These species have similar ecology and behavior and appear to be spaced out in their habitat.

Genus Melanerpes. Red-headed Woodpeckers (M. erythrocephalus) stored food in winter territories from which they chased other woodpeckers, Blue Jays (Cyanocitta cristata), and Tufted Titmice (Parus bicolor) (Kilham, 1958).

Genus Corvus. The Rook (C. frugilegus) is colonial and maintains Type D territories. Coombs (1960:408) states that "interspecific territorialism occurs between Rooks and Jackdaws [C. monedula]" and that he has observations of "Rooks threatening Jackdaws which happened to land in a Rook's territory, but none of territorial fighting between Rooks and Jackdaws or any other species, and no record of a Jackdaw threatening or attacking a Rook."

Genus Parus. Root (1964) found that the Plain Titmouse (P. inornatus) and the Chestnut-backed Chickadee (P. rufescens) did not maintain mutually exclusive territories, as they had been reported to do by Dixon (1954, 1960).

Interspecific territoriality between the Plain Titmouse and the Bridled Titmouse (P. wolweberi), reported by Dixon (1950) and Marshall (1957), is based on circumstantial evidence. These two species live in different habitats, but where their habitats mix they do not occur in the same flock.

The only evidence for interspecific territoriality between the Black-capped Chickadee (P. atricapillus) and the Carolina Chickadee (P. carolinus) is a single observation of a "vocal duel" in Illinois (Brewer, 1963).

Genus Oenanthe. Most cases of interspecific territoriality in Oenanthe concern migrants that are chased by breeding birds, wintering birds, or other migrants, and on the winter range (Hartley, 1949, 1950; Simmons, 1951; and Meinertzhagen, 1954). The responses of one species toward another varies (Meinertzhagen, 1954). Two of the three cases cited by Stresemann (1950) are based on distribution

(horizontal or vertical) rather than on observations of behavior; the third case was discussed above (p. 49).

Genera Oenanthe and Monticola. Simmons (1951) reports interspecific territoriality between chats and a female Blue Rock-thrush (M. solitarius) in winter.

Genus Sylvia. Raines (1945:202) states that "Blackcaps [S. atricapilla] would not allow Garden Warblers [S. borin] in their territory and vice versa, although other small warblers were tolerated." This instance certainly deserves further study.

Genus Lanius. Simmons (1951) reported interspecific territoriality between the Masked (L. nubicus) and the Red-backed (L. collurio) shrikes in winter.

Genera Agelaius and Quiscalus. Wiens (1965) has shown that the Red-winged Blackbird and the Common Grackle (Q. quiscula) do not maintain mutually exclusive territories. Common Grackles nested successfully within the territories of Red-winged Blackbirds. Grackles, regularly displaying from trees that were song and display perches of Red-winged Blackbirds, were rarely chased by Red-winged Blackbirds; other Red-winged Blackbirds were always chased. Grackles were chased when they approached a Red-winged Blackbird nest site. Nero (1956) reported persistent aggressiveness of Red-winged Blackbirds toward Common Grackles and a general aggressiveness toward other species (20 of 13 families) in the same marsh studied by Wiens.

Genus Cassidix. Brief observations of Great-tailed Grackles (C. mexicanus) and Boat-tailed Grackles (C. major) indicated that these species maintained territories that were largely exclusive (Selander and Giller, 1961). However, the territories did overlap and females of each species nested in the same tree.

Genera Zonotrichia *and* Melospiza. Kendeigh (1947) noted that White-throated Sparrows (*Z. albicollis*) and Song Sparrows (*M. melodia*) maintained non-overlapping territories, but he did not study the relationship.

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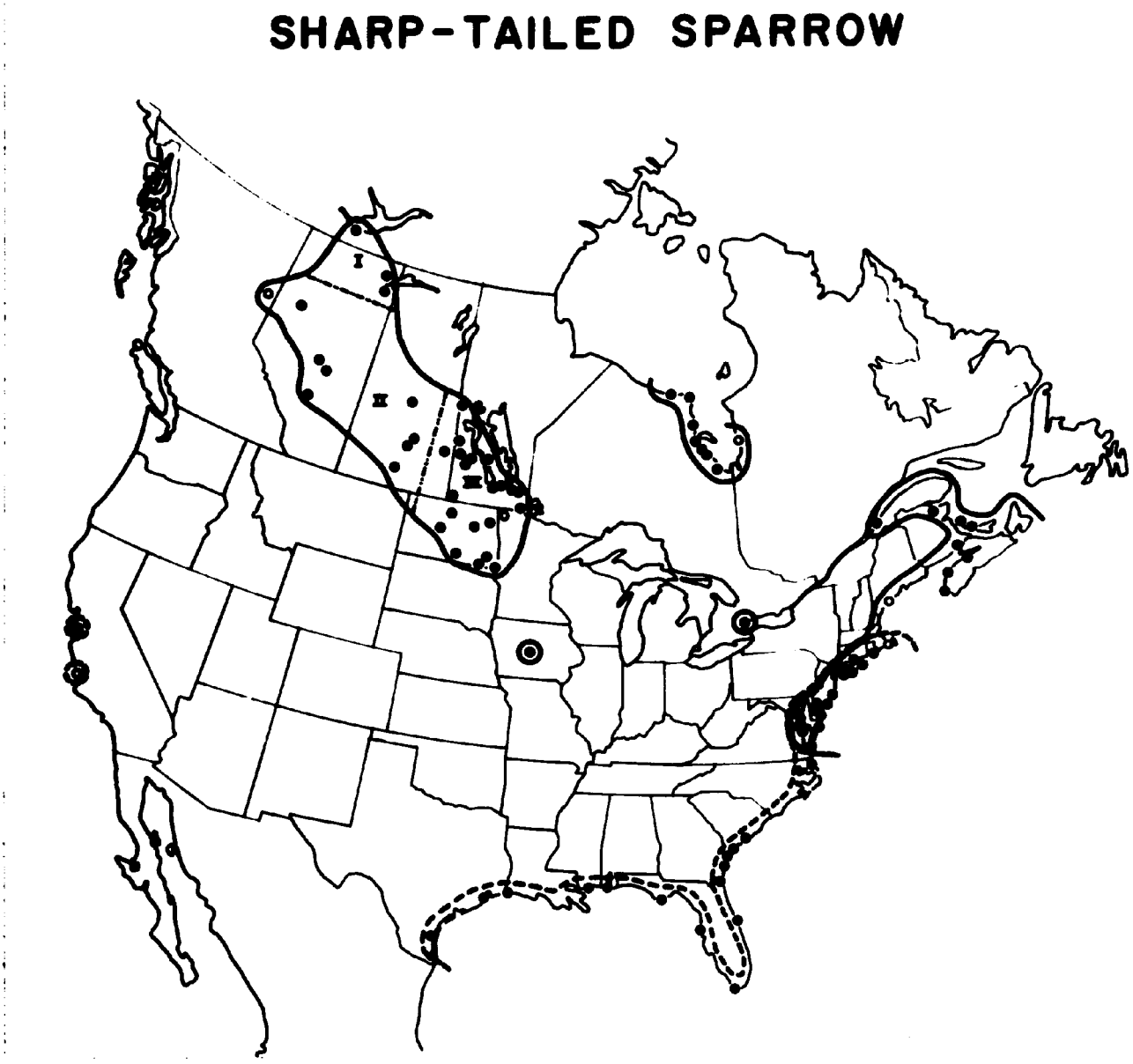


Figure 1. The breeding and winter ranges of the Sharp-tailed Sparrow. Black circles indicate localities at which the specimens examined were collected; white circles indicate additional localities reported in the literature. A solid line delimits the areas in which specimens were collected in June, July, and August, while the dashed line delimits the areas in which specimens were collected in December, January, and February.

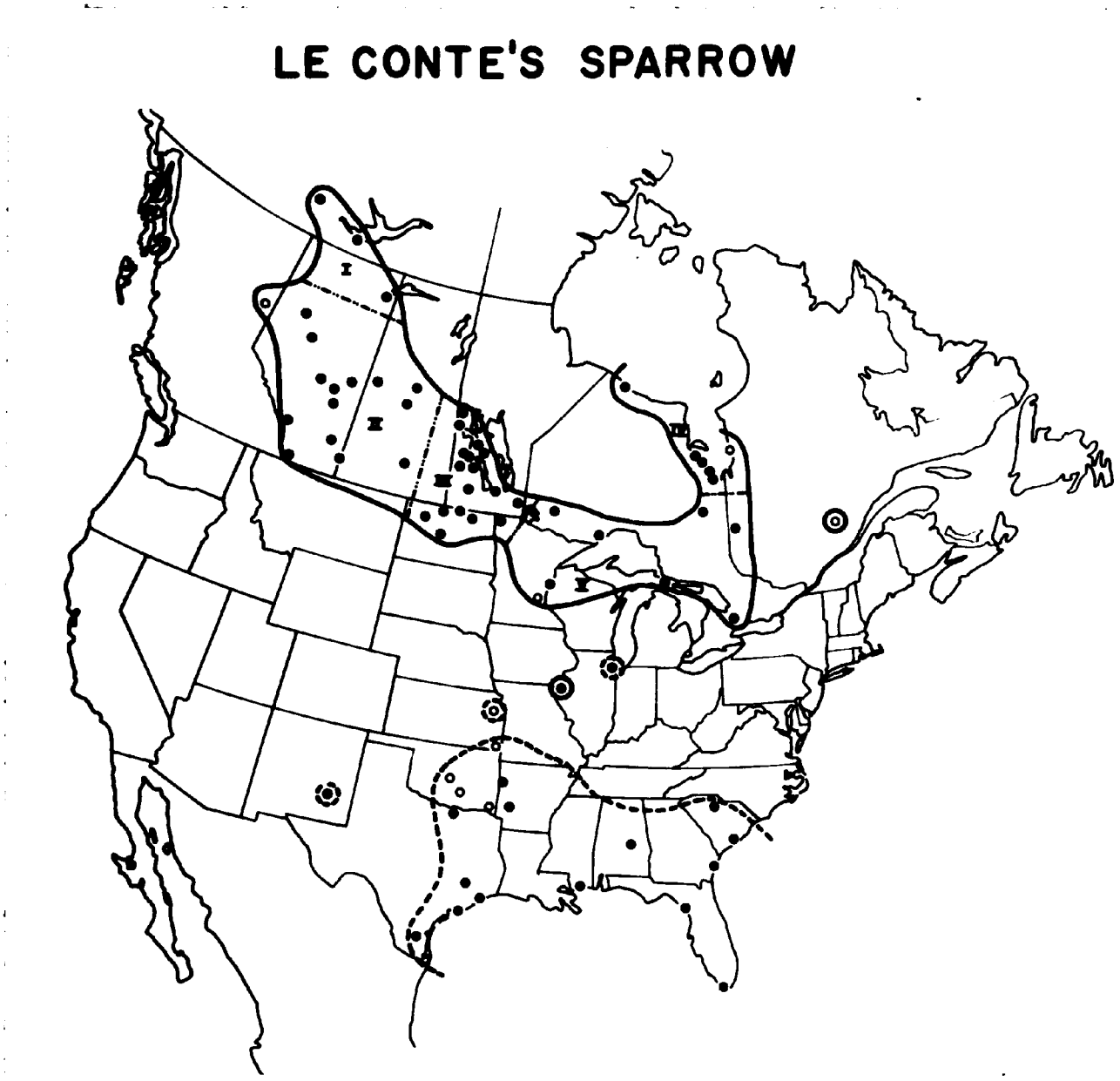
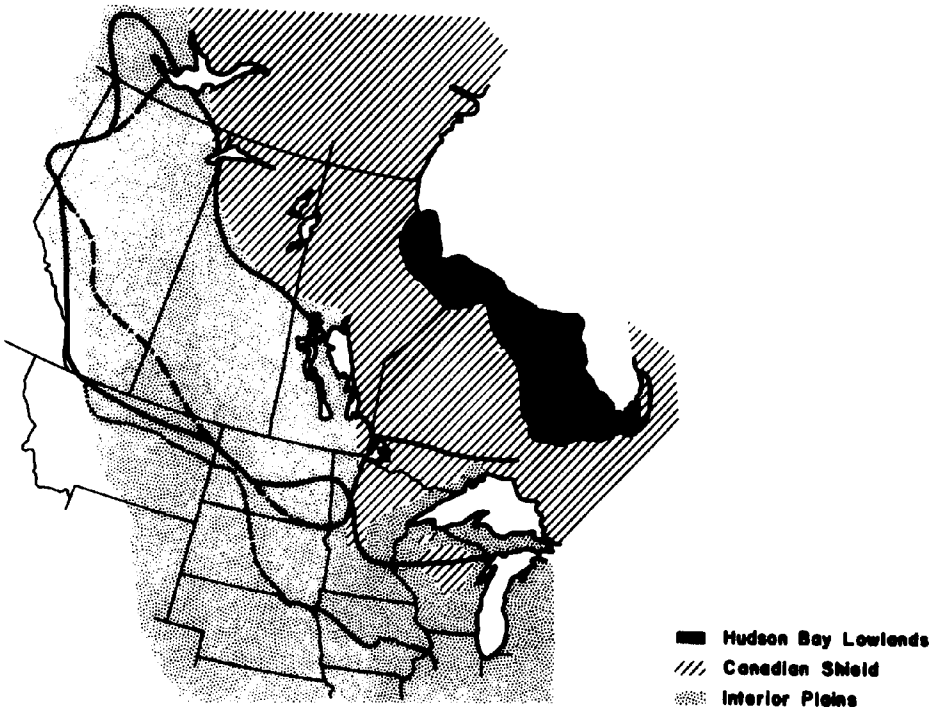


Figure 2. The breeding and winter ranges of the Le Conte's Sparrow. The symbols are the same as in Figure 1.

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

Figure 4. The ranges of Le Conte's and Sharp-tailed sparrows in relation to vegetation type. The symbols, other than those indicated in the key, are the same as in Figure 3.


Hudson Bay Lowlands
Canadian Shield
Interior Plains

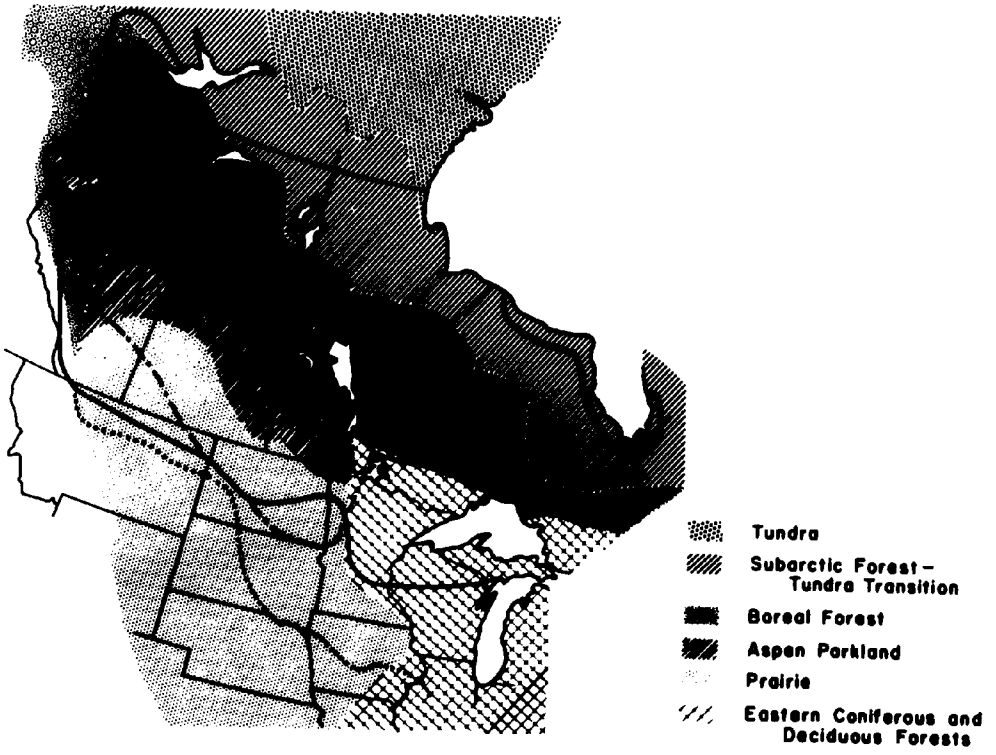

Tundra
Subarctic Forest – Tundra Transition
Boreal Forest
Aspen Parkland
Prairie
Eastern Coniferous and Deciduous Forests

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

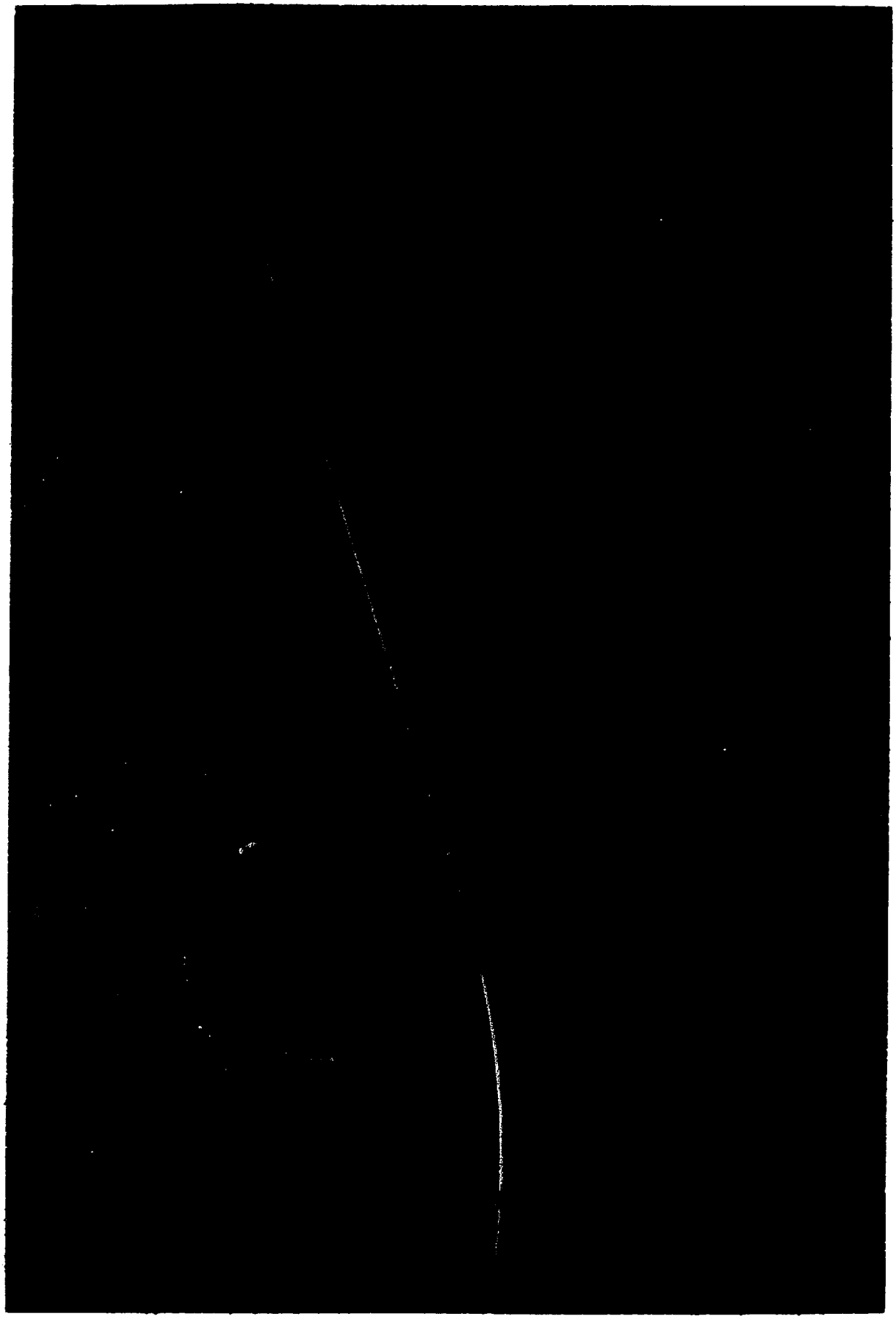


Figure 6. Vertical aerial photograph of the study area. (Courtesy John W. Winship and Bureau of Sport Fisheries and Wildlife.)

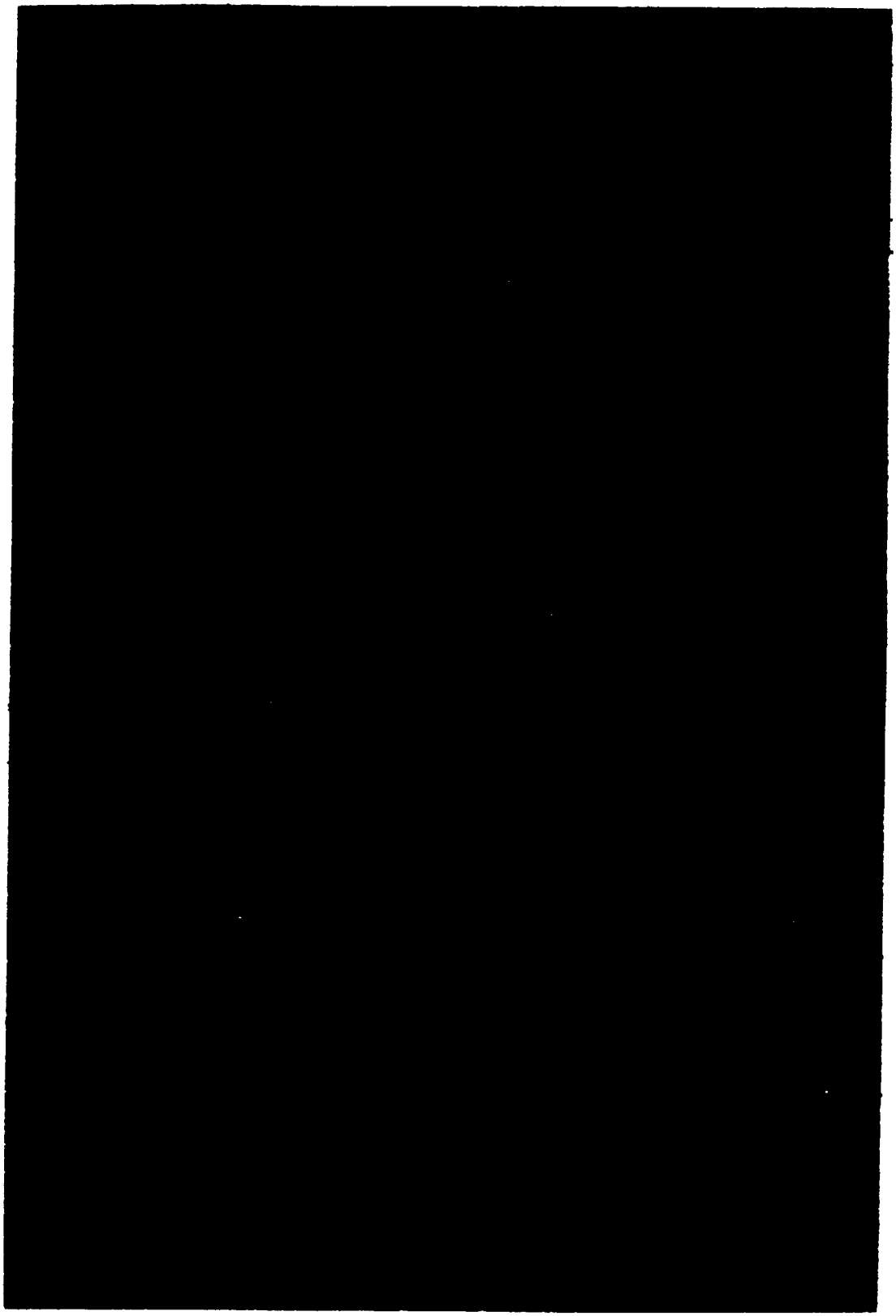
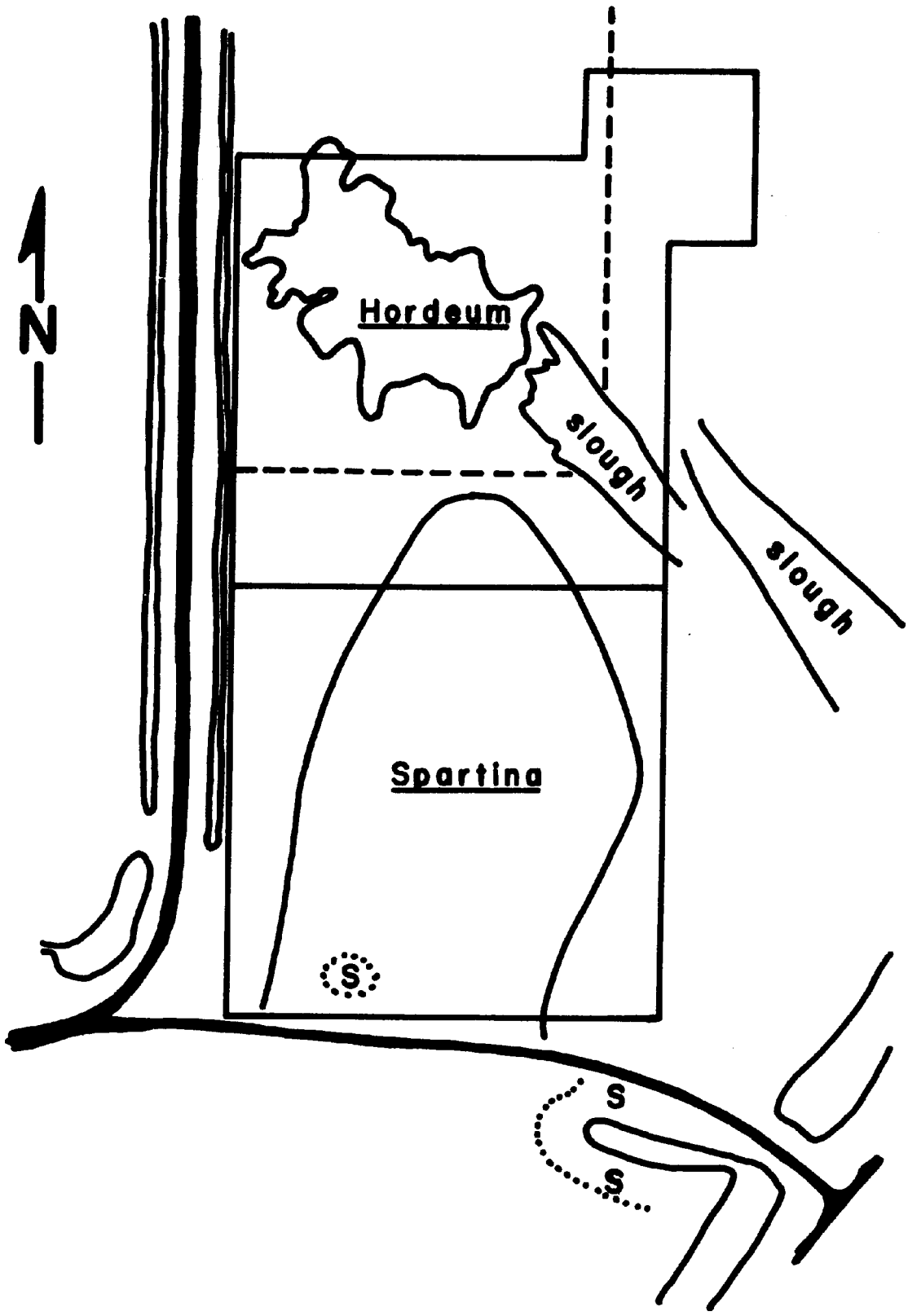


Figure 7. Diagram of study area. The extensive areas of Spartina and Hordeum are shown. The rest of the area within the large rectangle is predominantly a mixture of Spartina and Hordeum. The S, surrounded by dots, represents areas of Scolochloa. The large rectangular area is the 1966 study area, the southern half of which includes the 1965 study area. The dashed lines indicate the extent of the area last hayed in 1964.


N
Hordeum
slough
slough
Spartina
S
S
S

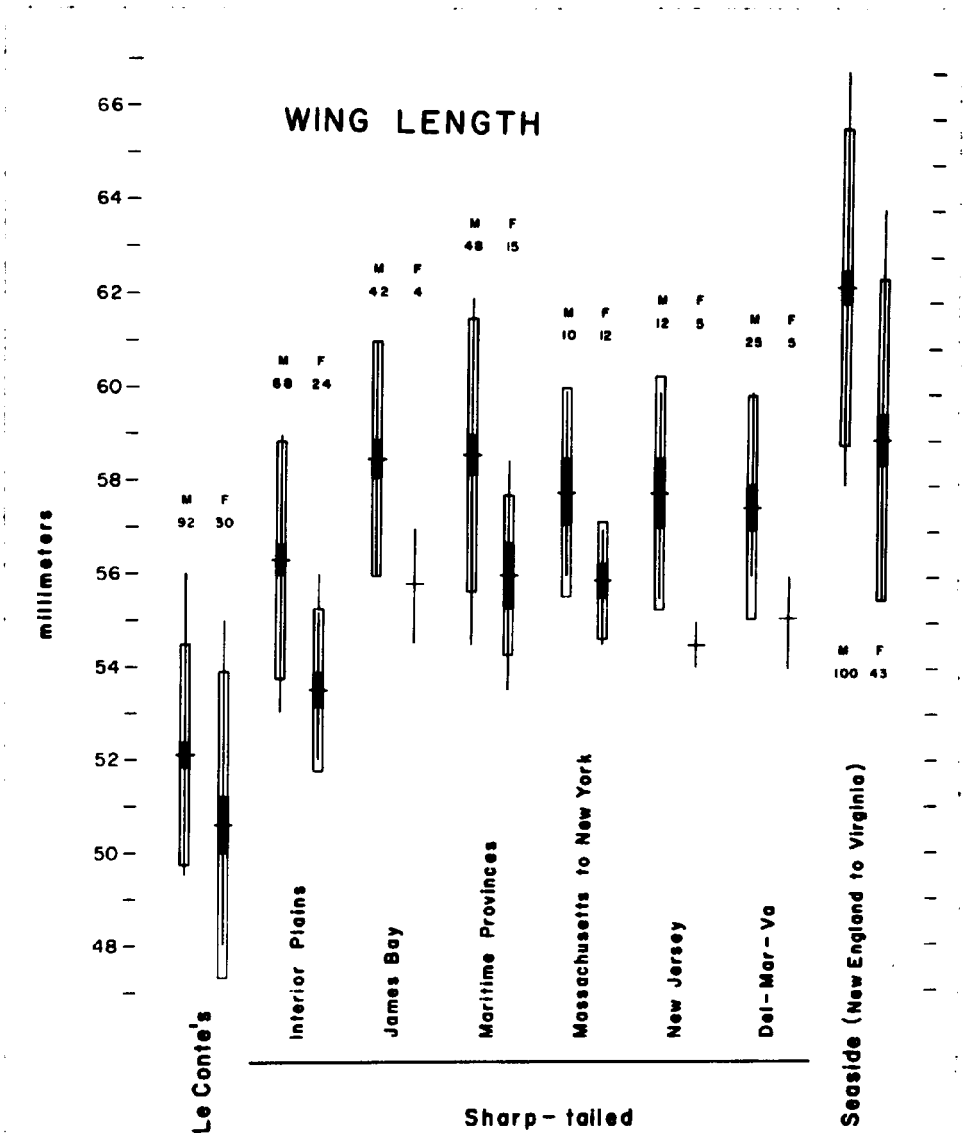


Figure 8. Comparison of wing lengths of the Le Conte's Sparrow, the Seaside Sparrow, and six populations of the Sharp-tailed Sparrow. The observed range and mean $\pm$ 2 standard deviations and $\pm$ 2 standard errors of the mean are given for males (M) and females (F). The number of specimens in each sample is also given. The statistics are given in Tables 1, 2, 3, and 5.

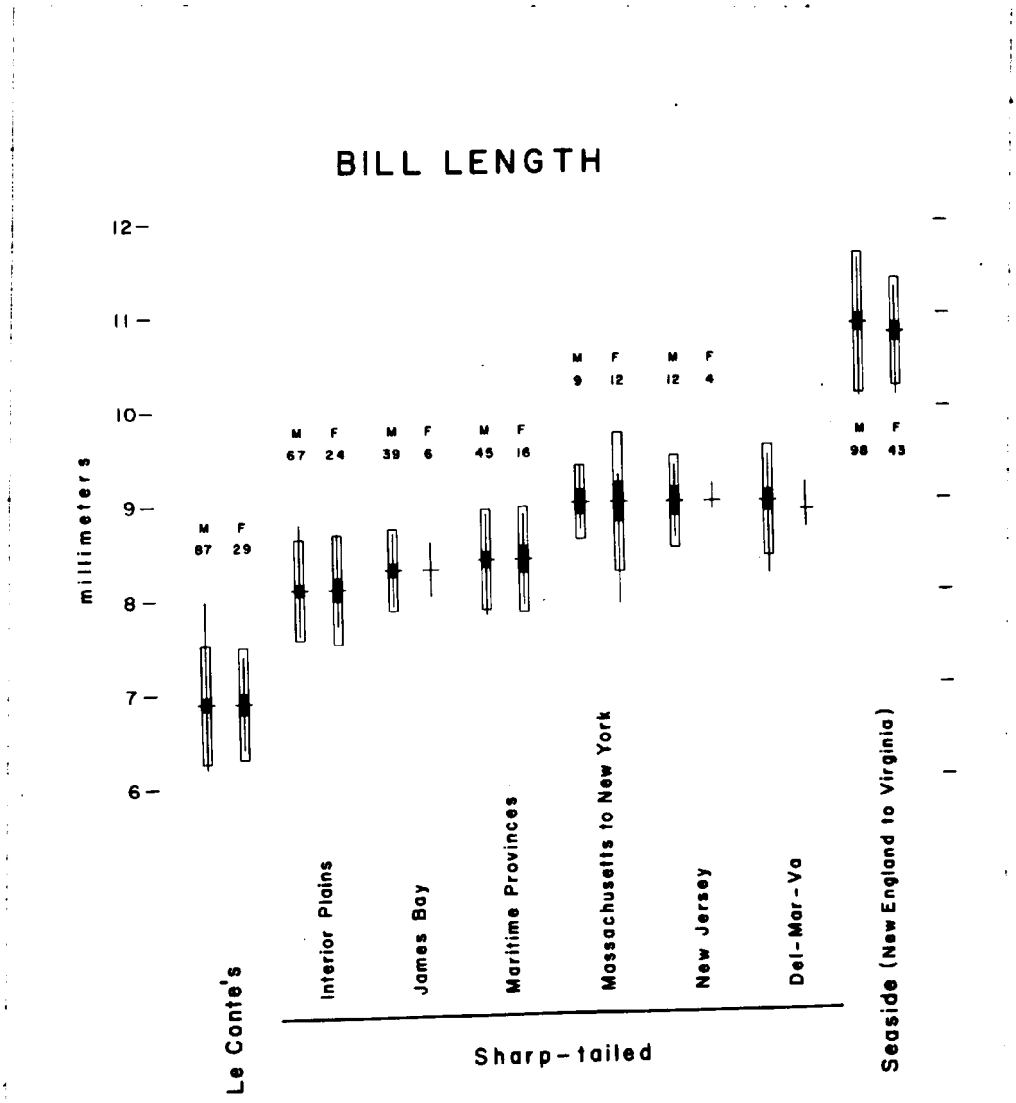


Figure 9. Comparison of bill lengths of the Le Conte's Sparrow, the Seaside Sparrow, and six populations of the Sharp-tailed Sparrow. The symbols are the same as in Figure 8. The statistics are given in Tables 1, 2, 3 and 5.

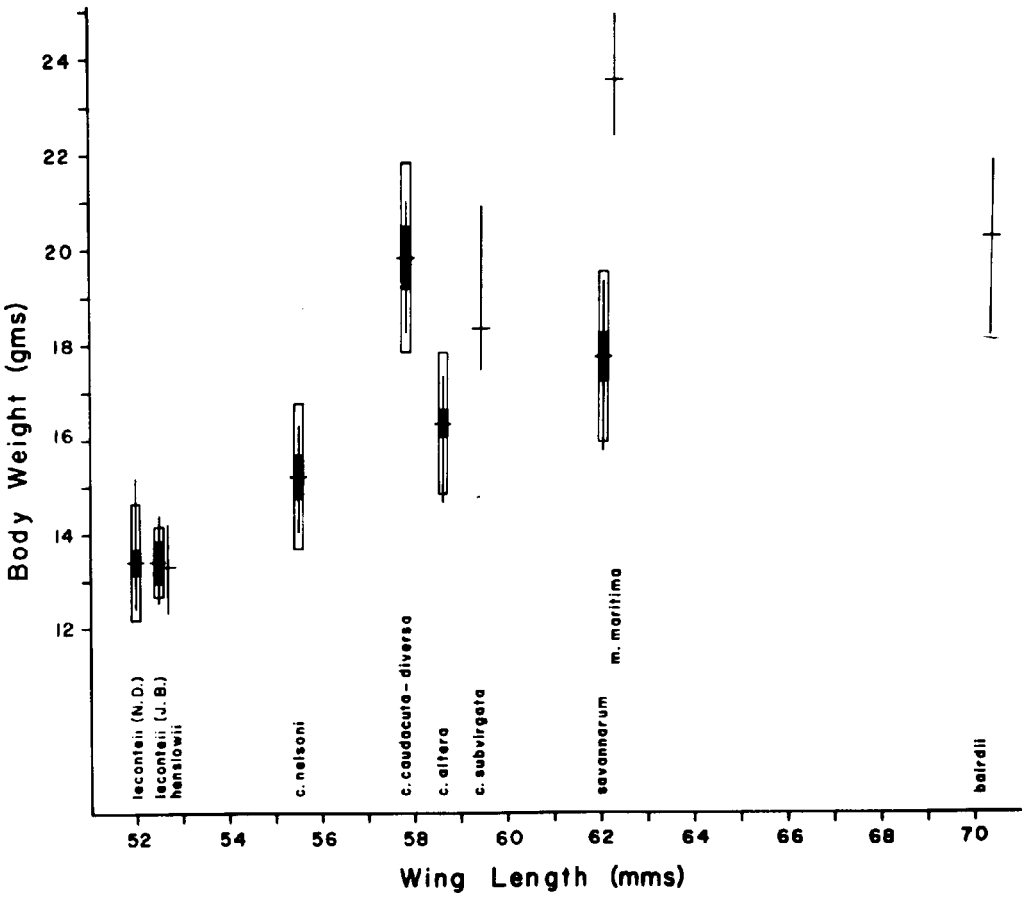


Figure 10. The relationship between body weight and wing length among several populations of sparrows. The symbols are the same as in Figure 8. The statistics are given in Table 4.

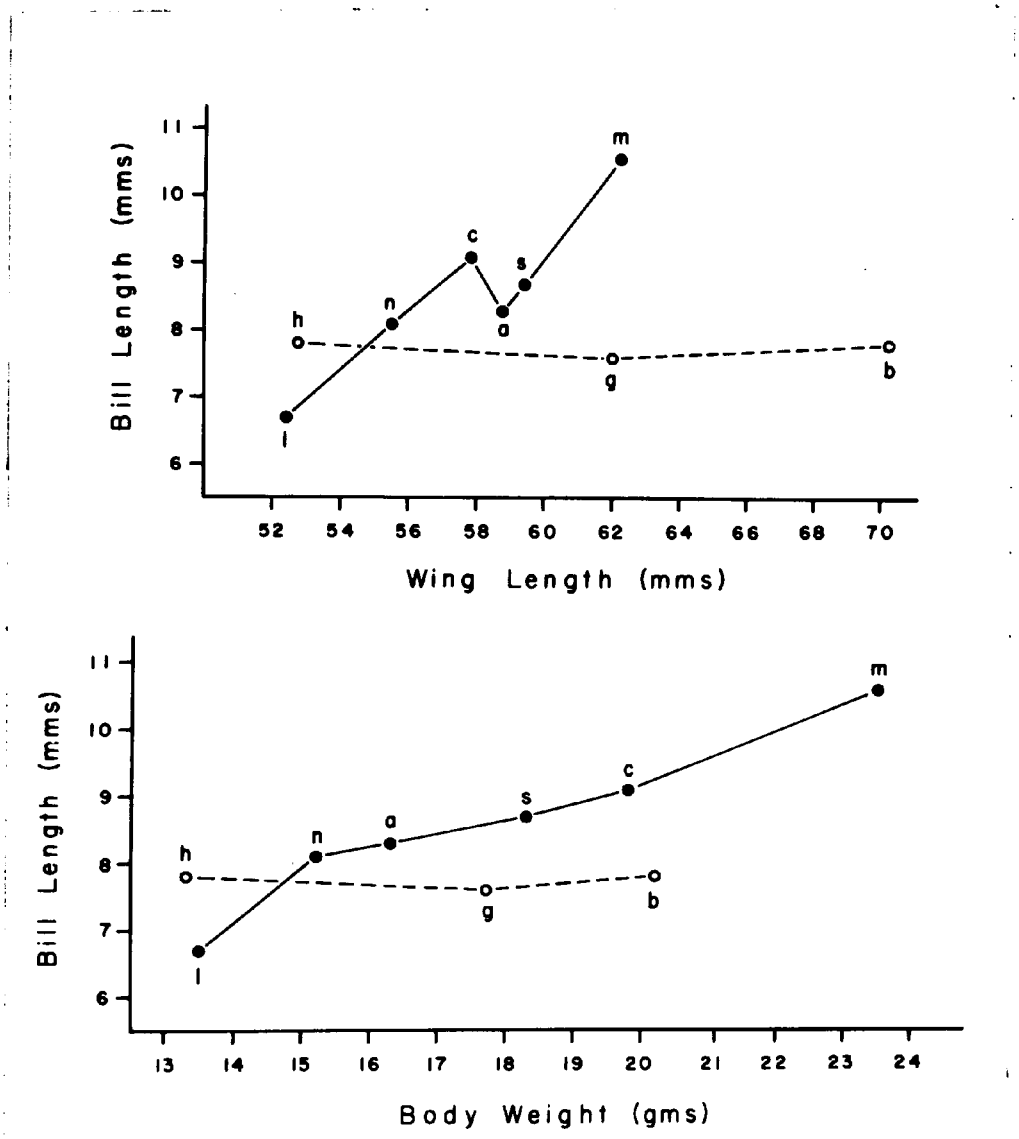
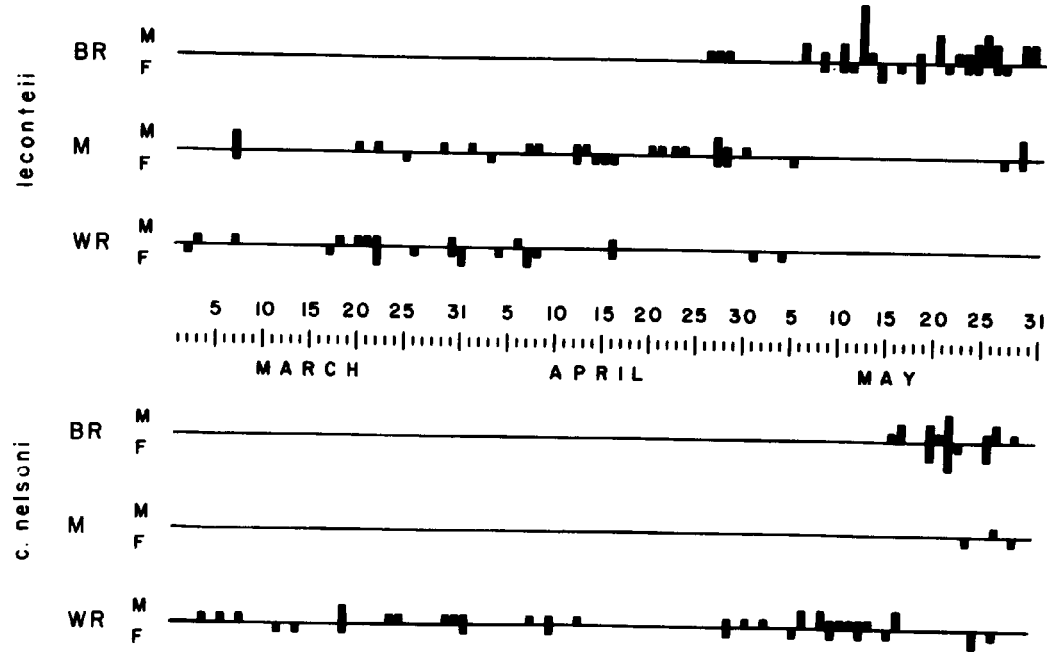


Figure 11. The relationship between bill length and wing length (upper) and between bill length and body weight (lower) among several populations of sparrows. Only means are given. Populations: l, leconteii; n, c. nelsoni; a, c. altera; s, c. subvirgata; c, c. caudacuta; m, m. maritima; h, henslowii; g, savannarum; and b, bairdii.

Figure 12. Pre-breeding migration of the Le Conte's and Sharp-tailed (nelsoni) sparrows. Individual specimens 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 (M). The males (M) are plotted above the line, and the females (F) are plotted below the line.

Figure 13. Post-breeding migration of the Le Conte's and Sharp-tailed (nelsoni) sparrows. Specimens are plotted in the same way as in Figure 12.

PRE-BREEDING MIGRATION



POST-BREEDING MIGRATION

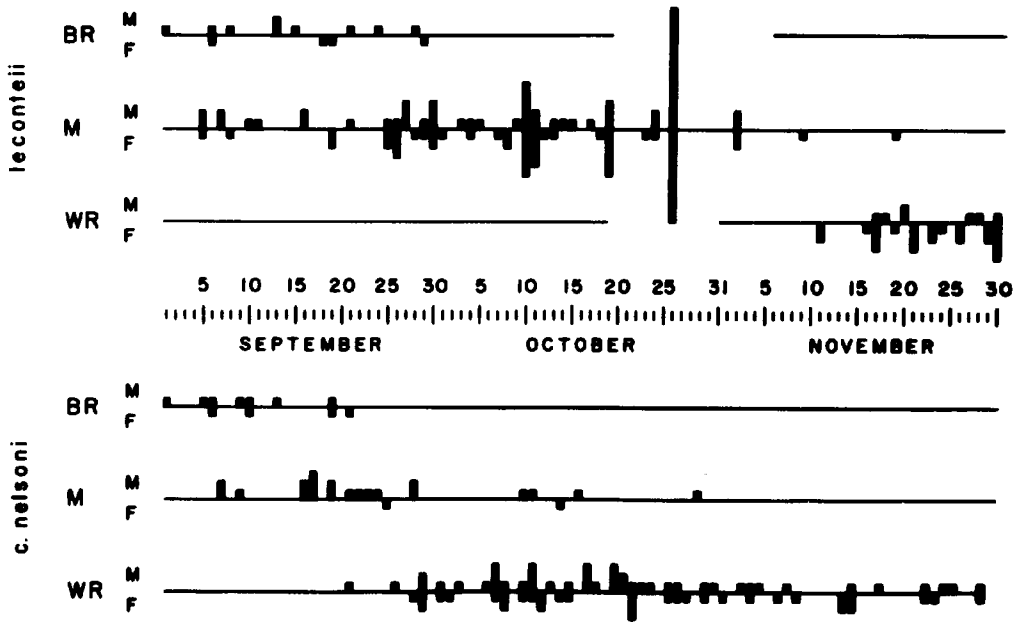
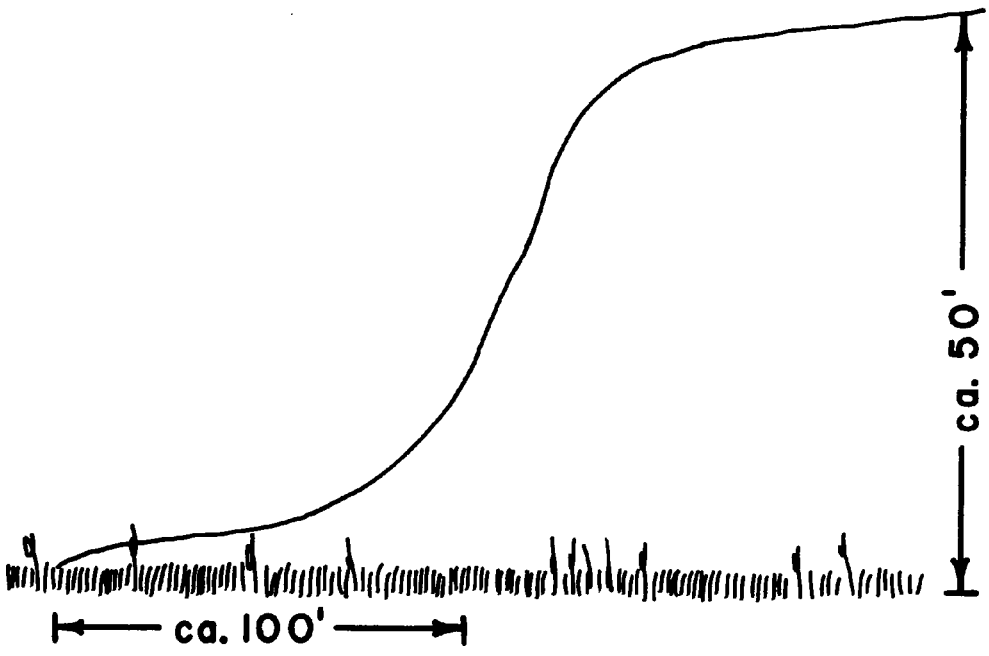


Figure 14. Typical song flights of the Le Conte's Sparrow (upper) and the Sharp-tailed Sparrow (lower). Le Conte's Sparrows give introductory notes on the upward flight and the buzz on the downward flight (see text). Sharp-tailed Sparrows give one to three songs in horizontal flight at a height and, then, drop to the ground.



Le Conte's Sparrow



Sharp-tailed Sparrow

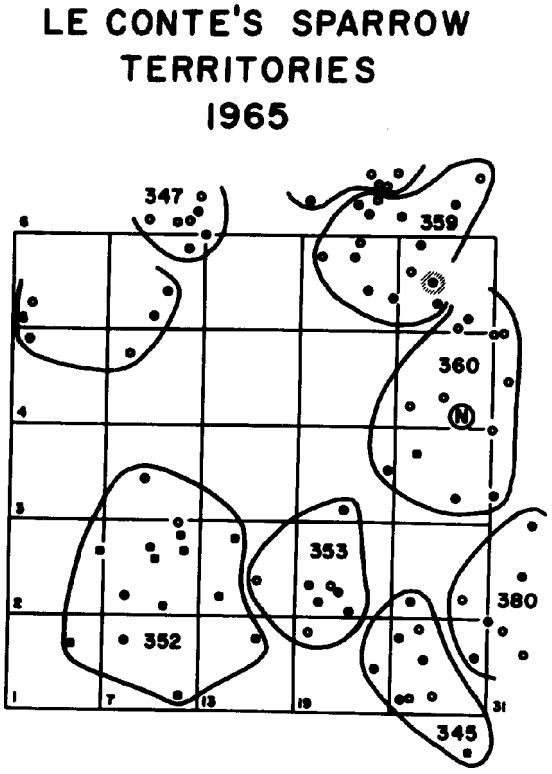


Figure 15. Le Conte's Sparrow territories in 1965. Black circles denote identified (color-marked) singing individuals, and black squares denote identified non-singing individuals; white circles denote unidentified singing birds; black-and-white circles denote flight-songs; and the N indicates a nest-site. The numbers are the last three digits of the band number. Heavy lines delimit territories. The broken territorial boundaries of 359 and 360 indicate where there was a seasonal change in boundary or an overlap of territories, as the dot marked by diagonal lines represents 360.

Figure 16. Le Conte's Sparrow territories in 1966. In addition to the symbols used in Figure 15, the triangles indicate locations where the birds were mist-netted. Changes in territories are described in the text.

LE CONTE'S SPARROW TERRITORIES 1966

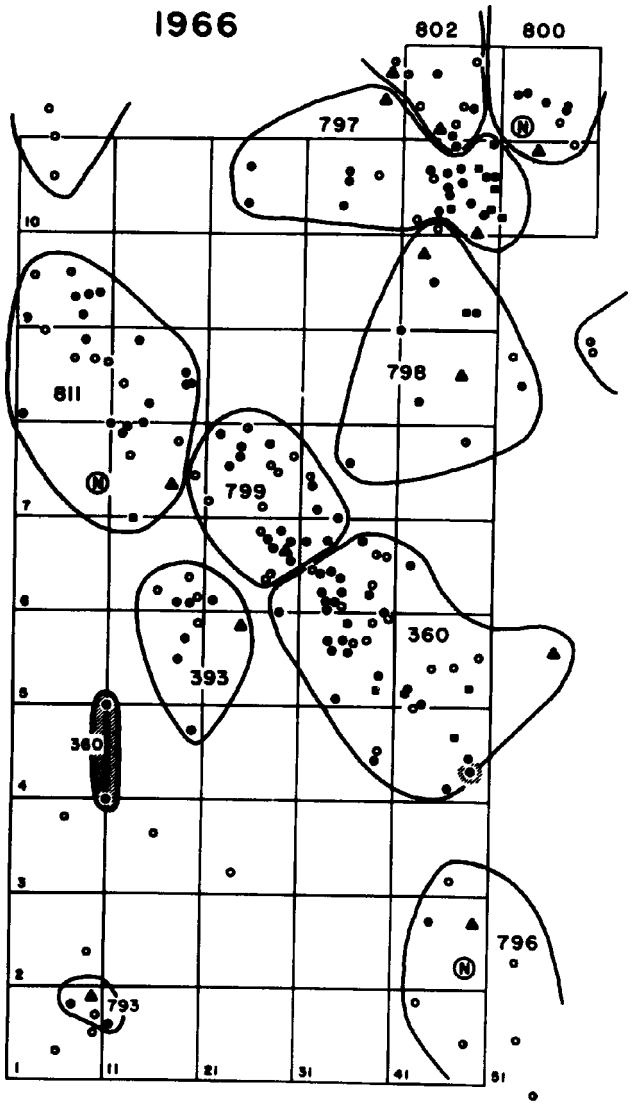


Figure 17. Activity of male Sharp-tailed Sparrows between 0800 and 1130 hours on 2 July 1965. There were three marked birds: solid line, dashed line, and alternating dashes and double dots. The activity of two or three unmarked birds is represented by dotted lines. The s indicates singing; when the identity of the singer might be in doubt, the s is underlined appropriately. A single arrowhead indicates the point where a bird stopped; a double arrowhead indicates the direction in which the bird was seen flying. A tail to an arrow indicates the point at which a flying bird was first spotted; no tail indicates the starting point of a flight.

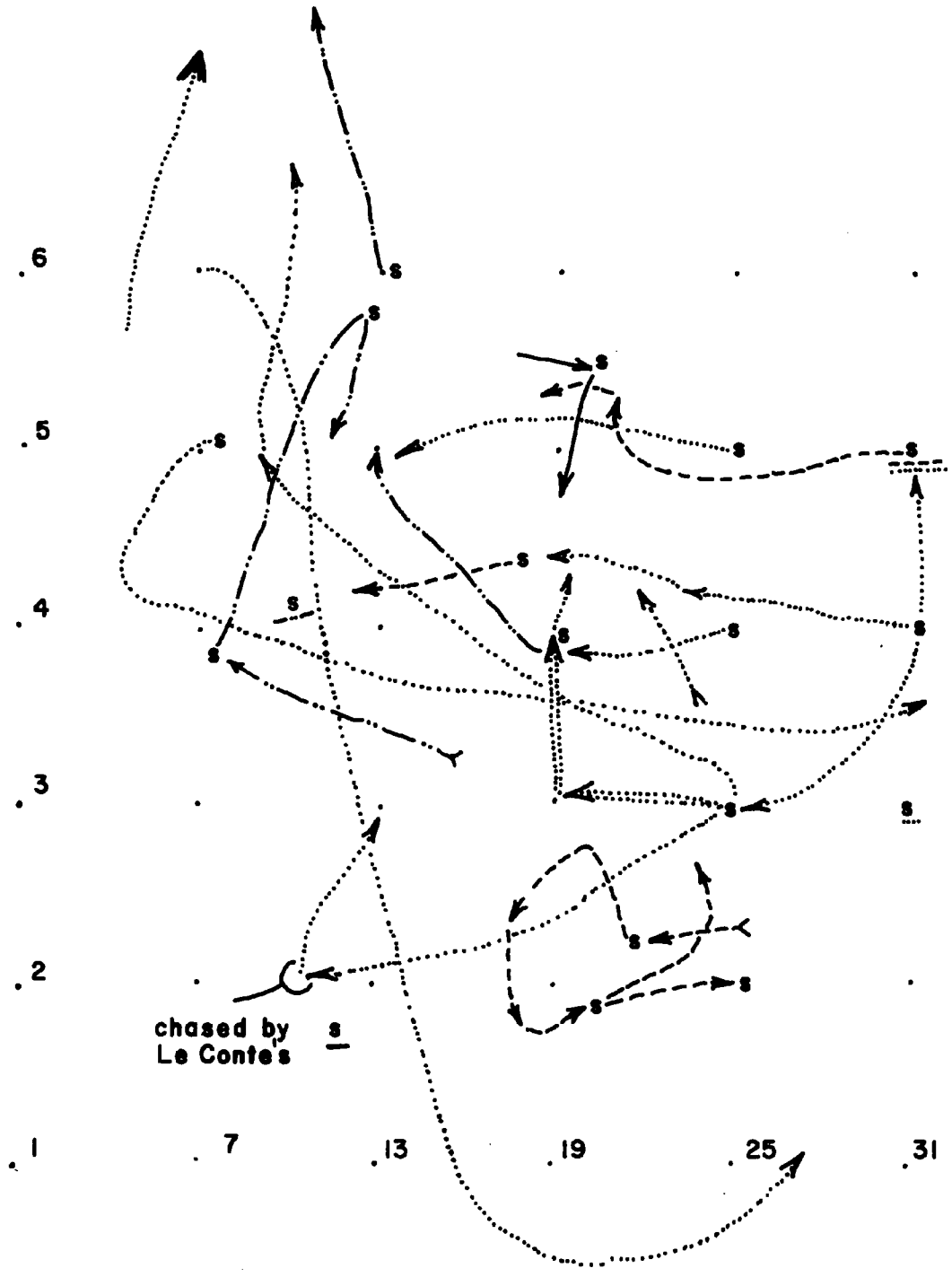

6
5
4
3
2
1
7
13
19
25
31
chased by
Le Contes
s

Figure 18. Activity of male Sharp-tailed Sparrows between 1900 and 2000 hours on 12 July 1966. There were two marked birds: solid line and dashed line. The activity of at least two unmarked birds is represented by dotted lines. In addition to the other symbols used in Figure 17, an fs indicates a position of a flight song.

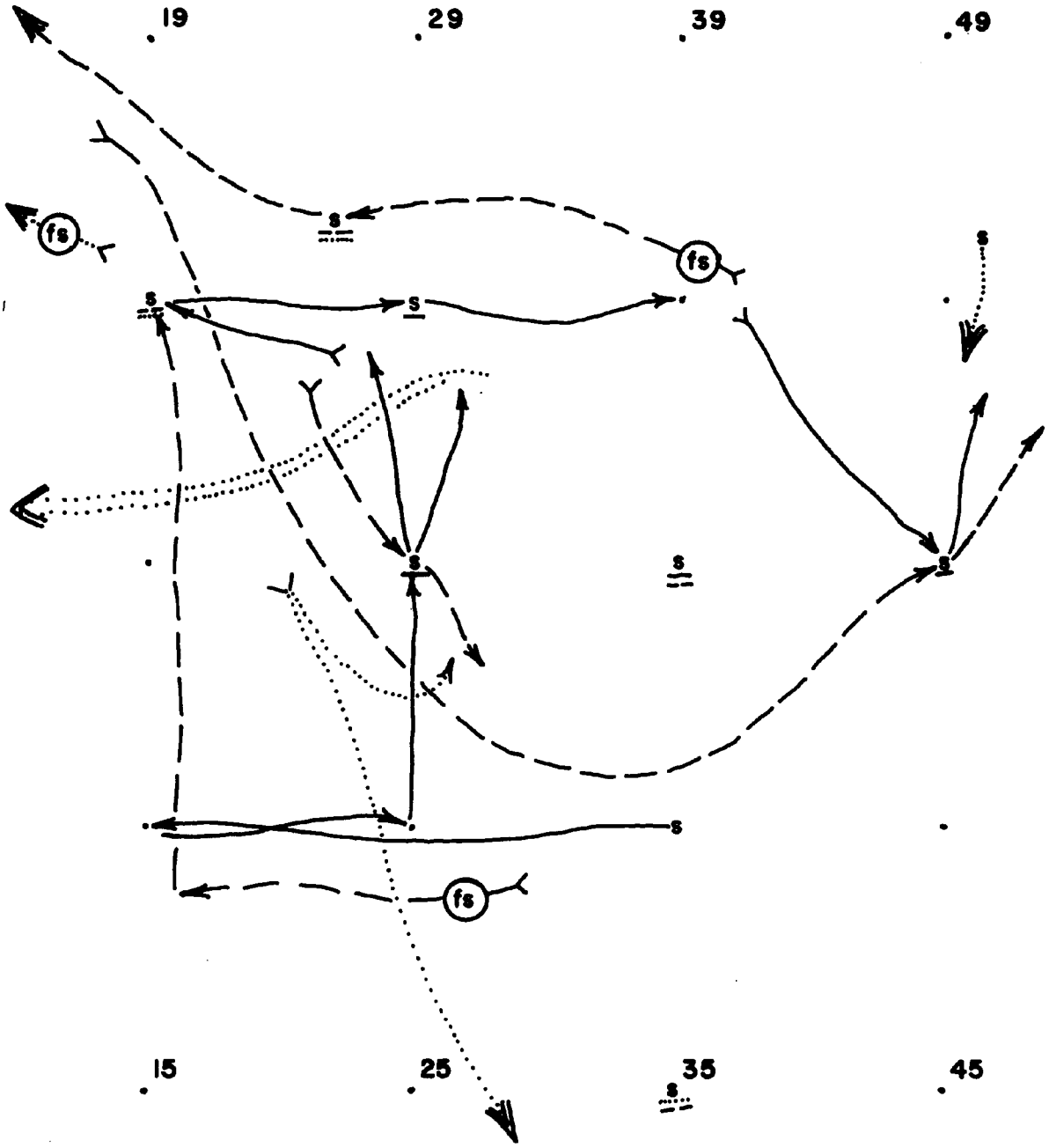

19
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fs
fs
s
s
s
s
s
s
s
s
fs
15
25
35
45

Figure 19. The sequence of molts in several species of sparrows. The first year's cycle is shown. The dashed lines indicate the degree of variation that can occur in a particular molt.

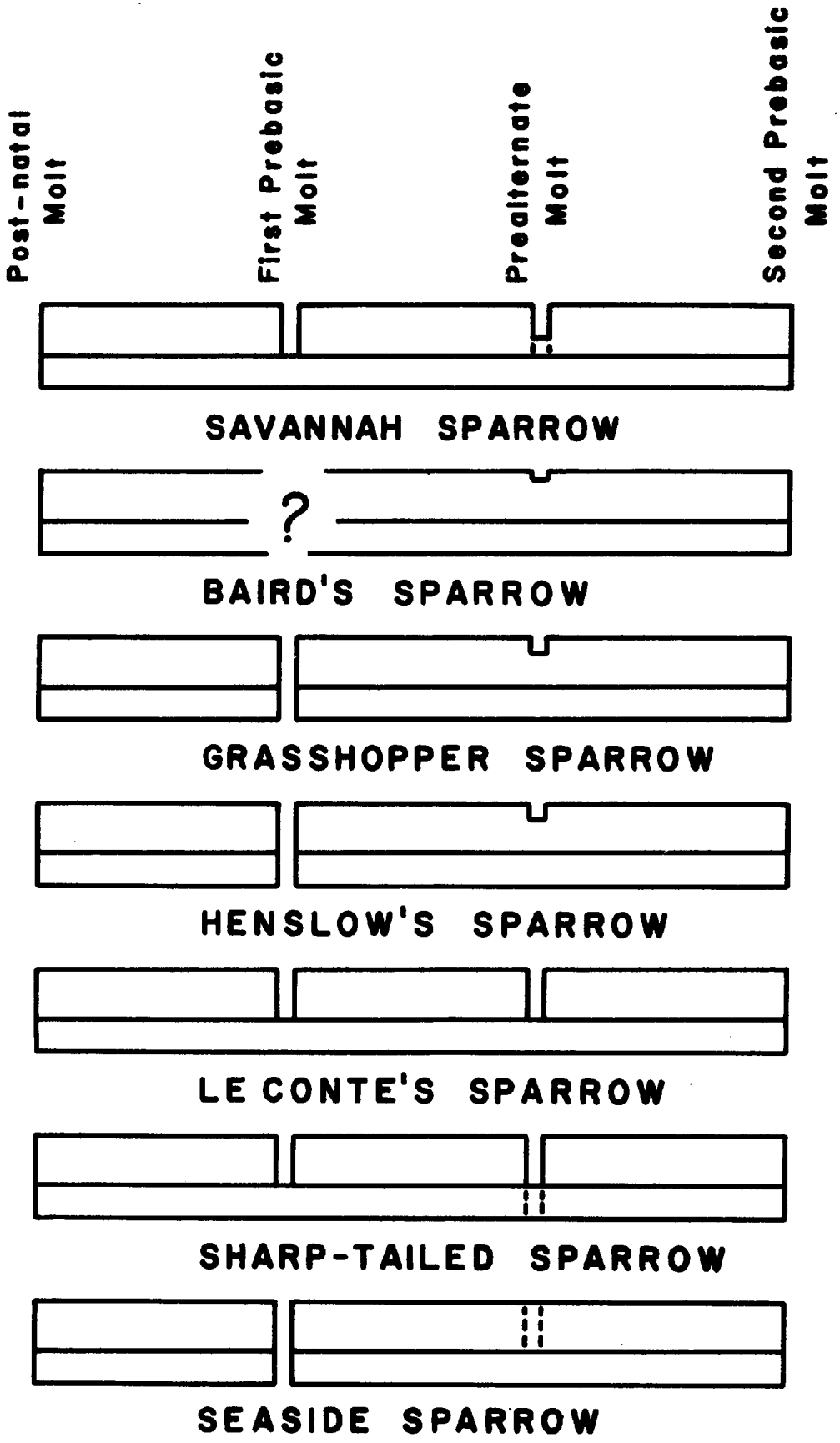
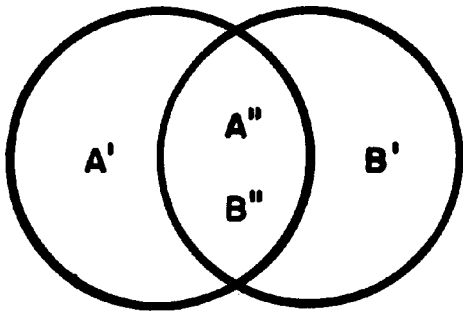

Post-natal Molt
First Prebasic Molt
Prealternate Molt
Second Prebasic Molt
SAVANNAH SPARROW
?
BAIRD'S SPARROW
GRASSHOPPER SPARROW
HENSLOW'S SPARROW
LE CONTE'S SPARROW
SHARP-TAILED SPARROW
SEASIDE SPARROW



Figure 20. Dorsal views of a Sharp-tailed Sparrow (left), a Le Conte's Sparrow (right), and a probable hybrid between the two species.

Figure 21. The evolution of bill length in hypothetical populations.



Geographic Ranges of two species,
A and B

I. No gene flow between A' and A" or between B' and B"



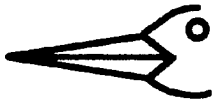
A' = 6 mm



A" = 8 mm



B" = 8 mm

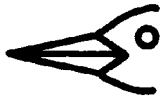


B' = 10 mm

II. Gene flow between A' and A" and between B' and B"



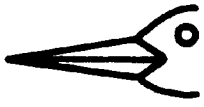
A' = 6.5 mm



A" = 7.5 mm



B" = 8.5 mm



B' = 9.5 mm

Table 1. Measurements of Le Conte's Sparrow populations.

Wing Length

Area	Sex	N	Mean (± 2 S.E.)	Range	S.D.
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

Area	Sex	N	Mean (± 2 S.E.)	Range	S.D.
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 (± 9.07)	6.2 - 8.0	0.32
	F	29	6.9 (± 0.11)	6.4 - 7.4	0.30

Table 2. Measurements of Sharp-tailed Sparrow (*nelsoni*) populations.

Wing Length

Area	Sex	N	Mean (± 2 S.E.)	Range	S.D.
I	M	10	56.4 (± 0.83)	54.5 - 58.5	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

Area	Sex	N	Mean (± 2 S.E.)	Range	S.D.
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

Table 3. Measurements of some male Seaside Sparrow populations.

		Wing Length		
Race	N	Mean (± 2. S.E.)	Range	S.D.
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		
Race	N	Mean (± 2. S.E.)	Range	S.D.
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

Table 4. Weights and wing lengths of males of some sparrow populations.

	N	Mean Wing Length	Weight Mean (± 2 S.E.)	S.D.	Range
Baird's Sparrow					
North Dakota	5	70.2	20.2	-	18.1-21.8
Grasshopper Sparrow					
Michigan	13	62.0	17.7 (± 0.50)	0.90	15.7-19.3
Henslow's Sparrow					
Michigan	8	52.7	13.3	-	12.3-14.2
Le Conte's Sparrow					
North Dakota	26	52.0	13.4 (± 0.25)	0.63	12.4-15.2
James Bay	10	52.5	13.4 (± 0.43)	0.68	12.5-14.4
Sharp-tailed Sparrow					
North Dakota	12	55.5	15.2 (± 0.45)	0.78	14.0-16.3
James Bay	30	58.6	16.3 (± 0.28)	0.77	14.6-17.3
Maine[1]	21	59.4	18.3	-	17.4-20.9
New Jersey	10	57.8	19.8 (± 0.63)	1.01	18.2-21.0
Seaside Sparrow					
New Jersey	6	62.2	23.5	-	22.3-24.9

[1]From Montagna (1940).

Table 5. Measurements of Sharp-tailed Sparrow populations.

Wing Length

	Sex	N	Mean (± 2 S.E.)	S.D.	Range
c. nelsoni	M	68	56.3 (± 0.31)	1.28	53.0–59.0
	F	24	53.5 (± 0.36)	0.88	52.0–56.0
c. altera	M	42	58.5 (± 0.39)	1.27	56.0–61.0
	F	4	55.8	–	54.5–57.0
c. subvirgata	M	48	58.6 (± 0.43)	1.48	54.5–62.0
	F	15	56.0 (± 0.71)	1.37	53.5–58.5
c. caudacuta (Massachusetts to New York)	M	10	57.8 (± 0.71)	1.13	56.0–60.0
	F	12	55.9 (± 0.40)	0.70	54.5–57.0
c. caudacuta and *c. diversa* (New Jersey)	M	12	57.8 (± 0.73)	1.27	55.5–60.0
	F	5	54.5	–	54.0–55.0
c. diversa (DelMarVa)	M	25	57.5 (± 0.48)	1.21	56.0–60.0
	F	5	55.1	–	54.0–56.0

Bill Length

	Sex	N	Mean (± 2 S.E.)	S.D.	Range
c. nelsoni	M	67	8.1 (± 0.06)	0.27	7.6–8.8
	F	24	8.1 (± 0.11)	0.29	7.7–8.7
c. altera	M	39	8.3 (± 0.07)	0.22	7.9–8.7
	F	6	8.3	–	8.0–8.6
c. subvirgata	M	45	8.4 (± 0.08)	0.27	7.8–8.9
	F	16	8.4 (± 0.14)	0.29	7.9–8.9
c. caudacuta (Massachusetts to New York)	M	9	9.0 (± 0.13)	0.21	8.7–9.4
	F	12	9.0 (± 0.21)	0.73	7.9–9.3
c. caudacuta and *c. diversa* (New Jersey)	M	12	9.0 (± 0.14)	0.25	8.6–9.4
	F	4	9.0	–	8.9–9.2
c. diversa (DelMarVa)	M	26	9.0 (± 0.11)	0.30	8.2–9.5
	F	4	8.9	–	8.7–9.2