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ECOGEOGRAPHICAL VARIATION IN SIZE AND PROPORTIONS OF SONG SPARROWS (*MELOSPIZA MELODIA*)

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INTRODUCTION

The correlation of morphological variation of plants and animals with environmental variables has interested biologists for many years. Small, genetically controlled variations for which environmental factors act as selective agents are generally believed to be the building blocks of evolution. Intraspecific differences that may lead to speciation are frequently coincident with variations in the environment within the species' range.

I studied variation in the wide ranging and morphologically highly variable North American Song Sparrow, *Melospiza melodia,* in relation to the totality of environmental factors represented by specific major biotic communities as recognized and described by ecologists. My purpose was to determine if particular morphological differences in the birds coincided with the distribution of biotic communities, thus indicating their morphological adaptation to the same factors that control the composition and distribution of those biotic communities. I believed that information on the nature and extent of morphological variation in Song Sparrows and its relation to factors known to control the composition and distribution of biotic communities would be significant in understanding the reasons for the marked intraspecific variation in animals and would provide a rewarding approach to this phase of evolutionary biology.

In the present study I have correlated measurements and proportions of Song Sparrows with Life Areas (Aldrich 1963, 1966), Ecoregion Provinces, Ecoregion Sections (Bailey 1976), and combinations of Life Areas and Ecoregion Sections, in an attempt to determine the probable adaptive value of the morphological variation. Plumage coloration, which is known to vary greatly geographically, was not considered. My rationale for using Life Areas and Ecoregions was that both are based primarily on climax vegetation, which imparts a specific identifying aspect to them, and that both are virtually visible expressions of the environmental factors that delimit them. Although Song Sparrows do not use climax vegetation extensively, at least during the breeding season, in any part of their geographical range (Appendix I), climax vegetation is an indicator of combined climatic and physiographic factors, as well as of the types of habitats of both climax and seral communities, which do impinge directly on Song Sparrows, and to which the birds must be adapted in order to survive. The significance of the dominant climax vegetation as an indicator of the total environment of a geographical area is treated at length by Weaver and Clements (1938:89–90), Carpenter (1939), Clements and Shelford (1939), Pitelka (1941), Dice (1943), Odum (1953), and Kendeigh (1954).

Many previous studies (summarized in Mayr 1951; Power 1970; Selander 1971) have dealt with the effects of single environmental factors, such as temperature, rainfall, or soils, on size proportions or color of birds. A few workers, however, have studied the relations between variation in morphological features and all environmental factors that characterize ecogeographical units. For example, Marshall and Behle (1942) described two races of Song Sparrows living in adjacent ecologically distinct zones in Utah. Aldrich and Friedmann (1943) described the association of morphological variation in Ruffed Grouse (*Bonasa umbellus*) with ecogeographic units throughout the entire species range. Aldrich (1963) showed that geographical races of American grouse species tend to be correlated with the

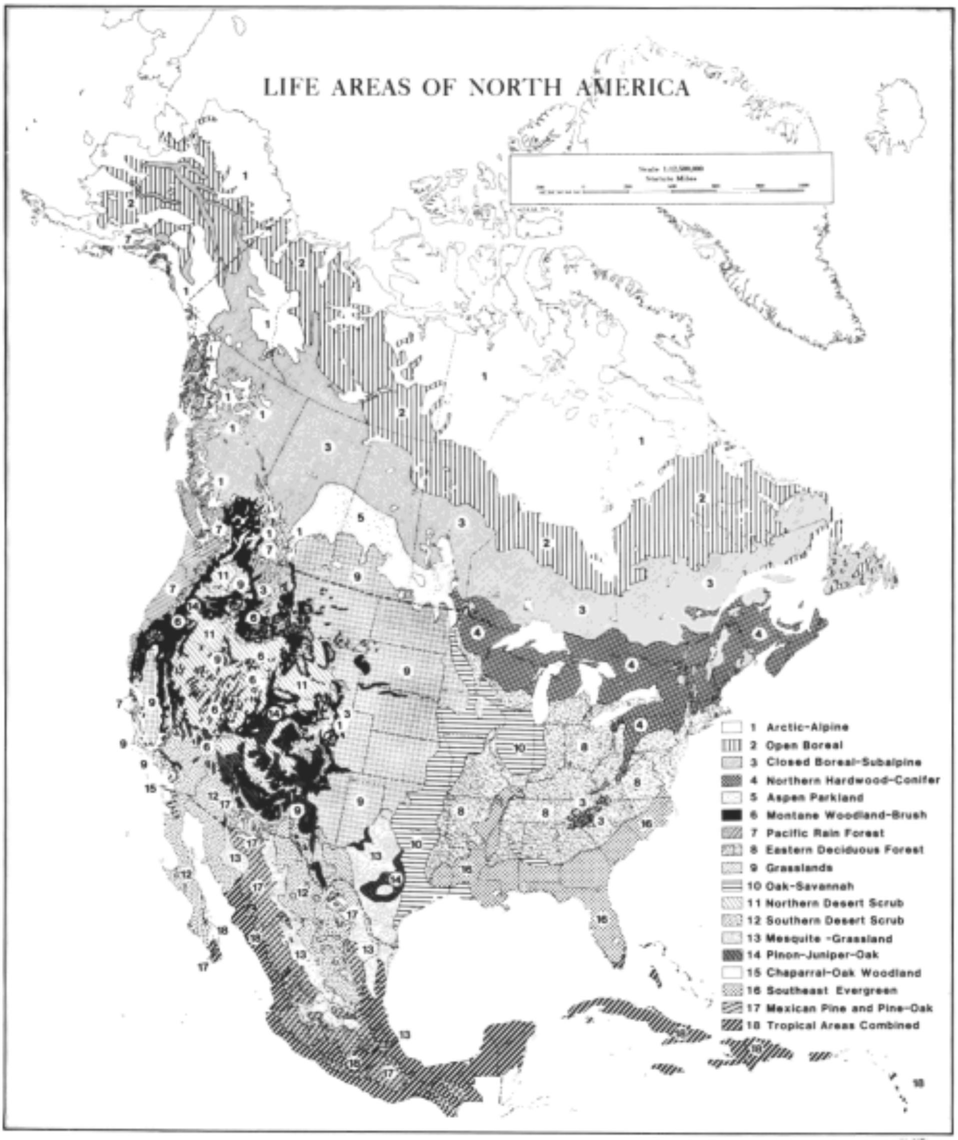

FIG. 1. Life Areas of North America. Based on Aldrich (1966).

ecological climax areas in which they live, and such ecogeographical units, called "Life Areas," were mapped. Rea (1973) correlated variations in Scaled Quail (*Callipepla squamata*) with desert scrub and short-grass prairie ranges. Aldrich and Weske (1978) related color and size variations in House Finches (*Carpodacus mexicanus*) to the Biotic Provinces of Dice (1931, 1943) and Ecoregions of Bailey (1976).

The Life Areas of North America (Fig. 1) were first mapped, described and discussed in relation to the distribution of subspecies of North American grouse (Aldrich 1963). Life Areas are based on climatic climax dominant vegetation of

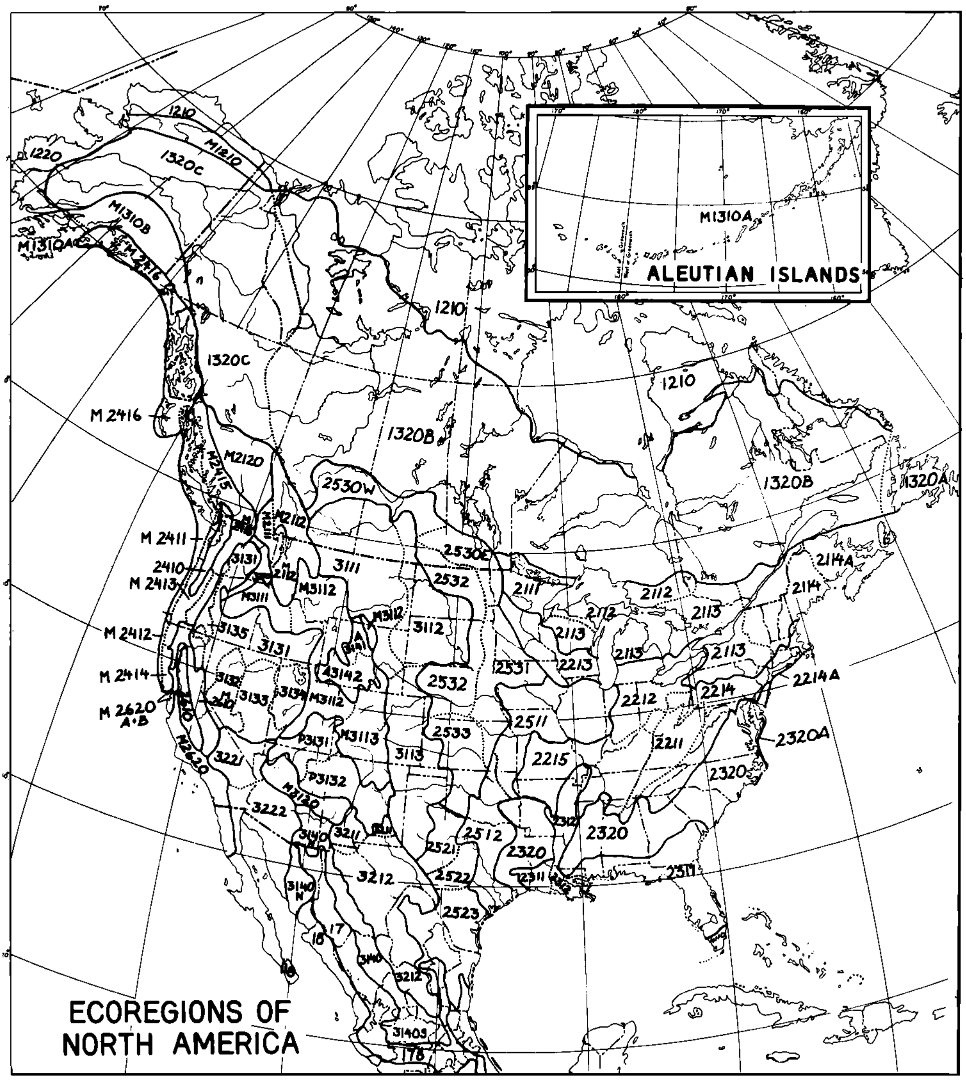

FIG. 2. Ecoregions of North America. Modified from Bailey (1976), and expanded based on Dice (1943), Leopold (1950), Rowe (1959), Aldrich (1966), and Crowley (1967).

specific physiognomic types and thus resemble the Formations of Weaver and Clements (1938) or Biomes of Clements and Shelford (1939). In contrast, however, they include a few distinct and extensive ecotones between Formations or Biomes, such as Northern Hardwood-Conifer, Oak-Savannah, and Aspen Parkland, and also extensive fire-maintained subclimaxes such as Southeast Evergreen and Chaparral-Oak Woodland. Some boundaries of Life Areas based on Küchler (1964) were revised by Aldrich (1966) after the first Life Area map was published. These changes are chiefly in the distribution of the Grasslands and Oak-Savannah Life Areas. In the present study the Open and Closed Boreal Life Areas of Aldrich (1966) are combined into a single "Boreal Life Area" (Fig. 1).

The Ecoregions (Fig. 2) are based primarily on Bailey (1976) for the United

States, but modified to include Canada and Mexico based on Dice (1943), Leopold (1950), Rowe (1959), Aldrich (1966), and Crowley (1967). Ecoregions are continuous geographical areas, like the Biotic Provinces of Dice (1943). In this respect they differ from Life Areas, which are as discontinuous as the climax vegetation types on which they are based. Ecoregions are characterized by the occurrence of one or more important ecological associations that differ, at least in proportional area covered, from associations of adjacent regions. In general, Ecoregions are characterized also by a distinctive flora, fauna, climate, landform, soil, and ecological climax. They are divided into hierarchical levels including Domain, Division, Province, and Section in decreasing order of inclusiveness. Provinces and Sections are further divided into lowland and highland types. A Province is a subdivision that corresponds to a broad vegetation region having a uniform regional climate and characteristic types of zonal soils. Generally, each Province is characterized by a single climax association, but two or more climaxes may be represented within a single Province. The Ecoregion Provinces of Bailey (1976) are similar to the Biotic Provinces of Dice (1943) but are more detailed and more exactly ecologically oriented. An Ecoregion Section is based on local climatic variation and characterized by a single climax association as defined by Küchler (1964), except in mountainous areas where zones of more than one climax type occur.

METHODS

In the present study I have employed the Life Area (Fig. 1), and the Ecoregion Province and Section (Fig. 2), and combinations thereof as data grouping units for comparing mean measurements of Song Sparrows. I have further divided the Ecoregion Sections into their component zones (called "Life Belts") which are equivalent to the Life Areas appearing as elevational belts in Figure 1. In mountainous regions these are the elevational zones recognized, but not mapped, by Bailey (1976). Composition of the Ecoregion Section/Life Area units appearing in Tables 5, 6, and 9 (*Tables 1–9 are found on pp. 52–78*) are indicated by a prefix number that identifies the Life Area (Fig. 1; Tables 1, 2), and a second number (following the dash), that identifies the Ecoregion Section (Fig. 2; Tables 5, 6). The letters M, P, and A identify the Ecoregion as mountainous, plateau, or altiplano, respectively. The portions of Life Areas segregated in Ecoregion Sections and forming the Section's Life Belts are of a single climax community and are equivalent to the "Life Areas" of Aldrich's (1966) figure 1.

Specimens of Song Sparrows used in the present study were taken from areas representing most of the breeding range of that species and are chiefly from the collections of the National Museum of Natural History, Washington, D.C., and the Museum of Vertebrate Zoology, University of California at Berkeley. No specimens from California offshore islands were included. Only specimens taken from May through August were used to avoid the inclusion of migrants. This restricted period of collection also insured that the specimens would be more comparable from the standpoint of seasonal plumage wear.

Measurements used were the chord of the folded wing, length of the wing-tip from end of longest secondary to tip of longest primary, tail length from insertion of two middle tail feathers to the tip of the longest feather, total culmen length from depression in forehead separating culmen from cranium to tip of culmen, tarsus length from the posterior proximal end of the tarsometatarsus to the anterior distal end of the most distal tarsal scute, middle toe length from the end of the most distal tarsal scute to the distal end of the toe at its junction with the claw, height of maxilla from edge of the tomial notch to the opposite point on the dorsal surface of the maxilla, and width of maxilla at its widest point. In addition, ratios were determined for length of wing-tip to total wing length, height of maxilla to length of total culmen, width of maxilla to length of total culmen, length of tarsus to length of wing, and length of tail to length of wing. All measurements were made to 0.1 mm with a dial caliper equipped with needle points.

I grouped the 828 male and 406 female specimens by sex into the ecogeographic unit which they represent and determined the means and standard deviations of the measurements and their ratios for each group. The samples were arranged in descending order of magnitude of the means of each measurement and ratio to permit gross comparison of the relationship of populations representing the different ecogeographical units. I grouped the mean measurements and ratios for most male characters in three size categories and indicated the categories on maps which appear as figures in the appropriate character sections. The size categories were derived by dividing the total range (for males) of means of each measurement and ratio for Ecoregion Sections into three equal parts. The larger one-third of means is designated as "larger," "longer," or "higher," the middle one-third as "medium," and the smaller one-third as "smaller," "shorter," or "lower," depending on the nature of the character measured. If means are exceptionally large or small, so that they distort the division of values into three equal parts of the total, they are so indicated and were not included in computing the three size categories.

Means of measurements and their ratios of birds from adjoining Life Area, Ecoregion Province, and Ecoregion Section/Life Area units were compared with the Student's *t*-test to determine if differences were significant; *P* values of 0.05 or less were considered significant. The Student's *t*-test was used with these variables because it has been shown to be robust in the face of minor violations of assumptions found in this type of data (Boneau 1960; Lee-Ann Hayek, pers. comm.).

Finally, I arranged means of measurements and ratios representing Ecoregion Section/Life Area units along eight north to south transects and three east to west transects (Figs. 3, 4) and compared them by Student's *t*-test to determine significant character differences that might demonstrate progressive trends or sharp morphological changes related to ecogeographical differences. I compared the results of all of these analyses in an attempt to elucidate patterns of variation in Song Sparrows in relation to the ecogeographical units.

Means of each character for each sex for each of the 49 Ecoregion Section/Life Area units were compared by the Student's *t*-test to determine sexual dimorphism in those characters. Correlation of the variations in male and female characters and, in a few cases, correlation of variations in two different characters in the same sex, were determined. Correlation coefficients, *r*, as well as *P* values, were determined by standard programs of the Hewlett-Packard 67 calculator.

Measurements of all specimens used in this study are available for further analysis in the "species files" of the U.S. Fish and Wildlife Service offices, Bird Division, National Museum of Natural History, Washington, D.C. 20560.

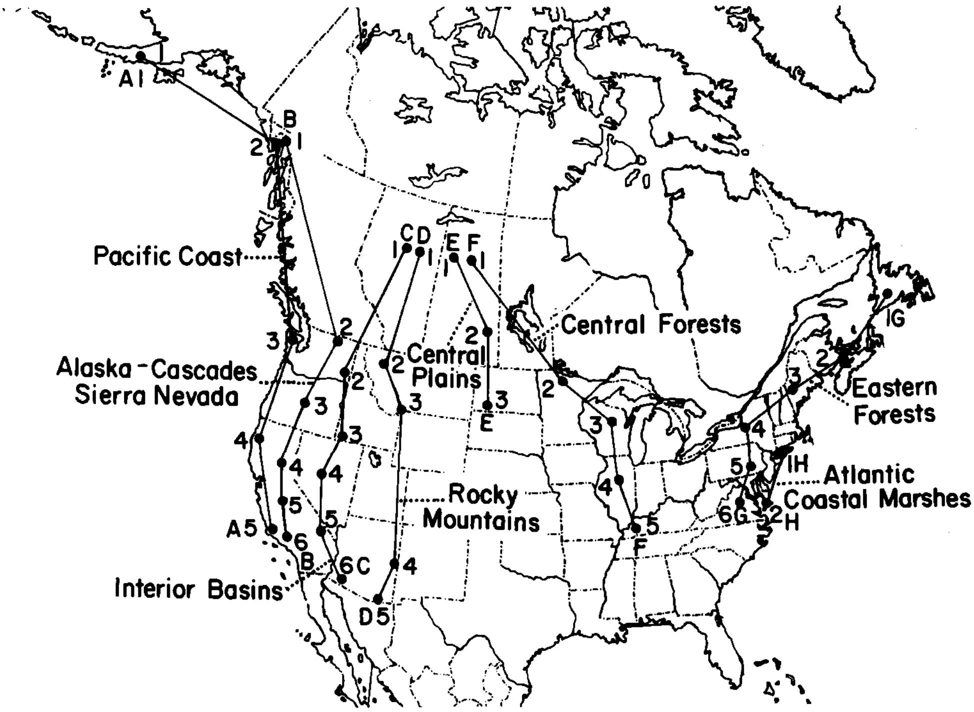

FIG. 3. Map of north-south transects connecting Ecoregion Section/Life Area units. A. Pacific Coast: 1—Alaska Range (Aleutians); 2—Alaska Pacific; 3—Sitka Spruce-Cedar-Hemlock; 4—Redwood Forest; 5—California Chaparral. B. Alaska Pacific-Cascades-Sierra Nevada: 1—Alaska Pacific; 2—Columbia Forest (montane); 3—Silver Fir-Douglas-fir (Cascades); 4—Sierran Forest (montane); 5—California Grassland (valley); 6—California Chaparral. C. Interior Basins: 1—Central Boreal; 2—Palouse Grassland; 3—Sagebrush-Wheatgrass; 4—Lahontan Saltbush-Greasewood; 5—Mojave Desert; 6—Sonoran Desert. D. Rocky Mountains: 1—Central Boreal; 2—Columbia Forest (moist); 3—Northern Rocky Mountains (montane); 4—Upper Gila Mountains Forest; 5—Mexican Shrub Steppe (north). E. Central Plains: 1—Central Boreal; 2—Aspen Parklands (east); 3—Short-grass Prairie east. F. Central Forests: 1—Central Boreal; 2—Spruce-Fir (Minnesota); 3—Northern Hardwoods (New York-Wisconsin); 4—Oak-Hickory-Bluestem Parkland; 5—Oak-Hickory Forest. G. Eastern Forests: 1—Newfoundland Boreal; 2—Northern Hardwood-Spruce (maritime); 3—Northern Hardwood-Spruce (New England); 4—Northern Hardwoods (New York-Wisconsin); 5—Appalachian Oak (deciduous); 6—Southeastern Mixed Forest. H. Atlantic Coastal Marshes: 1—Atlantic Coastal Marsh (north); 2—Atlantic Coastal Marsh (south).

WING MEASUREMENTS

TOTAL WING LENGTH

Sex differences.—Males have longer wings than females in all 49 Ecoregion Section/Life Area samples of more than one specimen of each sex. Male wings are significantly longer in 41 populations (all except 3-1320, 3-1320A, 4-2111, 7-M2413, 9-3111, 6-M3111, 11-3112 and 13-3140).

Differences by Life Area (Fig. 1; Tables 1, 2).—Means of total wing lengths arranged in order of decreasing size for males are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutian)	59	81.43	38	78.27
11	Northern Desert Scrub	96	68.56	40	64.64
14	Piñon-Juniper-Oak	50	68.19	30	64.14
10	Oak-Savannah	2	67.90	0	—
17	Mexican Pine-Oak	18	67.79	3	63.87
9	Grasslands	49	67.72	31	64.18
7	Pacific Rain Forest	107	67.62	71	63.83
6	Montane Woodland-Brush	26	67.53	16	63.85
5	Aspen Parkland	6	67.32	3	64.67
3	Boreal	22	66.30	6	63.85
13	Mesquite-Grassland	14	66.06	6	61.95
12	Southern Desert Scrub	25	65.97	12	62.32
4	Northern Hardwood-Conifer	112	65.96	40	62.92
8	Eastern Deciduous Forest	115	65.45	46	62.36
15	Chaparral-Oak Woodland	31	62.47	12	58.55

The correlation between male and female wing lengths is high ($r = 0.99$, $P < 0.001$).

Significant differences between mean wing lengths of adjacent Life Areas are: Arctic-Alpine > Boreal (♂, ♀); Northern Hardwood-Conifer > Eastern Deciduous Forest (♂); Grasslands > Eastern Deciduous Forest (♂, ♀); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Mexican Pine-Oak > Mesquite-Grassland (♂, ♀); Grasslands > Mesquite Grassland (♂, ♀).

In addition to differences in mean wing lengths of birds from different Life Areas, mean wing lengths of birds from different Ecoregion Sections within Life Areas differ significantly as follows:

Boreal

3-1320B Central Boreal > 3-1320a Newfoundland Boreal (♂)

Northern Hardwood-Conifer

4-2111 Spruce-Fir (N. Minnesota) > 4-2113 N. Hardwoods (New York-Wisconsin) (♀)

Pacific Rain Forest

7-M2416 Alaska Pacific Forest > 7-2410 Willamette-Puget Forest (♂)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀)
7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2415 Cascades Forest (♀)

Eastern Deciduous Forest

8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂)

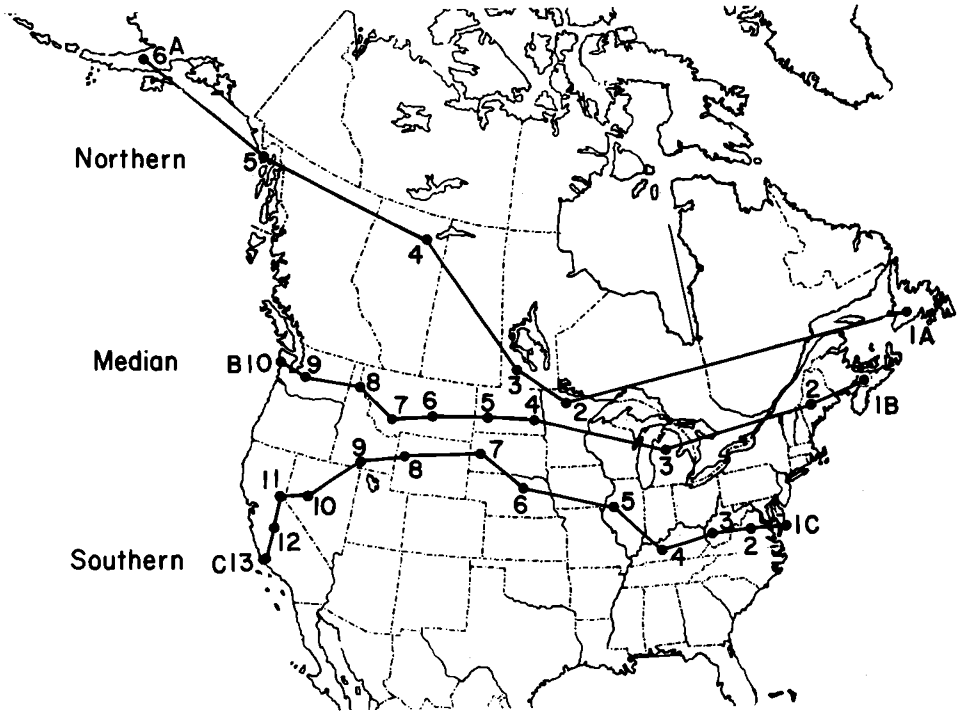

FIG. 4. Map of east-west transects connecting Ecoregion Section/Life Area units. A. Northern: 1—Newfoundland Boreal; 2—Spruce-Fir (Minnesota); 3—Aspen Parklands (east); 4—Central Boreal; 5—Alaska Pacific; 6—Alaska Range (Aleutians). B. Median: 1—Northern Hardwoods-Spruce (Maritime); 2—Northern Hardwoods-Spruce (New England); 3—Northern Hardwoods (New York-Wisconsin); 4—Tall-grass Prairie (west); 5—Short-grass Prairie (east); 6—Short-grass Prairie (west); 7—Northern Rocky Mountains (montane); 8—Columbia Forest (moist); 9—Silver Fir-Douglas-fir (Cascades); 10—Sitka Spruce-Cedar-Hemlock. C. Southern: 1—Atlantic Coastal Marshes (south); 2—Southeastern Mixed Forest; 3—Mixed Mesophytic Forest; 4—Oak-Hickory Forest; 5—Oak-Hickory-Bluestem Parkland; 6—Tall-grass Prairie (west); 7—Short-grass Prairie (east); 8—Northern Rocky Mountains (montane); 9—Sagebrush-Wheatgrass; 10—Lahontan Saltbush-Greasewood; 11—Sierran Forest (montane); 12—California Grassland (valley); 13—California Chaparral.

Northern Desert Scrub

11-3131 N. Desert Scrub (sagebrush) > 11-3132 N. Desert Scrub (Lahontan Greasewood) (♂)

Mexican Pine-Oak

17- Mexican Pine-Oak (S. Mexico) > 17-M2620 California Chaparral (Pine-Oak in Baja California) (♂)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of total wing lengths arranged in order of decreasing size for males are:

		♂ N	Mean	♀ N	Mean
M1310	Alaska Range (Aleutians)	59	81.43	38	78.27
A3140	Wyoming Basin	9	69.43	1	68.50
M3110	Rocky Mountains Forest	47	68.62	19	64.76
3130	Intermountain Sagebrush	108	68.55	56	64.56
17	Mexican Pine-Oak	15	68.25	15	63.87
M2410	Pacific Forest	93	67.97	60	65.08
2510	Prairie Parkland	2	67.90	0	—
3110	Short-grass Prairie	7	67.71	11	64.46
2530	Tall-grass Prairie	13	67.37	6	64.47
2610	California Grassland	3	67.10	4	61.80
3120	Palouse Grassland	21	67.08	9	64.14
2410	Willamette-Puget Forest	16	66.69	10	62.35
2110	Laurentian Forest	47	66.39	20	62.90
1320	Boreal Forest	22	66.30	6	63.85
M2110	Columbia Forest	13	66.23	5	63.46
P3130	Colorado Plateau	0	—	2	63.10
3140	Mexican Shrub Steppe	14	66.09	6	61.95
M2610	Sierran Forest	8	66.05	5	62.90
3220	American Desert	25	65.97	12	62.32
2210	Eastern Deciduous Forest	149	65.73	52	62.33
M3120	Upper Gila Mountains Forest	6	65.42	5	62.62
2320	Southeastern Mixed Forest	84	65.29	44	62.13
M2620	California Chaparral	57	61.37	25	56.39

Male and female wing lengths are highly correlated ($r = 0.97$, $P < 0.001$).

Significant differences between mean wing lengths in adjoining Ecoregion Provinces are: Alaska Range (Aleutian Islands) > Boreal Forest (♂, ♀); Laurentian Forest > Eastern Deciduous Forest (♂); Alaska Range (Aleutian Islands) > Pacific Forest (♂, ♀); Pacific Forest > Willamette Puget Forest (♀); California Grassland > California Chaparral (♂, ♀); Rocky Mountains Forest > Columbia Forest (♂); Mexican Pine-Oak (S) > Mexican Highlands Shrub Steppe (S) (♂, ♀); Intermountain Sagebrush > American Desert (♂, ♀); Tall-grass Prairie > Eastern Deciduous Forest (♂, ♀); Rocky Mountains Forest > Palouse Grassland (♂).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 5, 6).—When average wing lengths of populations in adjacent Ecoregion/Life Area units are compared, significant differences are: 1-M1310 Aleutians > 7-M2416 Alaska Pacific (♂, ♀); 7-M2416 Alaska Pacific > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwoods (♂, ♀); 7-M2413 Pacific Forest (inland) > 9-M2412 Redwoods (♂, ♀); 6-M2610 Sierran Montane > 15-M2620 California Chaparral (♂, ♀); 6-M3112 N. Rocky Mts. Montane > 14-M3111 Oregon Montane (Piñon-Juniper) (♂); 11-3131 N. Desert Scrub (Sagebrush) > 11-3132 N. Desert Scrub (Lahontan Saltbush) (♂); 11-3131 N. Desert Scrub (Sagebrush) > 9-3120 Palouse Grassland (♂); 6-M3112 N. Rocky Mts. Montane >

7-M2112 Columbia Forest (moist) (♂); 3-1320B Central Boreal > 3-1320A Newfoundland Boreal (♂); 4-2114A Northern Hardwoods (Maritime) > 3-1320A Newfoundland Boreal (♂); 8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂); 10-2511 Oak Savannah > 8-2215 Oak-Hickory Forest (♂); 9-2610 California Grassland > 15-M2620 California Chaparral (♂, ♀).

In some cases, Life Belts (Life Areas) within the same Ecoregion Section differ significantly: 15-M2620 California Chaparral (chaparral) > 9-M2620 California Chaparral (grass) (♂); 17-M2620 California Chaparral (Pine-Oak) > 15-M2620 California Chaparral (chaparral) (♂); 9-M3111 Oregon Montane (grass) > 14-M3111 Oregon Montane (Piñon) (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B California Chaparral (San Francisco Bay Marsh South) (♂, ♀); 14-3132 Lahontan Saltbush (Piñon) > 11-3132 Lahontan Saltbush (N. Desert) (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620A California Chaparral (San Francisco Bay Marsh North) (♀).

Relative lengths of wings of males in different Ecoregion Sections are shown in Figure 5.

North-south transects. A north to south transect along the Pacific coast (Figs. 3, 6, transect A) shows a cline of significant progressive decreases in male and female wing lengths in succeeding populations from the Aleutian Islands tundra to the California redwoods, then a nonsignificant increase to the California Chaparral-Oak. The general trend along the coast is a marked north-south cline of decreasing wing length.

A more interior transect from coastal Alaska southeastward along the Cascades and Sierras to the California Chaparral (Figs. 3, 6, transect B) shows a significant decrease in male wing length to the Columbia Montane of northern Washington and in female wing length to the Cascades, then no change in either sex from there to the Sierra Forest, and finally, a significant decrease in wing lengths of both sexes passing from the Sierra Forest to the California Chaparral. The general trend is a less precipitous north to south cline of decreasing wing length than in the coastal transect.

A transect from the Central Boreal south through the interior basins to the Sonoran Desert of southern Arizona (Figs. 3, 6, transect C) shows a significant increase in male but not female wing lengths between the Palouse Grassland of eastern Washington and the Sagebrush-Wheatgrass of the Northern Great Basin of southern Oregon and Idaho, a decrease in wing length significant in males and insignificant in females from there to the Lahontan Saltbush-Greasewood Section in the central western Great Basin, then little change from there to the Sonoran Desert of southern Arizona. No continuous cline is evident along the interior basins transect. Rather increases and decreases between ecological units fluctuate. Male wing length is maximal in the Sagebrush-Wheatgrass, and female wing length greatest in the Central Boreal.

A transect from the Central Boreal down the Rocky Mountains (Figs. 3, 6, transect D) shows a nonsignificant decrease in wing lengths of both sexes as far as the moist Columbia Forest of northern Idaho and northwestern Montana, then a significant increase in male wing length to the northern Rocky Mountains Forest of western Wyoming and Montana, followed by a significant decrease in wing lengths of both sexes from there to the Upper Gila Mountains Forest of middle

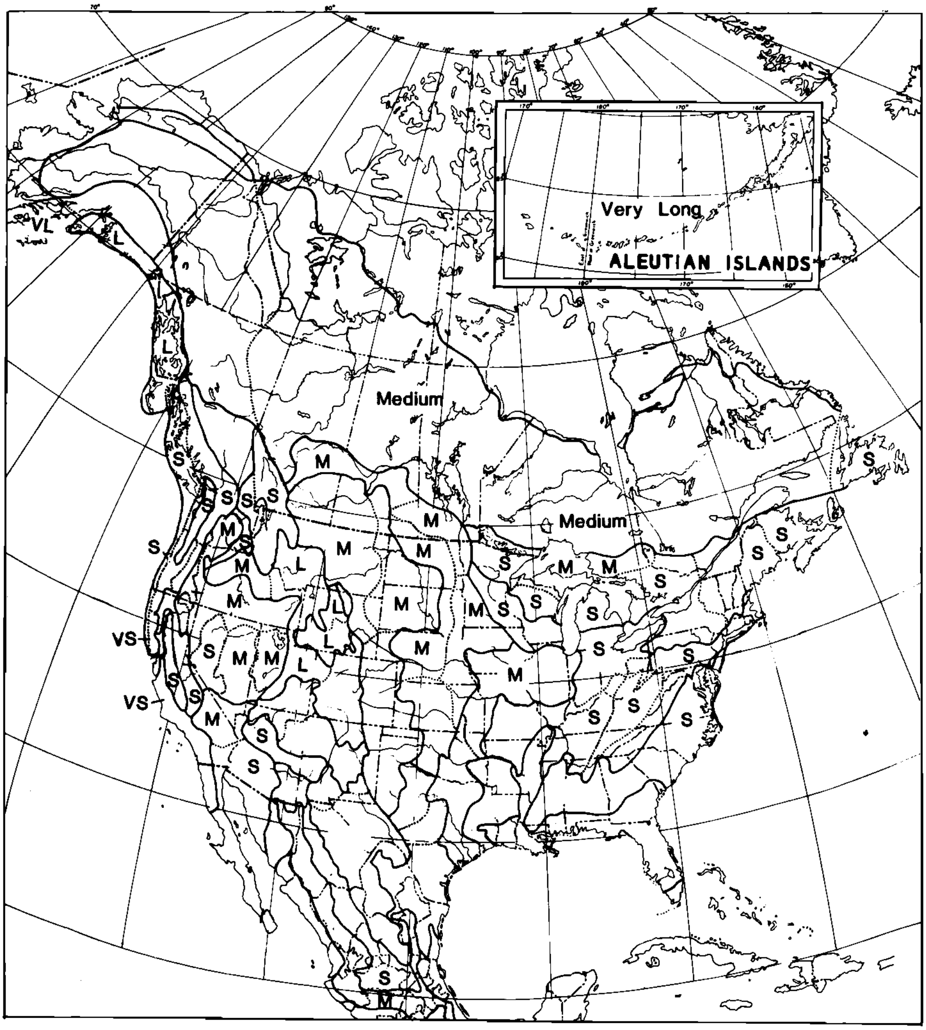

FIG. 5. Relative wing lengths of males in different Ecoregion Sections. L = Longer; S = shorter; M = middle one-third of means; VL = very long; VS = very short.

Arizona and New Mexico. Apparently wing length along the Rocky Mountains transect does not show a north-south cline but rather increases and decreases in relation to local ecological factors. Maximum wing lengths for both males and females are found in the northern Rockies, minimum male wing length in the Upper Gila Mountains Forest, and minimum female wing length in the Mexican Shrub Steppe of Arizona.

Along a transect from the Central Boreal Section southward in the Great Plains grasslands (Figs. 3, 6, transect E), wing length initially decreases very slightly to the Aspen Parkland Belt, then very slightly increases from there to the Short-grass Prairie of western North Dakota and eastern Montana. Maximum male wing

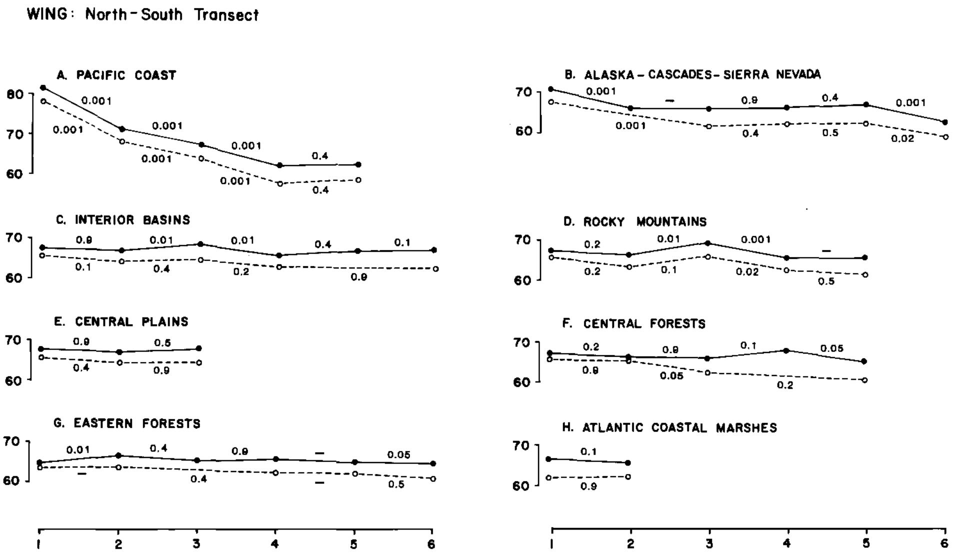

FIG. 6. North-south transects of mean wing lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference. Solid line male, dashed line female.

length is found in birds of the Short-grass Prairie, and for females in the Central Boreal. Minimum wing length is found in males in the Aspen Parkland and in females of the Short-grass Prairie. Thus, no trend is shown in this Great Plains transect.

On the transect from the Central Boreal Section southward through the Central Forests (Figs. 3, 6, transect F), wing length decreases significantly in females, but not males, from the Spruce-Fir of northern Minnesota to the Northern Hardwood of Wisconsin, and decreases significantly in males from the Prairie Parkland of Illinois to the Oak-Hickory Forest of western Kentucky. Maximum male wing lengths are found in birds of the Prairie Parkland and maximum female wing lengths in birds of the Central Boreal. Minimum wing lengths for both sexes occur in birds of the Oak-Hickory Forest.

Along a transect from the Newfoundland Boreal southward through eastern forest areas (Figs. 3, 6, transect G), wing length increases significantly in males, but not females, to the Maritime Northern Hardwoods-Spruce, thence little change in either sex southward to the Appalachian Oak Section (deciduous forest belt) of Pennsylvania and southern New England, then a significant decrease in males, but not females, from the Appalachian Oak into the Southeastern Mixed Forest of eastern Maryland and eastern Virginia. Maximum wing lengths of both sexes are in the Maritime Northern Hardwoods-Spruce and minima of both sexes, in the Southeastern Mixed Forest. After an initial increase from Newfoundland, the trend in the eastern forest transect is a north-south decrease in wing length.

Birds along a transect in the Atlantic Coastal Marshes (Figs. 3, 6, transect H) show little change in wing length from the marshes of New York and New Jersey to those of Maryland and Virginia.

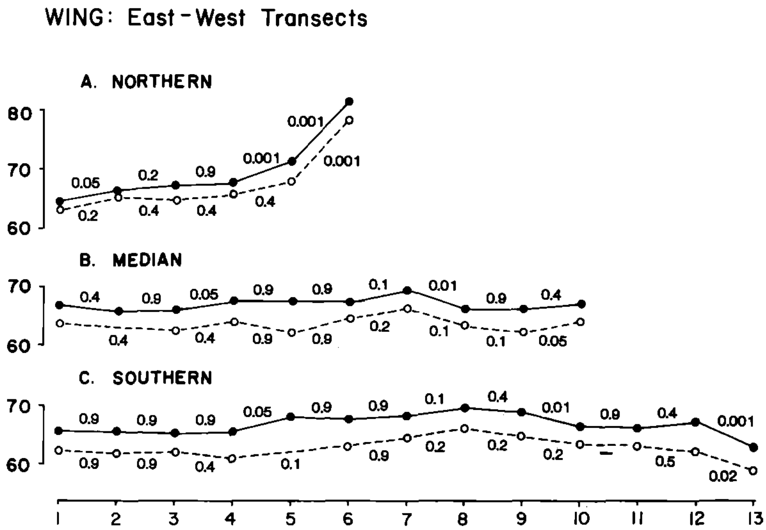

FIG. 7. East-west transects of mean wing lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference. Solid line male, dashed line female.

Although in all eight north-south transects the total decreases (both significant and nonsignificant) in wing length outnumber the increases, the different transects differ considerably in this respect. Whereas decreases considerably outnumber increases in the Pacific Coast, Alaska-Cascades-Sierra Nevada, and Central Forest transects, the numbers of increases and decreases are more even in the Interior Basins, Rocky Mountains, Central Plains and Eastern Forest transects.

Contrary to the usual trends in progressing from north to south, significant increases in wing length occur between the more northern Palouse Grassland and more southern Northern Desert Scrub (♂), between more northern Columbia Forest (moist) and more southern Northern Rockies (Montane) (♂, ♀), and between the more northern Newfoundland Boreal and more southern Northern Hardwood-Spruce (Maritime) (♂). In these cases it appears that some factor, such as higher elevation producing a colder climate, or more open habitat resulting from a dryer climate, may offset the effect of generally increasing temperature resulting from the southward progression.

East-west transects. In the northernmost transect (Figs. 4, 7, transect A) average wing length increases significantly in males and nonsignificantly in females from Newfoundland Boreal to the Spruce-Fir (near Boreal) of northern Minnesota and southwestern Ontario; little change occurs from there to the Central Boreal of Northern Alberta, but then a significant increase occurs in males but not females from there to coastal Alaska, then a significant increase in both sexes to the Aleutian Tundra. The general trend in this most northern transect is a consistent increase in average wing length from east to west.

In a median east to west transect (Figs. 4, 7, transect B) no significant change occurs from the Maritime Northern Hardwoods-Spruce to the Northern Hardwood of Wisconsin, then a significant increase in wing length is found in males, but not females, from there to the Tall-grass Prairie of eastern North Dakota, and the montane Woodlands of the northern Rockies, then a significant decrease in males and nonsignificant decrease in females from there to the moist Columbia Forest, then little change to the Cascades, then a significant increase in females but not males from there to the wet Sitka Spruce-Cedar-Hemlock Forest of the Pacific Coast. The general trend of this median transect is an increase from the Northern Hardwood-Conifer Forests to the Grasslands and continuing to the northern Rockies, then a decrease from there to the Cascades, followed by an increase to the Pacific coastal forests. Thus, the longest wings are in birds of the Pacific coastal, Rocky Mountains, and Great Plains Grassland units, with greatest values for both sexes in the northern Rockies Montane Woodland. Minimum wing length is found in males of the New England Northern Hardwoods-Spruce and in females of the Cascades.

In the southernmost east to west transect (Figs. 4, 7, transect C) wing length does not change significantly between the Atlantic coastal marshes of Maryland and Virginia and the Oak-Hickory Forest of western Kentucky, then increases significantly in males from there to the Oak-Savannah of Illinois, then shows a series of nonsignificant decreases and increases from there to the middle Rocky Mountains, then little if any change from there to the Sagebrush-Wheatgrass of the northern Great Basin, then a significant decrease in males and nonsignificant decrease in females from there to the Lahontan Saltbush-Greasewood of western Nevada, then no significant change from there to the California Valley Grassland, but a significant decrease in both sexes from there to the western California Chaparral. The general trends in this transect are a pronounced increase in wing length from the Eastern Deciduous Forests and coastal marshes to the interior grasslands, then a slight increase in females but not males from there to the Northern Rocky Mountains. A marked decrease in male wing length occurs within the Northern Desert Scrub of the Great Basin from the southern Idaho Sagebrush-Wheatgrass to the western Nevada Lahontan Saltbush-Greasewood, followed by a slight increase to the California Central Valley Grassland, then a pronounced decrease to the Chaparral of coastal California. Maxima for wing lengths of both sexes are in the Middle Rockies Montane Woodland; minima for both sexes are in the California Chaparral.

In general the east-west transects indicate an increase in wing length from east to west in the boreal forest, relatively long wings in the grasslands northern Rocky Mountains and northern desert scrub, and relatively short wings in eastern deciduous forests and California Chaparral.

Discussion.—In all populations wings of males average longer than those of females. There is good agreement between sexes in wing length in Life Areas. There is some difference between males and females in order of wing length between Ecoregion Provinces, particularly: Pacific Forest, California Grassland, Willamette-Puget Forest, and Mexican Shrub Steppe.

Taking all data together from comparison of mean wing lengths classified by Life Area, Ecoregions, and combinations of the two, there is a general trend of decreasing wing length from north to south which is modified locally by elevation and density of vegetation. Wing lengths are greater at higher elevations in montane forests and more open plant associations such as tundra, grasslands, savannas, and deserts at the same latitudes. Thus, wings are longest, by far, in the Aleutian

Tundra, but are also long in northern grasslands, northern montane forests, and northern deserts. They are somewhat shorter in the northern lowland forest, still shorter in the southern forests and southern deserts, and shortest in the California Chaparral, particularly in the San Francisco Bay Salt Marsh seral stage of the Chaparral-Oak Woodland Life Area.

Wing-tip Length

Sex differences.—Wing-tips of males average longer than those of females in 39 of 49 Ecoregion Section/Life Area samples, eight significantly so, including 8-2211, 4-2214, 7-M2411, 7-M2412, 15-M2620, 6-M3112, 9-3120, 11-3131. Females have longer wing-tips than males in 10 populations, but in none were differences significant statistically.

Differences by Life Area (Fig. 1, Tables 1, 2).—Means of wing-tip lengths arranged in order of decreasing size for males are:

		♂ N	Mean	♀ N	Mean
5	Aspen Parkland	6	10.52	3	11.03
3	Boreal	22	10.44	6	9.92
1	Arctic-Alpine (Aleutian)	58	9.92	37	10.10
9	Grasslands	50	9.82	31	9.06
7	Pacific Rain Forest	104	9.62	71	8.51
6	Montane Woodland-Brush	26	9.51	15	8.66
10	Oak-Savannah	2	9.50	0	—
4	Northern Hardwood-Conifer	111	9.26	40	9.04
8	Eastern Deciduous Forest	114	9.10	46	8.91
11	Northern Desert Scrub	97	9.08	41	8.43
12	Southern Desert Scrub	26	8.82	12	8.10
14	Piñon-Juniper	49	8.45	30	7.79
17	Mexican Pine-Oak	18	8.32	3	8.43
15	Chaparral-Oak Woodland	30	7.35	12	6.42
13	Mesquite-Grassland	14	7.20	6	6.42

Male and female mean measurements are highly correlated ($r = 0.97$, $P < 0.001$).

Significant differences in mean wing-tip lengths in adjoining Life Areas are: Boreal Forest > Northern Hardwood-Conifer (♂); Aspen Parkland > Grasslands (♀); Grasslands > Chaparral-Oak Woodland (♂, ♀); Grasslands > Mesquite-Grassland (♂, ♀); Grassland > Eastern Deciduous Forest (♂); Grassland > Northern Desert Scrub (♂, ♀); Montane-Woodland-Brush > Piñon-Juniper (♂, ♀); Southern Desert Scrub > Mesquite-Grassland (♂, ♀); Mexican Pine-Oak > Mesquite-Grassland (♂, ♀).

Significant differences between mean wing-tip lengths of birds in different Ecoregion Sections within Life Areas are:

Boreal

3-1320B Central Boreal > 3-1320A Newfoundland Boreal (♂)
3-2114 New England Mountains (boreal) > 3-1320A Newfoundland Boreal (♂)

Pacific Rain Forest

7-M2411 Sitka Spruce-Cedar-Hemlock > 7-2410 Willamette-Puget Forest (♂)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2413 Pacific Forest (inland) (♂)
7-M2416 Alaska Pacific Forest > 7-2410 Willamette-Puget Forest (♂)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀)
7-M2415 Cascades Forest > 7-M2412 Redwood Forest (♀)

Eastern Deciduous Forest

8-2212 Beech-Maple Forest > 8-2211 Mixed Mesophytic Forest (♂, ♀)
8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂)
8-2211 Mixed Mesophytic Forest > 8-2320 Southeastern Mixed Forest (♀)

Grasslands

9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂)
9-3111 Short-grass Prairie (west) > 9-2610 California Grassland (valley) (♀)

Northern Desert Scrub

11-3131 Sagebrush-Wheatgrass > 11-3132 Lahontan Saltbush-Greasewood (♂)

Piñon-Juniper-Oak

14-3131 Northern Desert Scrub (Piñon) > 14-M3120 Upper Gila Mountains (Piñon) (♂)
14-3132 Lahontan Saltbush-Greasewood (Piñon) > 14-M3120 Upper Gila Mountains (Piñon) (♂)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of wing-tips arranged in order of decreasing size for males are:

		♂ N	Mean	♀ N	Mean
1320	Boreal	22	10.44	6	9.92
2530	Tall-grass Prairie	13	10.35	6	10.02
3110	Short-grass Prairie	8	10.28	11	9.87
M1310	Alaska Range (Aleutians)	58	9.92	37	10.10
2110	Laurentian Forest	47	9.89	20	9.85
2610	California Grassland	3	9.80	4	8.18
3120	Palouse Grassland	21	9.51	9	8.36
2510	Prairie Parkland	2	9.50	0	—
M3110	Rocky Mountains Forest	47	9.46	19	8.78
M2610	Sierran Forest	8	9.22	5	8.12
2210	Eastern Deciduous Forest	151	9.22	51	8.57
A3140	Wyoming Basin	9	9.21	1	10.10
M2410	Pacific Forest	93	9.09	60	8.53
3130	Intermountain Sagebrush	107	8.99	57	8.35
2320	Southeastern Mixed Forest	85	8.94	45	8.78
M2110	Columbia Forest	11	8.93	5	8.26

3220	American Desert	25	8.84	12	8.10
17	Mexican Pine-Oak	15	8.75	3	8.43
P3130	Colorado Plateau	0	—	2	7.50
2410	Willamette-Puget Forest	16	8.23	10	7.96
3140	Mexican Shrub Steppe	14	7.20	6	6.42
M2620	California Chaparral	56	7.07	25	6.30
M3120	Upper Gila Mountains Forest	6	7.02	5	6.98

Male and female mean wing-tip lengths are highly correlated ($r = 0.89$, $P < 0.001$).

Significant differences between mean wing-tip lengths in adjoining Ecoregion Provinces are: Laurentian Forest > Eastern Deciduous Forest (♂, ♀), Alaska Range (Aleutians) > Pacific Forest (♂, ♀), Pacific Forest > Willamette-Puget Forest (♂), California Grassland > California Chaparral (♀), Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂, ♀), Rocky Mountains Forest > Intermountain Sagebrush (♂), Tall-grass Prairie > Eastern Deciduous Forest (♂, ♀), Short-grass Prairie > Wyoming Basin (♂).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 5, 6).—When I compared average wing-tip lengths of birds in adjoining Ecoregion/Life Area units, some differences were significant: 3-1320B Central Boreal > 3-1320A Newfoundland Boreal (♂); 4-2214A N. Hardwoods (Maritime) > 3-1320A Newfoundland Boreal (♂, ♀); 8-2212 Beech-Maple Forest > 8-2211 Mixed Mesophytic Forest (♂, ♀); 8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂); 8A-2214A Atlantic Salt Marsh (north) > 8A-2320A Atlantic Salt Marsh (south) (♂); 7-M2411 Sitka Spruce Pacific Forest > 7-M2413 Pacific Forest (inland) (♂); 6-M3112 N. Rockies (montane) > 11-M3112 N. Rockies (sagebrush) (♂); 9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (chaparral) (♂, ♀); 11-3131 Great Basin Sagebrush > 11-3132 Lahontan Saltbush-Greasewood (♂); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂); 3-1320B Central Boreal > 4-2111 Spruce-Fir (Minnesota) (♂); 6-M3112 N. Rockies (montane) > 11-3131 Great Basin Sagebrush (♂); 1-M1310 Aleutian Islands > 7-M2416 Alaska Pacific (♀); 7-M2411 Sitka Spruce Pacific Forest > 7-M2412 Redwoods (♂; ♀); 4-2114A N. Hardwoods-Spruce (Maritime) > 4-2114 N. Hardwood-Spruce (N. England) (♀); 6-M2610 Sierras (montane) > 15-M2620 California Chaparral (♂, ♀); 8-2320 Southeastern Mixed Forest > 8-2211 Mixed Mesophytic Forest (♀); 17- Mexican Pine-Oak (S) > 13 Mexican Shrub Steppe (S) (♂, ♀).

In the above comparisons in only one case do birds differ significantly in Life Belts within an Ecoregion/Life Area unit: 6-M3112 Northern Rocky Mountains Montane Forest male wing-tip averages longer than that of males of 11-M3112 Northern Rockies Sagebrush.

Relative lengths of wing-tips of males in different Ecoregion Sections are shown in Figure 8.

North-south transects. In the Pacific coastal north to south transect (Figs. 3, 9, transect A), wing-tip length shows a pronounced clinal decrease in succeeding populations, with maxima in both sexes in the Aleutian Tundra, and minima in

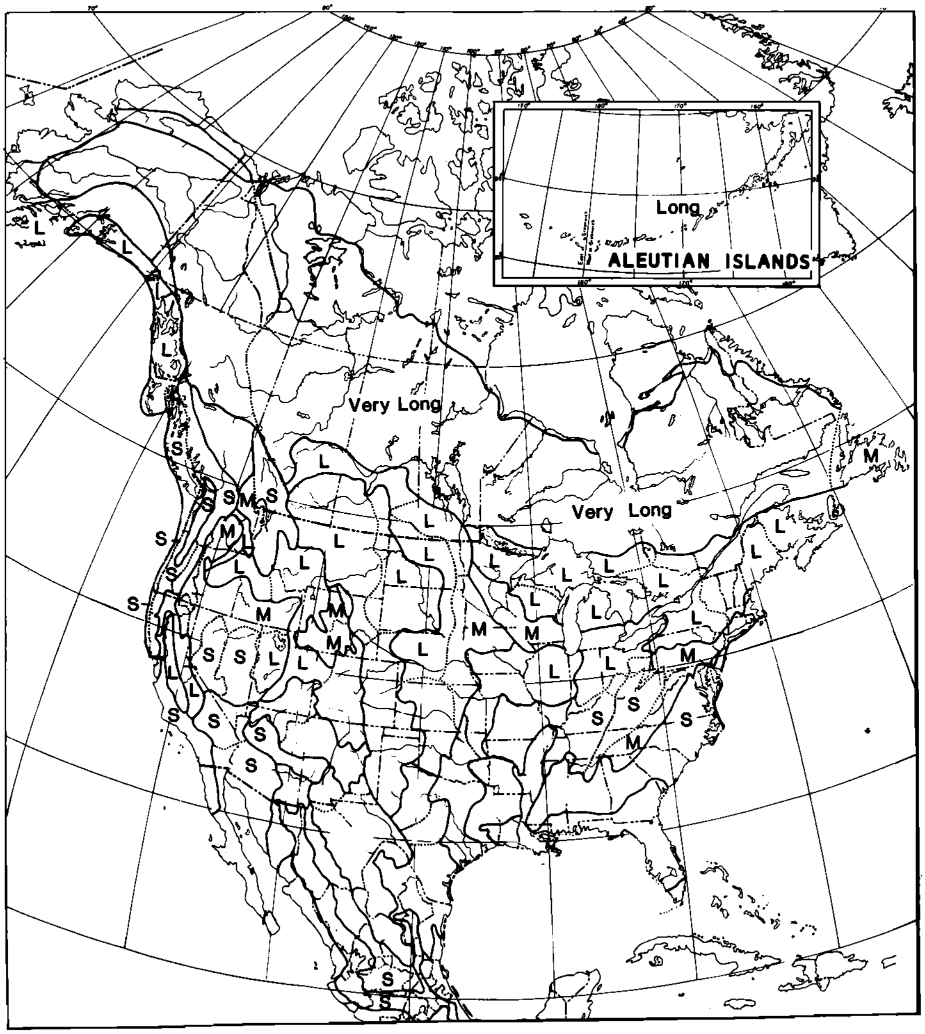

FIG. 8. Relative wing-tip lengths of males in different Ecoregion Sections. L = longer; S = shorter; M = middle one-third of means.

the California Chaparral (♂) and Redwood Forest (♀). The decreases are significant for each step from Alaska Pacific to the Redwood Forest for males, and from the Aleutian Tundra to the Redwood Forest for females.

A transect southward along the Alaska-Cascades-Sierra route (Figs. 3, 9, transect B) indicates a gradual decrease from a maximum wing-tip length in Alaska Pacific in both sexes to the California Grassland, then significant decreases to a minimum in both sexes in the California Chaparral.

Along a transect from the Central Boreal southward through the interior basins to the Sonoran Desert (Figs. 3, 9, transect C), the progression is irregular with a decrease in both sexes from maximal wing-tip lengths in the Central Boreal to minima in the Lahontan Saltbush-Greasewood. Significant decreases between

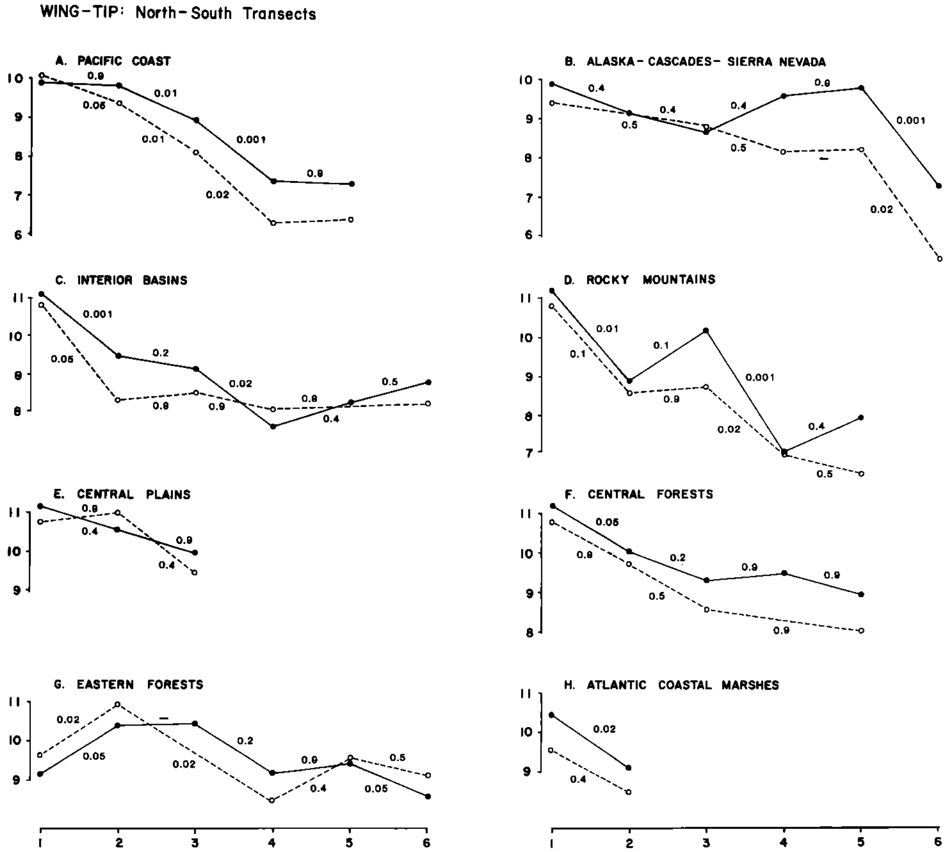

FIG. 9. North-south transects of mean wing-tip lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

sections occur in both sexes from the Central Boreal to the Palouse Grassland and in males from the Sagebrush-Wheatgrass to the Lahontan Saltbush-Greasewood, followed by an insignificant increase in both sexes from there to the Sonoran Desert.

A transect from the Central Boreal south along the Rocky Mountain system (Figs. 3, 9, transect D) shows a trend of decreasing wing-tip length in both sexes from maxima in the Central Boreal to minimum for males in the Upper Gila Mountains and for females in the Mexican Shrub Steppe. The initial significant decrease in males from the Central Boreal to the moist Columbia Forest is reversed by a nonsignificant increase from there to the northern Rockies. This is followed by a significant decrease in both sexes to the Upper Gila Mountains.

A transect through the Central Plains (Figs. 3, 9, transect E) shows no significant trends, although wing-tip length decreases slightly from north to south. The maximum mean for males is in the Central Boreal and for females in the Aspen Parkland. Minima for both sexes are in the Short-grass Prairie.

A transect southward through the Central Forests (Figs. 3, 9, transect F) shows a trend of decreasing wing-tip length in both sexes. Maxima for both sexes are in the Central Boreal, and minima in the Oak-Hickory. The decrease in males is significant from the Central Boreal to the Spruce-Fir of Minnesota, then occurs gradually from there to the Oak-Hickory Forest.

A transect southward through the Eastern Forests (Figs. 3, 9, transect G) shows irregular and alternating increases and decreases in both sexes with significant increases in both sexes from the Newfoundland Boreal to the Laurentian Forest (Maritime), then a significant decrease in females to Laurentian Forest (New York-Wisconsin), then little change from there to the Applachian Oak (deciduous). A final significant decrease occurs in males from the Appalachian Oak (deciduous) to the Southeastern Mixed Forest. Maximum male wing-tip length is found in birds of the New England Laurentian Forest, and maximum female wing-tip length in Maritime Laurentian Forest birds. Minimum male wing-tip length is in the Southeastern Mixed Forest, and minimum female wing-tip length in the New York Laurentian Forest. Overall wing-tip length decreases from the Maritime Laurentian southward to the Southeastern Mixed Forest, and northward to Newfoundland.

The transect in the Atlantic Coastal salt marshes (Figs. 3, 9, transect H) shows a significant decrease in male and nonsignificant decrease in female wing-tip lengths from the northern to the southern marshes.

The conclusion to be drawn from the north-south transects is that mean wing-tip length declines overall from north to south with pronounced decreases in Pacific Coast, Alaska-Cascades-Sierra Nevada, Central Forests, and Atlantic Coastal marshes transects. Other transects, although indicating an overall decrease, are interrupted by local and sometimes significant increases between sections.

East-west transects. In the northernmost transect (Figs. 4, 10, transect A), wing-tip length gradually increases in both sexes from the Newfoundland Boreal to the Aspen Parklands. From the Central Boreal to Alaska Pacific male wing-tip length decreases significantly, and from there to the Aleutian Islands female wing-tip length increases significantly. The maximum male mean is in the Central Boreal, and maximum female in the Aspen Parkland. Minimum male wing-tip is in the Newfoundland Boreal, and female in the Alaska Pacific.

In the median transect (Figs. 4, 10, transect B), despite an initial significant decrease in females, no sustained trend is apparent in either sex from the Maritime Laurentian Forest as far as the Short-grass Prairie. A decreasing trend appears in both sexes from there to the Sitka Spruce-Cedar-Hemlock on the Pacific Coast. The longest male wing-tips occur in both New England Laurentian and Short-grass Prairie, and longest female wing-tips in Maritime Laurentian. The shortest mean wing-tips are in the Cascades (♂) and Sitka Spruce-Cedar-Hemlock (♀).

Along the southern transect (Figs. 4, 10, transect C), progression is irregular without obvious trends from the Atlantic Coastal marshes to a maximum in the Short-grass Prairie (♀) and Tall-grass Prairie (♂), then a sharp decline in males to the Lahontan Saltbush with another pronounced peak in males, but not females in the California Grasslands. From there, wing-tip length decreases significantly in both sexes to a minimum in the California Chaparral.

The overall trend in all three east-west transects is toward slightly longer wing-

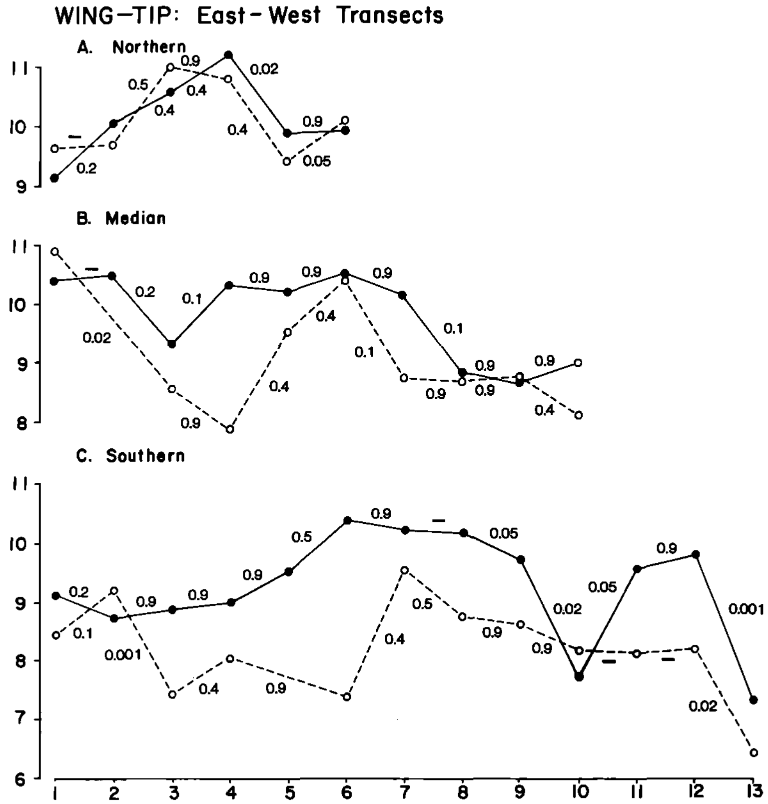

FIG. 10. East-west transects of mean wing-tip lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

tips in the Central Boreal Forest and Great Plains Grasslands and Parklands, then much smaller size on the Pacific Coast, particularly in California Chaparral.

Discussion.—There are trends of decreasing wing-tip length from north to south and from the high short-grass prairies and Rocky Mountains toward both coasts, but particularly the Pacific. As in the case of total wing length, it appears that wing-tips are longer in more northern, more open, and higher regions and shorter in more southern, lower, and more heavily vegetated regions, although northern deserts also seem to be in the shorter groups unlike total wing length. Also like total wing length, within each vegetation life-form area the more northern populations have longer wing-tips. Despite these similarities, wing-tip lengths are poorly correlated with total wing lengths among males in the same Ecoregion Province ($r = 0.41$, $P < 0.1$).

RATIO OF WING-TIP TO WING LENGTH

Sex differences.—In 29 (59%) of the 49 samples, males had higher ratios of wing-tip length to total wing length than did females, and in 20 samples (41%) females had higher ratios. Three of the male ratios were significantly higher, 8-2211, 9-2532, and 9-3120, as were three of the female ratios (4-2114A, 8-2320, and 11-3182). Thus, the proportions of wing-tip to wing length are quite similar in males and females unlike either total wing or wing-tip length which are considerably larger in males than in females.

Differences by Life Areas (Fig. 1, Table 7).—Means of wing-tip/wing length ratios arranged in order of decreasing size are:

		♂ N	Mean	♀ N	Mean
3	Boreal	21	.157	6	.155
5	Aspen Parkland	6	.156	3	.171
9	Grasslands	49	.145	31	.141
6	Montane Woodland-Brush	26	.141	16	.137
4	Northern Hardwood-Conifer	113	.140	40	.144
10	Oak-Savannah	2	.140	0	—
8	Eastern Deciduous Forest	117	.139	45	.143
12	Southern Desert Scrub	25	.134	12	.130
11	Northern Desert Scrub	97	.132	40	.131
7	Pacific Rain Forest	112	.132	71	.132
14	Piñon-Juniper-Oak	50	.127	30	.124
17	Mexican Pine-Oak	18	.124	3	.132
1	Arctic-Alpine (Aleutians)	57	.122	38	.128
15	Chaparral-Oak Woodland	30	.118	12	.109
13	Mesquite-Grassland	14	.109	6	.104

Male and female mean ratios are highly correlated ($r = 0.94$, $P < 0.001$).

Significant differences between adjacent Life Areas in wing-tip to wing length ratios are: Boreal Forest > Arctic-Alpine (♂, ♀); Boreal Forest > Northern Hardwood-Conifer (♂); Grasslands > Northern Desert Scrub (♂, ♀); Montane Woodland-Brush > Pacific Rain Forest (♂); Montane Woodland-Brush > Piñon-Juniper-Oak (♂, ♀); Mexican Pine-Oak > Mesquite-Grassland (♂, ♀); Grasslands > Chaparral-Oak (♂, ♀); Grasslands > Mesquite-Grassland (♂, ♀); Aspen Parkland > Grasslands (♀).

Significant differences in mean ratios of wing-tip to wing length of birds in different Life Areas within Ecoregion Sections are:

Boreal

3-1320B Central Boreal > 4-1320A Newfoundland Boreal (♂)

Northern Hardwood-Conifer

4-2111 Spruce-Fir (Minnesota) > 4-2214 Appalachian-Oak (N. Hardwood-Conifer) (♂)

4-2114A N. Hardwood-Spruce (maritime) > 4-2214 Appalachian-Oak (N. Hardwood-Conifer) (♀)

4-2114A N. Hardwood-Spruce (maritime) > 4-2114 N. Hardwood-Spruce (New England) (♀)

Pacific Rain Forest

7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2413 Pacific Forest (inland) (♂)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♀)

Eastern Deciduous Forest

8-2212 Beech-Maple Forest > 8-2211 Mixed Mesophytic Forest (♂)
8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂)
8-2211 Mixed Mesophytic Forest > 8-2320 Southeastern Mixed Forest (♀)

Northern Desert Scrub

11-3131 Sagebrush-Wheatgrass > 11-3132 Lahontan Saltbush-Greasewood (♂)

Piñon-Juniper

14-3131 Sagebrush-Wheatgrass (Piñon) > 14-3132 Gila Mountains (Piñon) (♂)

Mexican Pine-Oak

17- Mexican Pine-Oak (south) > 17-M2620 California Chaparral (Pine-Oak; north) (♂)

Differences by Ecoregion Province (Fig. 2; Table 8).—Means of wing-tip to wing length ratios arranged in order of decreasing proportions of males are:

		♂ N	Mean	♀ N	Mean
1320	Boreal Forest	21	.157	6	.155
2530	Tall-grass Prairie	13	.154	6	.155
3110	Short-grass Prairie	7	.153	11	.153
2110	Laurentian Forest	43	.148	20	.156
2610	California Grassland	3	.146	4	.132
3120	Palouse Grassland	21	.142	9	.130
2210	Eastern Deciduous Forest	147	.140	51	.137
2510	Prairie Parkland	2	.140	0	—
M2610	Sierran Forest	8	.139	5	.130
M3110	Rocky Mountain Forest	46	.138	19	.135
2320	Southeastern Mixed Forest	83	.136	44	.140
M2110	Columbia Forest	11	.134	5	.140
M2410	Pacific Forest	93	.134	60	.132
3220	American Desert	25	.134	12	.130
A3140	Wyoming Basin	9	.132	1	.147
3130	Intermountain Sagebrush	106	.131	56	.130
17	Mexican Pine-Oak	15	.128	3	.132
2410	Willamette-Puget Forest	16	.124	10	.128
P3130	Colorado Plateau	0	—	2	.129
M1310	Alaska Range (Aleutians)	57	.122	38	.128
M2620	California Chaparral	56	.115	25	.112
3140	Mexican Shrub Steppe	13	.109	6	.104
M3120	Upper Gila Mountains Forest	6	.107	5	.112

Male and female ratios are highly correlated ($r = 0.88$, $P < 0.001$).

Adjacent Ecoregion Provinces that differ significantly in wing-tip to wing length ratios are: Yukon Forest (Boreal) > Alaska Range (Aleutian Islands) (♂, ♀); Laurentian Forest > Eastern Deciduous Forest (♂, ♀); Pacific Forest > Alaska Range (Aleutians) (♂); Pacific Forest > Willamette-Puget Forest (♂); California Grassland > California Chaparral (♂); Boreal Forest > Columbia Forest (♂, ♀); Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂, ♀); Rocky Mountains Forest > Intermountain Sagebrush (♂); Short-grass Prairie > Wyoming Basin (Sagebrush) (♂).

Differences by Ecoregion Section/Life Area (Fig. 2, Table 9).—Adjoining Ecoregion Section/Life Area units that differ significantly in ratios are: 17-Mexican Pine-Oak (S) > 13-3140 (S) Mexican Highlands Shrub Steppe (S) (♂); 7-M2416 Alaska Pacific Forest > 1-M1310 Alaska Range (Aleutian Islands) (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2413 Cedar-Hemlock-Douglas-fir (inland) (♂); 3-1320B Central Boreal > 3-1320A Newfoundland Boreal (♂); 8-2212 Beech-Maple > 8-2211 Mixed Mesophytic Forest (♂, ♀); 8A-2214A Atlantic Coastal Marsh (north) > 8A-2320A Atlantic Coastal Marsh (south) (♂); 6-M2610 Sierran Montane > 15-M2620 California Chaparral (chaparral) (♂); 6-M2610 Sierran Montane > 9-M2620 California Chaparral (grassland) (♂); 9-3111 Short-grass Prairie (W) > 11-M3112 Douglas-fir Forest (Northern Desert Scrub belt) (♂); 11-3131 Sagebrush-Wheatgrass (Northern Desert Scrub) > 11-3132 Lahontan Saltbush-Greasewood (Northern Desert Scrub) (♂); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (♂, ♀); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂); 8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♂).

Life Belts (Life Areas) within the same Ecoregion Section that differed significantly are: 4-2214 Appalachian Oak (N. Hardwood-Conifer) > 8A-2214A Appalachian Oak (Atlantic Coastal Marsh) (north) (♂); 8A-2320A Atlantic Coastal Marsh (south) > 8-2320 Southeastern Mixed Forest (♂); 9-M2620 California Chaparral (grassland) > 9-M2620B San Francisco Bay Marsh (south) (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B San Francisco Bay Marsh (south) (♂, ♀); 6-M3112 N. Rockies (Montane Forest) > 11-M3112 N. Rockies (Sagebrush) (♂).

Relative ratios of wing-tip length to wing length of males in different Ecoregion Sections are shown in Figure 11.

North-south transects. In the Pacific Coast transect (Figs. 3, 12, transect A), after an initial significant increase in ratio of wing-tip to wing length in both sexes from the Aleutian Islands to Alaska Pacific, the ratio decreases progressively to the California Chaparral. This decrease is by significant steps from Alaska Pacific to the Redwood Forest in males and to Sitka Spruce-Cedar-Hemlock in females. The maximum ratio in both sexes is in the Alaska Pacific Section and minimum in the California Chaparral.

In the Alaska-Cascades-Sierra Nevada transect (Figs. 3, 12, transect B) ratios of wing-tip to wing length do not change significantly in either sex between sections from Alaska Pacific south to the California Grasslands (valley), but show slight, irregular increases and decreases differing in the two sexes. Ratios in both sexes

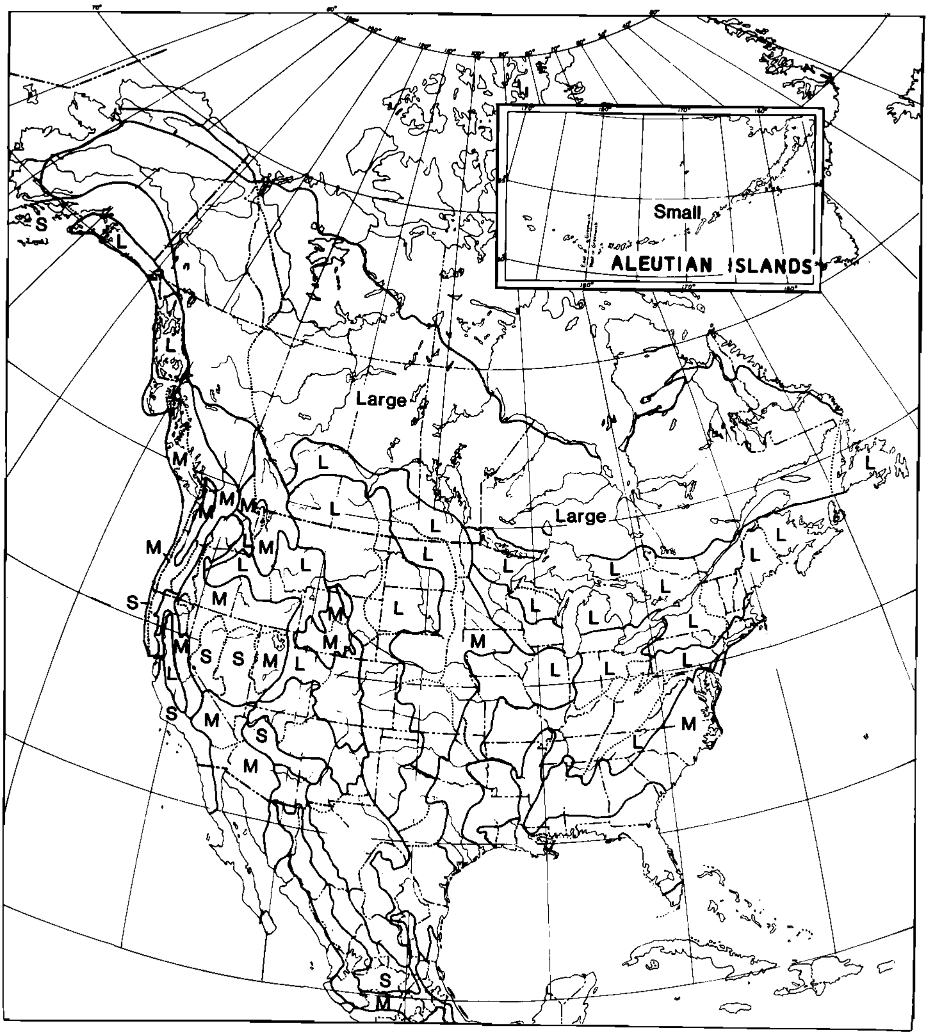

FIG. 11. Relative ratios of wing-tip to wing length of males in different Ecoregion Sections. L = larger; S = smaller; M = middle one-third of means.

decrease significantly from the California Grasslands to the California Chaparral. The maximum ratio for males is in the California Grassland and for females in the Cascades. Minimum ratios for both sexes are in the California Chaparral.

In the Interior Basins transect (Figs. 3, 12, transect C), wing-tip to wing length ratios decrease significantly in both sexes from the Central Boreal south to the Palouse Grassland, and in males from Sagebrush-Wheatgrass to Lahontan Greasewood of the western Great Basin followed by little change to the Sonoran Desert. Maximum ratios for both sexes are in Central Boreal. Minimum ratios for both sexes are in Lahontan Saltbush-Greasewood. The overall trend is a decrease southward in both sexes.

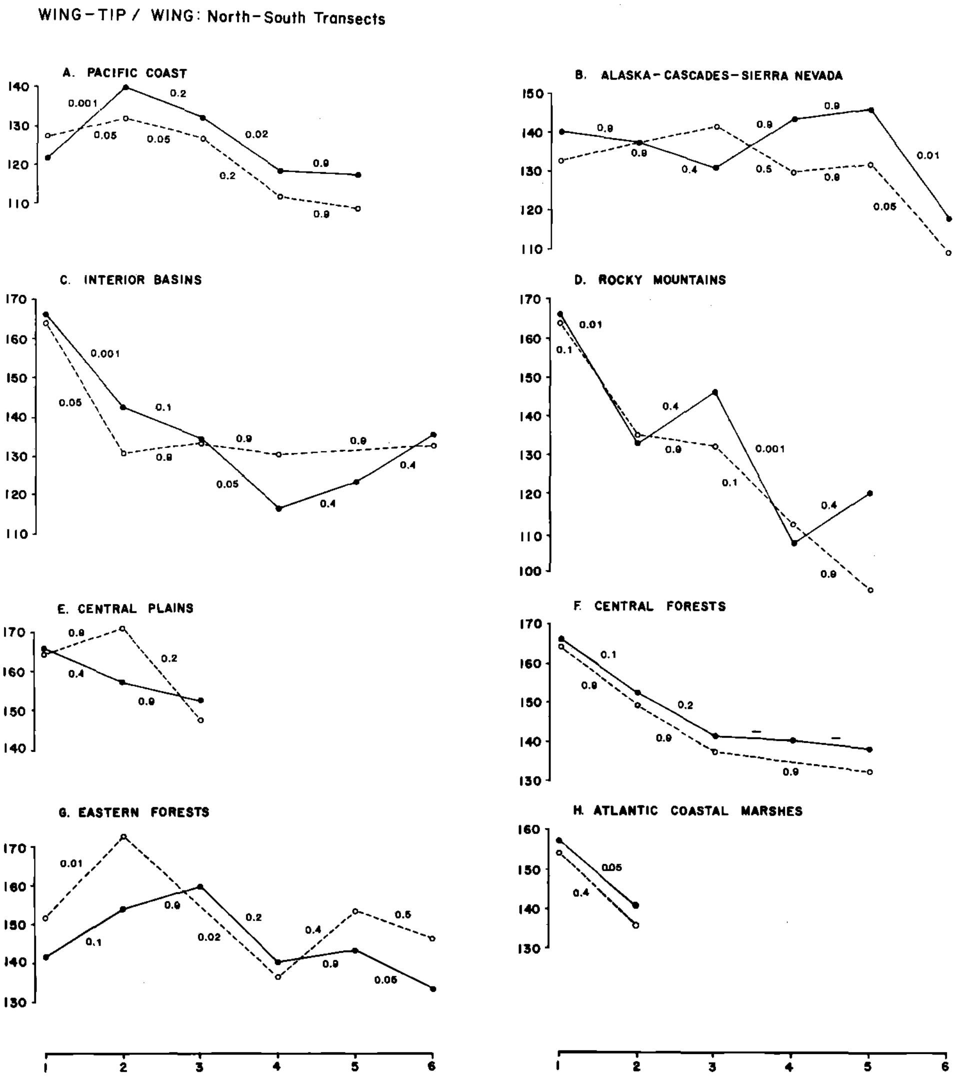

FIG. 12. North-south transects of mean wing-tip to wing length ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

Along the Rocky Mountains transect (Figs. 3, 12, transect D), the trend is definitely decreasing in both sexes from maxima in the Central Boreal. The decrease in males is significant from the Central Boreal to the moist Columbia Forest, and from the Northern Rockies to the Upper Gila Mountains Forest then no significant change occurs in either sex to the Mexican Shrub Steppe. Maximum ratios for both sexes are in the Central Boreal. The minimum ratio for males is in the Upper Gila Mountains Forest and for females in the Mexican Shrub Steppe.

In the Central Plains transect (Figs. 3, 12, transect E) size slightly decreases toward the south in both sexes to the Short-grass Prairie. Maxima are in the

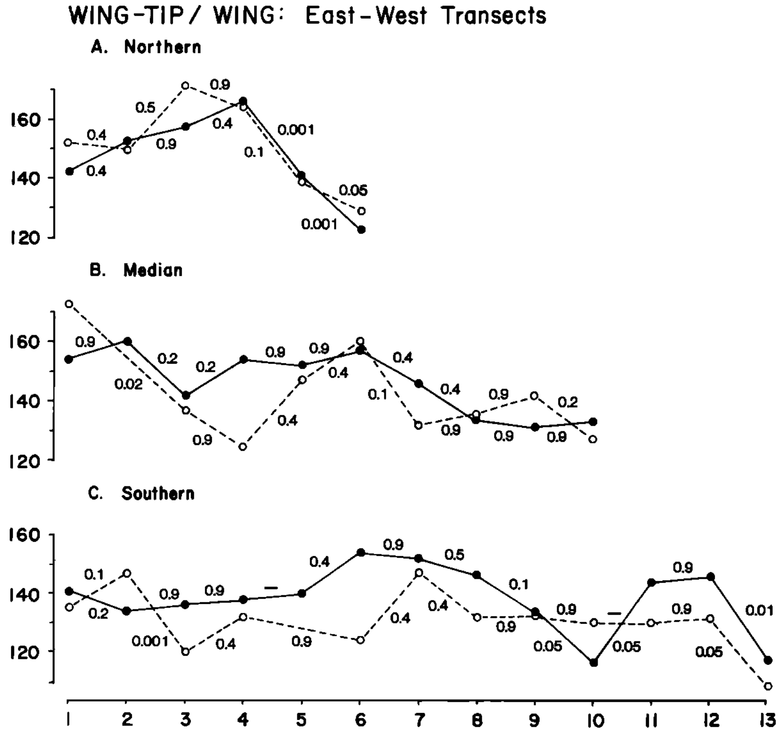

FIG. 13. East-west transects of mean wing-tip to wing length ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

Central Boreal for males and Aspen Parkland for females. Minima for both sexes are in the Short-grass Prairie.

In the Central Forest transect (Figs. 3, 12, transect F) ratios of both sexes decline moderately with seeming progressive decreases from the Central Boreal to the Oak-Hickory Forest.

A transect in the Eastern Forests (Figs. 3, 12, transect G) shows no trend in ratios of either sex. The maximum for males is in the New England Northern Hardwoods-Spruce, and for females, in the Maritime Northern Hardwoods-Spruce. The minimum for males is in the Southeastern Mixed Forest, and for females, in the New York Northern Hardwoods. Opposite, sometimes significant, differences occur between sections in both sexes along the transect, which tend to counteract one another. The relatively small ratio for Newfoundland, which is smaller in both sexes than Appalachian Oak (deciduous), is indicative of the lack of trend.

The Atlantic Coastal Marsh transect (Figs. 3, 12, transect H) shows a significant decrease in male ratios from north to south. In females the wing-tip ratio of the southern section is smaller, but not significantly so, than that of the northern marshes.

East-west transects. In the northern transect (Figs. 4, 13, transect A) ratios increase moderately in both sexes without statistically significant increments, from the Newfoundland Boreal to the Central Boreal, then decrease sharply in both sexes, in two places significantly, from the Central Boreal to the Aleutian Islands. The maximum value for males is in the Central Boreal, and for females, in the Aspen Parklands. Minima for both sexes are in the Aleutian Islands.

In the median transect (Figs. 4, 13, transect B), ratios alternately increase and decrease in both sexes from the Maritime Northern Hardwoods-Spruce to the western Short-grass Prairie, then decline, without significant steps, to the Sitka Spruce-Cedar-Hemlock on the Pacific Coast. The maximum value is for males in the Northern Hardwoods-Spruce (New England), and for females, in the Northern Hardwoods-Spruce (Maritime). The minimum ratio is for males in the Cascades, and for females, in the Tall-grass Prairie.

In the southern transect (Figs. 4, 13, transect C), no trends in values occur from the Atlantic Coastal Marshes to the Sagebrush-Wheatgrass, but ratios in males decline significantly from there to the western Great Basin Lahontan Saltbush-Greasewood, and increase significantly between there and the Sierran Forest, and then both sexes decrease significantly from the California Grassland to the California Chaparral. The maximum ratio is for males in the western Tall-grass Prairie, and for females both in the Southeastern Mixed Forest and eastern Short-grass Prairie. Minima for both sexes are in the California Chaparral.

Discussion.—The ratio of wing-tip length to total wing length does not differ appreciably between the sexes in contrast to both total wing length and wing-tip length. Both males and females tend to have larger ratios in grasslands and more northern regions except for the more sedentary populations of the Aleutian Tundra and Pacific Forest which have relatively small ratios. Populations in the boreal and higher mountain forests, and all grasslands have the largest ratios; those in the southern woodlands, chaparral, and southern deserts, as well as Pacific Rain Forests and the Aleutian Islands have the smaller ones. In both north-south and east-west transects wing-tip to wing length ratios generally decrease, except in areas of grassland or high elevation, in which birds have larger ratios. Birds in eastern lowland forests have higher ratios than those in western lowland forests. It is interesting that the wing-tip to wing length ratios are smallest among Aleutian Islands birds which have the longest total wing length of all populations. Sedentary populations on the Pacific Coast appear to have smaller ratios than more migratory ones, particularly those in eastern forests and grasslands. Within Life Areas the more northern sections have greater ratios.

Discussion of All Wing Measurements

Means of total wing length generally decrease from north to south, except where influenced locally by changes in elevation and density of vegetation. Wing lengths are greater at higher elevations and in more open plant associations at the same latitudes. Thus, wings are very long in the Aleutian Islands but are also long in the northern grasslands and northern deserts. They are somewhat shorter in the northern forests, even shorter in the southern forests and southern deserts, and shortest in the California Chaparral. Thus, as an indicator of overall size of the birds, wing length conforms to Bergmann's ecogeographic rule with larger size in colder climates. However, this rule may be modified by relative heat loss by evaporation (James 1970), and by relative body water loss by evaporation (Hamilton 1958), resulting in larger size of birds in dryer climates (Ripley 1950). Life form of the vegetation may affect wing length independent of body size (Davis 1951; Pitelka 1951; Hamilton 1961; Rand 1961). More extensive flights and, thus, greater use of wings may be required to escape predators in more open habitats such as grasslands and deserts. Linsdale (1938) suggested that high winds in open country contribute to longer wings in the same way that flying great distances does. Also, populations with long migrations may require long wings (Behle 1942; Mayr 1956; Hamilton 1961), and such populations are usually the more northern ones (Appendix II), the non-migratory Aleutian populations being notable exceptions.

Studies on other species of birds also have shown correlations between long wings and cold climates (e.g., Miller 1941; Behle 1942; Calhoun 1947; Hawbecker 1948; Traylor 1950; Davis 1951; Pitelka 1951; Snow 1954; Hamilton 1958, 1961; Williamson 1958; Bowers 1960; Rand 1961; Johnston and Selander 1964, 1971; Packard 1967; Power 1969, 1970; Jackson 1970; James 1970; Johnston 1972; Niles 1973). Kendeigh (1969) discussed the physiological basis for Bergmann's rule. He found that, in general, larger birds are favored physiologically for living in cold climates because of less stress on body temperature regulation. However, he noted that this advantage may be offset in some cases because the larger birds require more food from the environment. Other investigators noted exceptions to this ecogeographic rule in which large size was not correlated with northern distribution (Rensch 1938; Mayr and Vaurie 1948; Pitelka 1951; Snow 1954; Hamilton 1958; Moreau 1960; Rand 1961). Longer wings of Song Sparrows also may be correlated with dryer climates of grasslands and deserts as noted by Hamilton (1958) for vireos, by Power (1970) for Red-winged Blackbirds, and by James (1970) for other species, supporting the modification of Bergmann's rule to include effect of atmospheric moisture on body size suggested by James (1970).

As with total wing length, wing-tips are longer in more northern latitudes, more open situations, and at higher elevations, and shorter in more southern, lower, and more heavily vegetated regions, presumably reflecting both larger overall size of the birds as well as flight habits.

However, when the ratios of wing-tip length to total wing length are considered, the picture is quite different. Means of male wing-tip and wing length, paired by Ecoregion Province, are poorly correlated ($r = 0.41$, $n = 22$, $P < 0.1$). More rounded wings, that is, with shorter wing-tip to wing length ratios, are found in the northern Aleutian tundra and Pacific Rain Forest as well as in the southwestern chaparral, woodlands, and deserts. The more rounded wings appear to be characteristic of the more sedentary populations such as those of the Aleutian Islands, Pacific Forest, the more southern deserts and woodlands, and California Chaparral. The more pointed wings resulting from longer wing-tip to wing length ratios are found in the more migratory populations of the northeastern forests and mountains and those that must fly farther to seek cover in the grasslands. The data indicate that wing shape may be a better indicator of flight habits than total wing length. Correlations of wing length and shape with migratory habit and habitat have been noted also by Rensch (1938), Davis (1951), Dilger (1956), Hamilton (1958, 1961), and Rand (1961). Power (1970) summarized the multiplicity of environmental and behavioral factors that may affect wing length and shape. Despite these, it is the best indicator of body size available (McCabe and McCabe 1932; Pitelka 1951; Power 1969).

In most cases, male wings and wing-tips average longer than those of females. However, when we consider ratios of wing-tip to total wing length, the sexes practically do not differ. The consistently longer wings and wing-tips of males presumably reflect greater overall size in that sex, while the similar ratios of wing-tip to wing length in males and females presumably indicate a similar wing shape and, thus, similar flight patterns. All average measurements and ratios are highly significantly correlated for males and females from the same ecogeographical area.

BILL MEASUREMENTS

Total Culmen Length

Sex differences.—In 42 of 49 samples males have greater mean culmen lengths than females, in six instances (1-M1310, 3-1320A, 8-2214, 7-M2410, 14-M3111 and 12-3222) significantly so. Females have longer bills in six cases, but none is significant. In one sample both sexes have the same mean length of bill.

Differences by Life Area (Fig. 1, Tables 1, 2).—Means of total culmen lengths arranged in order of decreasing size are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutians)	58	18.29	37	17.88
7	Pacific Rain Forest	113	15.02	70	14.92
13	Mesquite-Grassland	14	14.73	6	14.32
17	Mexican Pine-Oak	18	14.47	3	14.43
15	Chaparral-Oak Woodland	32	13.99	12	13.62
6	Montane Woodland-Brush	26	13.98	16	13.86
14	Piñon-Juniper-Oak	51	13.92	29	13.82
9	Grasslands	50	13.90	31	13.82
11	Northern Desert Scrub	94	13.87	42	13.68
12	Southern Desert Scrub	25	13.84	13	13.49
10	Oak-Savannah	2	13.80	0	—
4	Northern Hardwood-Conifer	111	13.73	40	14.74
3	Boreal	21	13.70	6	13.18
5	Aspen Parkland	6	13.65	3	13.93
8	Eastern Deciduous Forest	114	13.55	47	13.48

Male and female mean culmen lengths are highly correlated ($r = 0.95$, $P < 0.001$).

Means of total culmen lengths differing significantly in adjoining Life Areas are: Arctic-Alpine (Aleutian Tundra) > Boreal Forest (♂, ♀); Grasslands > Eastern Deciduous Forest (♀); Pacific Rain Forest > Montane Woodland-Brush (♂, ♀); Mesquite-Grassland > Southern Desert Scrub (♂, ♀); Mesquite-Grassland > Grasslands (♂).

Significant differences in mean culmen lengths of birds from different Ecoregion Sections within Life Areas are:

Northern Hardwood-Conifer

4-2113 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♀)

Pacific Rain Forest

7-M2416 Alaska Pacific > 7-2410 Willamette-Puget Forest (♂)
7-M2416 Alaska Pacific > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂)

Eastern Deciduous Forest

8-2213 Maple-Basswood-Oak > 8-2211 Mixed Mesophytic Forest (♂)
8-2213 Maple-Basswood-Oak > 8-2215 Oak-Hickory Forest (♀)
8-2215 Oak-Hickory Forest > 8-2320 Southeastern Mixed Forest (♀)
8-2320 Southeastern Mixed Forest > 8-2214 Appalachian-Oak (deciduous) (♀)
8-2320 Southeastern Mixed Forest > 8-2211 Mixed Mesophytic Forest (♀)

Grasslands

9-2610 California Grasslands (valley) > 9-2532 Tall-grass Prairie (west) (♂)
9-3120 Palouse Grassland > 9-3112 Short-grass Prairie (east) (♂)

Northern Desert Scrub

11-3131 Sagebrush-Wheatgrass > 11-M3112 Douglas-fir Forest (sagebrush) (♂, ♀)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of total culmen length arranged in order of decreasing values of males are:

		♂ N	Mean	♀ N	Mean
M1310	Alaska Range (Aleutians)	58	18.29	37	17.88
M2410	Pacific Forest	92	15.15	60	14.94
2410	Willamette-Puget	16	14.79	10	14.71
17	Mexican Pine-Oak	15	14.79	3	14.43
3140	Mexican Shrub Steppe	14	14.73	6	14.32
2610	California Grassland	3	14.30	4	13.93
M2610	Sierran Forest	8	13.99	5	13.94
3120	Palouse Grassland	21	13.99	9	14.23
3130	Intermountain Sagebrush	104	13.99	56	13.80
P3130	Colorado Plateau	0	—	2	13.80
M2110	Columbia Forest	13	13.93	4	14.18
2320	Southeastern Mixed Forest	84	13.93	45	13.85
3220	American Desert	25	13.84	13	13.49
M2620	California Chaparral	57	13.83	25	13.44
M3110	Rocky Mountains Forest	46	13.81	19	13.69
2510	Prairie Parkland	2	13.80	0	—
2110	Laurentian Forest	46	13.78	21	13.39
2530	Tall-grass Prairie	13	13.72	6	13.70
1320	Boreal Forest	21	13.70	6	13.18
2210	Eastern Deciduous Forest	148	13.66	48	13.40
A3140	Wyoming Basin	9	13.46	1	13.10
3110	Short-grass Prairie	8	13.45	11	13.55
M3120	Upper Gila Mountains Forest	8	13.45	5	13.52

Male and female mean culmen lengths are highly correlated ($r = 0.98$, $P < 0.001$).

Significantly different means of culmen lengths in adjoining Ecoregion Provinces are: Southeastern Mixed Forest > Eastern Deciduous Forest (♂, ♀); Alaska Range (Aleutians) > Yukon Forest (Boreal) (♀); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); Pacific Forest > Sierran Forest (♂, ♀); Mexican Highlands Shrub Steppe > Upper Gila Mountains Forest (♂); Intermountain Sagebrush > American Desert (♀); Palouse Grassland > Rocky Mountains Forest (♀).

Bills tend to be longest in the Aleutian Tundra, becoming considerably shorter in southward progression through the Pacific Forests and into the arid southwestern United States, and then becoming longer again in Mexico. In general, shorter bills characterize populations from the Rocky Mountains eastward as well as those in the dryer southwestern mountains, deserts, and chaparral.

Differences by Ecoregion Section/Life Area (Fig. 2, Tables 5, 6).—When means of total culmen lengths are compared, adjacent Ecoregion Section/Life Area units that differ significantly are: 7-M2416 Alaska Pacific > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀); 7-M24111 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂); 14-M3111 Oregon Montane (Piñon-Juniper) > 6-M3112 N. Rockies Montane Forest (♂); 1-M1310 Alaska Range (Aleutian) > 7-M2416 Alaska Pacific Forest (♂, ♀); 7-M2112 Columbia Forest (moist) > 6-M3112 N. Rockies Montane Forest (♀); 5-2530E Aspen Parkland (east) > 9-3112 Short-grass Prairie (east) (♂); 8-A2320A Atlantic Coastal Marsh (south) > 8A-2214A Atlantic Coastal Marsh (north) (♂, ♀); 11-3131 N. Desert Scrub (sagebrush) > 11-M3112 N. Rockies (sagebrush) (♂, ♀); 9-3120 Palouse Grassland (grass) > 11-3131 N. Desert Scrub (sagebrush) (♀); 4-2112 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♀); 8-2320 Southeastern Mixed Forest > 8-2214 Appalachian-Oak (deciduous) (♀); 5-2530E Aspen Parkland (east) > 4-2111 Spruce-Fir (Minnesota) (♀); 7-M2112 Columbia Forest (moist) > 6-M3112 N. Rockies Montane (♀); 8-2320 Southeastern Mixed Forest > 8-2211 Mixed Mesophytic Forest (♀).

In five cases mean bill lengths of birds in Life Belts within the same Ecoregion Section differ significantly from each other: 8A-2320A Atlantic Salt Marsh (south) > 8-2320 Southeastern Mixed Forest (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B San Francisco Bay Marsh (south) (♂, ♀); 9-M2620 California Chaparral (grassland) > 9-M2620B San Francisco Bay Marsh (south) (♂); 14-M3111 Oregon Piñon-Juniper > 9-M3111 Oregon Grassland (♂); 6-M3112 Northern Rockies (Montane Woodland-Brush) > 11-M3112 Northern Rockies (N. Desert Scrub) (♀).

Relative lengths of culmens of males in different Ecoregion Sections are shown in Figure 14.

North-south transects. A north to south transect along the Pacific Coast (Figs. 3, 15, transect A) shows a progressive and pronounced decrease in mean culmen length in both sexes from the Aleutian Islands to the California Chaparral with significant differences in males between sections as far as the Redwood Forest, and in females as far as the Sitka Spruce-Cedar-Hemlock.

In a transect from Alaska Pacific southward along the Cascades and Sierra Nevada (Figs. 3, 15, transect B), after a significant decrease in males to the Columbia Forest (montane), and in females to the Cascades, alternating nonsignificant increases and decreases occur in both sexes to the California Chaparral, but

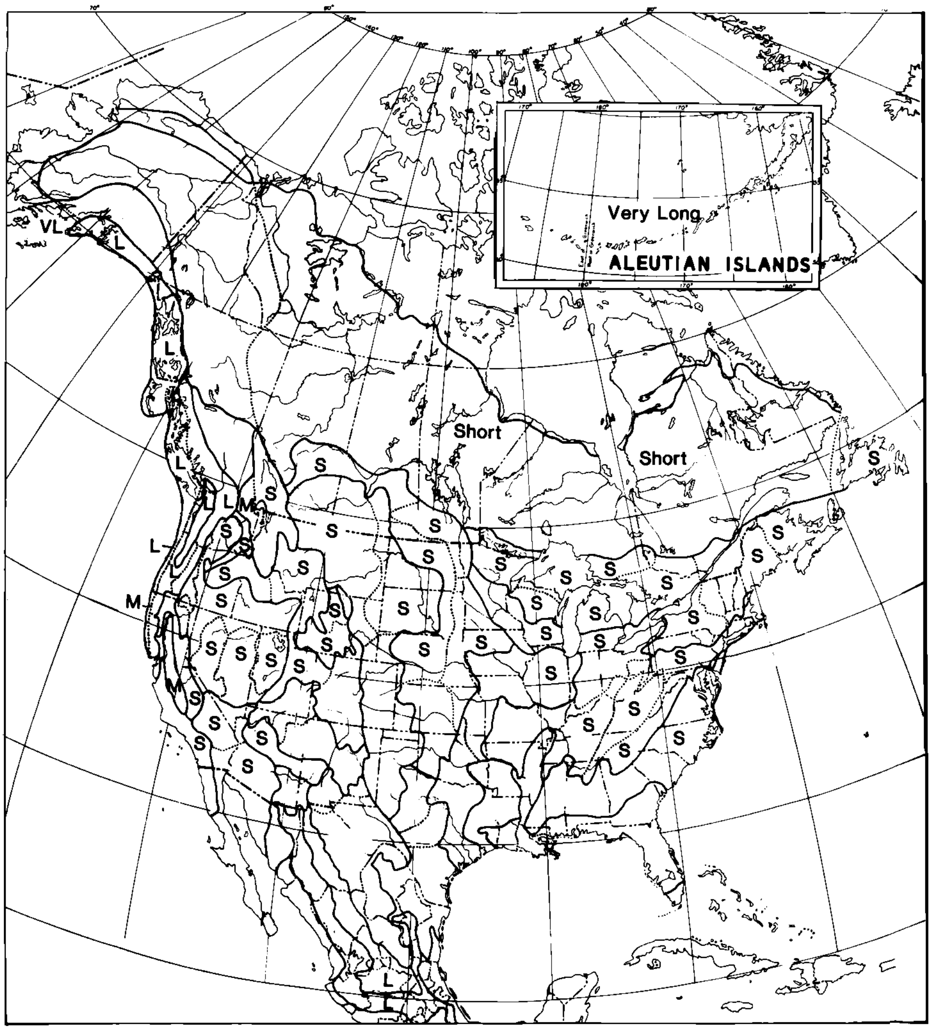

FIG. 14. Relative total culmen lengths of males in different Ecoregion Sections. L = longer; S = shorter; M = middle one-third of means; VL = very long.

with a decreasing trend. Maxima for both sexes are in Alaska Pacific, and minima in the California Chaparral.

A transect from the Central Boreal southward through the interior basins (Figs. 3, 15, transect C) shows no marked trend. The only significant difference between any two sections is a decrease in female culmen length between the Palouse Grasslands and Sagebrush-Wheatgrass Northern Desert Scrub. The maximum length for males is in the Lahontan Saltbush-Greasewood of the western Great Basin, and for females in the Palouse Grassland. Minima are in Mojave Desert for males, and Sonoran Desert for females.

A transect along the Rocky Mountains (Figs. 3, 15, transect D) shows no par-

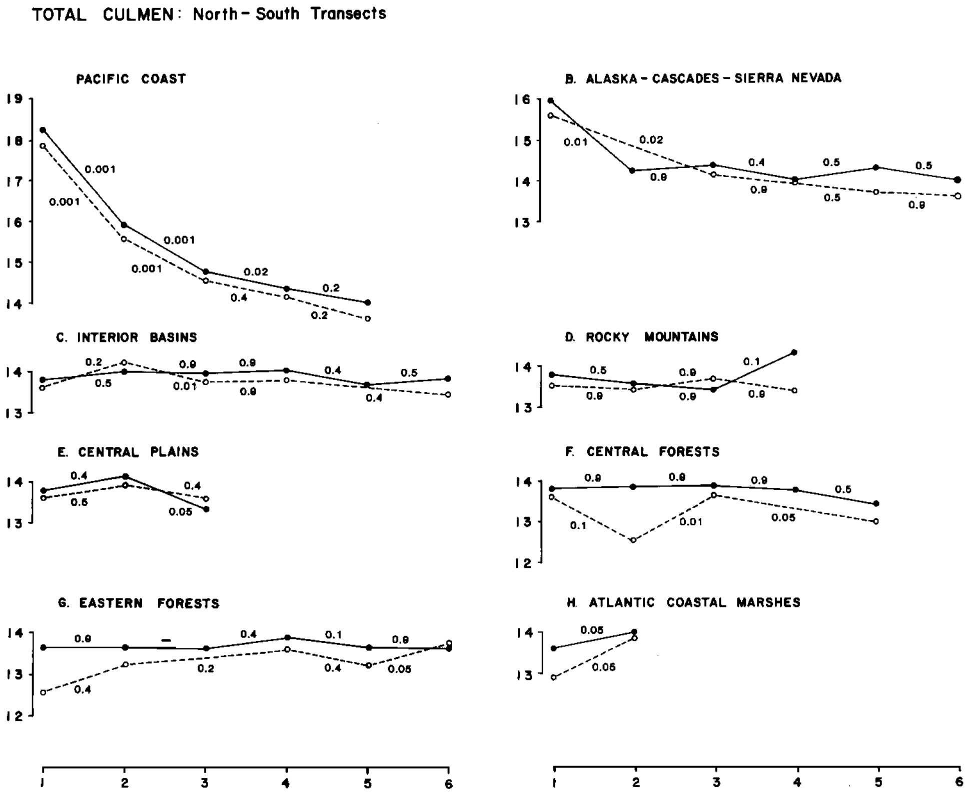

FIG. 15. North-south transects of mean total culmen lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

ticular trend and no significant steps. Maximum culmen length for males is in the Mexican Shrub Steppe, and for females in the Central Boreal. Minima are in the Upper Gila Mountains for males, and Mexican Shrub Steppe for females.

In the Central Plains transect (Figs. 3, 15, transect E) the longest bills in both sexes are in the Aspen Parkland and shortest in the Short-grass Prairie. The decrease in bill length between the Aspen Parkland and the Short-grass Prairie is significant in males.

A transect-through the central forests (Figs. 3, 15, transect F) shows maximum culmen lengths in both sexes in the Northern Hardwoods Forest (New York-Wisconsin). Female culmen length increases significantly from the Spruce-Fir of Minnesota to the Northern Hardwoods (New York-Wisconsin), followed by a significant decrease to the Oak-Hickory Forest. Minimum length for males is in the Oak-Hickory Forest, and for females in the Spruce-Fir (Minnesota).

The eastern forest transect (Figs. 3, 15, transect G) indicates a slight trend of increasing bill length from the Newfoundland Boreal to the northern Hardwoods of New York, then an insignificant decrease to the Appalachian Oak (deciduous forest) and then an increase, significant in females, to the Southeastern Mixed

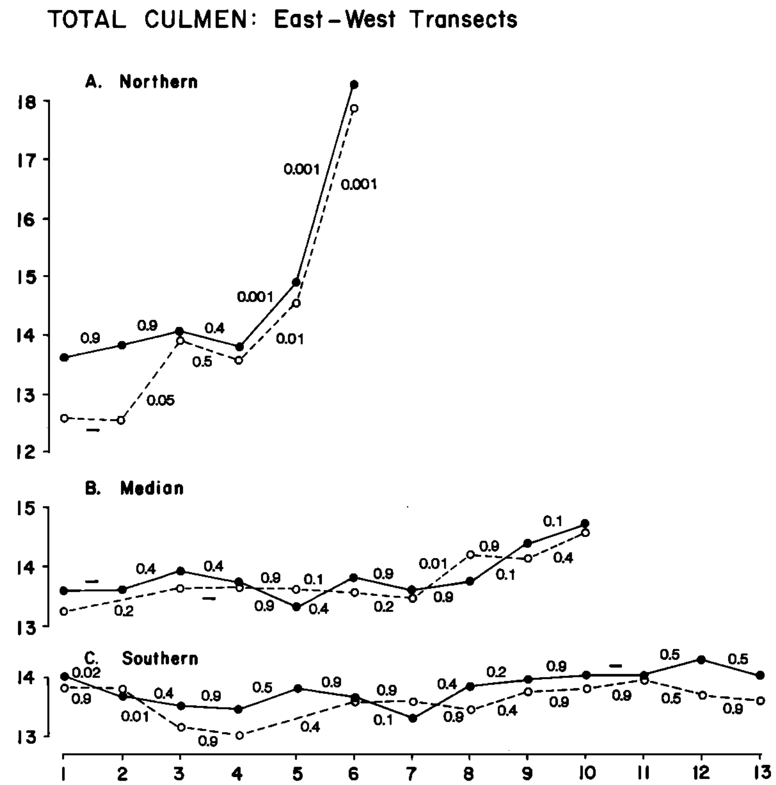

FIG. 16. East-west transects of mean total culmen lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

Forest. Maxima are in the Northern Hardwoods (New York) for males, and Southeastern Mixed Forest for females. Minima are in the Northern Hardwoods-Spruce (New England and Maritime) for males, and Newfoundland Boreal for females.

In the Atlantic Coastal Marsh transect (Figs. 3, 15, transect H) bill length increases significantly from the northern to the southern sections in both sexes.

East-west transect. The northern-most east to west transect (Figs. 4, 16, transect A) suggests a slight increase in mean bill length from Newfoundland Boreal to the Aspen Parkland, then little change to the Central Boreal, followed by a marked increase to maxima in the Aleutian Islands, with significant differences between sections. Minimum lengths are in the Newfoundland Boreal for males, and Spruce-Fir of northern Minnesota for females.

In the median transect (Figs. 4, 16, transect B), slight increases and decreases alternate, with little change indicated between the Northern Hardwoods-Spruce (Maritime) and the Northern Rockies Montane Forest. From there to the Sitka Spruce-Cedar-Hemlock of the Pacific Coast there is a pronounced increase in bill length with significant increases in females from the Northern Rockies Montane Forest to the Columbia Moist Forest. Maximum mean bill lengths are in Sitka

Spruce-Cedar-Hemlock Forest for both sexes, and minima in the Short-grass Prairie for males and the northern Hardwoods-Spruce (Maritime) for females.

Along the southern transect (Figs. 4, 16, transect C), mean bill lengths decrease from the Atlantic Coastal Marshes to the Oak-Hickory Forest, then remain unchanged to the Rocky Mountains. This is followed by a gradual increase to the California Grassland followed by a slight decrease to the California Chaparral. Maximum bill lengths for males are in the California Grassland, and for females in the Sierran Forest. Minima are in the Short-grass Prairie for males, and in the Oak-Hickory Forest for females.

Discussion.—Mean culmen lengths of populations grouped by Life Area, Ecoregion Province, and Ecoregion Section/Life Area units, tend to decrease from north to south. This trend is more pronounced west of the Rocky Mountains, and most pronounced along the Pacific Coast. The trend is reversed in Mexico and in the eastern forests and Atlantic coastal marshes where bill length increases from north to south. In addition, bill length generally increases from east to west, particularly from the Rocky Mountains to the Pacific Coast. This trend is most pronounced in the north, since bills of eastern birds tend to be longer and those of western birds to be shorter in the southern United States. This is particularly noticeable in the relatively short bills of birds in southern deserts and chaparral. Still farther south in the western part of the continent, in Mexico, bill size increases.

Males have longer bills than females in almost all cases, and in all cases in which differences are significant.

Height of Maxilla

Sex differences.—Within the 49 samples measured the maxilla averages higher in males in 37, higher in females in six, and is the same in both sexes in six. In five instances, male culmens are significantly higher (8A-2320A, 7-2410, 9-2610, 14-3131, and 12-3222), but in no cases are female culmens higher.

Differences by Life Area (Fig. 1, Tables 1, 2).—Means of height of maxilla arranged in decreasing order of magnitude for males are:

		♂ N	Mean	♀ N	Mean
8	Eastern Deciduous Forest	117	4.81	48	4.71
1	Arctic-Alpine (Aleutian)	59	4.76	38	4.69
10	Oak-Savannah	2	4.75	0	—
3	Boreal	21	4.70	6	4.57
4	Northern Hardwood-Conifer	114	4.68	41	4.66
5	Aspen Parkland	6	4.68	3	4.60
9	Grasslands	50	4.40	31	4.43
11	Northern Desert Scrub	98	4.31	42	4.26
14	Piñon-Juniper-Oak	53	4.30	30	4.30
6	Montane Woodland-Brush	26	4.29	16	4.24
15	Chaparral-Oak Woodland	32	4.24	12	4.25
7	Pacific Rain Forest	113	4.23	70	4.19
17	Mexican Pine-Oak	18	4.19	3	3.97
13	Mesquite-Grassland	14	4.16	6	4.10
12	Southern Desert Scrub	25	4.15	13	4.05

Male and female mean maxilla heights are highly correlated ($r = 0.97$, $P < 0.001$).

When means of adjacent Life Areas are compared, significant differences in height of maxilla are: Eastern Deciduous Forest > Northern Hardwood-Conifer (♂) and > Grasslands (♂, ♀); Grasslands > Northern Desert Scrub (♀); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Grasslands > Montane Woodland-Brush (♀); Grasslands > Chaparral-Oak Woodland (♂, ♀); Aspen Parkland > Grasslands (♂); Grasslands > Mesquite-Grasslands (♂, ♀).

Significant differences in mean height of maxilla between Ecoregion Sections within Life Areas are:

Northern Hardwood-Conifer

4-2113 Northern Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂)
4-2113 Northern Hardwoods (New York-Wisconsin) > 4-2114 N. Hardwoods-Spruce (New England) (♂)
4-2114 N. Hardwoods-Spruce (New England) > 4-2111 Spruce-Fir (Minnesota) (♀)

Pacific Rain Forest

7-M2415 Cascades Forest > 7-M2112 Columbia Forest (moist) (♂)
7-M2415 Cascades Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂)

Eastern Deciduous Forest

8-2214 Appalachian Oak (deciduous) > 8-2211 Mixed Mesophytic Forest (♂)
8-2320 Southeastern Mixed Forest > 8-2211 Mixed Mesophytic Forest (♂)

Grasslands

9-2532 Tall-grass Prairie (west) > 9-2610 California Grassland (valley) (♂)
9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂)
9-2610 California Grassland (valley) > 9-M3111 Grand Fir-Douglas-fir (grassland) (♂)
9-3112 Short-grass Prairie (east) > 9-3120 Palouse Grassland (♂, ♀)
9-3111 Short-grass Prairie (west) > 9-3112 Short-grass Prairie (east) (♀)

Piñon-Juniper-Oak

14-M3111 Grand Fir-Douglas-fir (Juniper) > 14-M3120 Upper Gila Mts. Forest (Piñon-Juniper) (♂)
14-3131 Sagebrush-Wheatgrass (Juniper) > 14-M3120 Upper Gila Mts. Forest (Piñon-Juniper) (♂)
14-3132 Lahontan Saltbush (Piñon-Juniper) > 14-M3120 Upper Gila Mts. Forest (Piñon-Juniper) (♂)
14-3131 Sagebrush-Wheatgrass (Juniper) > 14-3132 Lahontan Saltbush (Juniper) (♂)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Mean maxilla heights representing Ecoregion Provinces arranged in order of decreasing magnitude for males are:

		♂ N	Mean	♀ N	Mean
2320	Southeastern Mixed Forest	87	4.97	46	4.90
2610	California Grassland	3	4.93	4	4.40
M1310	Alaska Range (Aleutians)	59	4.76	38	4.69
2510	Prairie Parkland	2	4.75	0	—
2210	Eastern Deciduous Forest	152	4.74	52	4.68
2110	Laurentian Forest	47	4.71	21	4.66
1320	Boreal Forest	21	4.70	6	4.57
3110	Short-grass Prairie	7	4.69	11	4.56
2530	Tall-grass Prairie	13	4.68	6	4.55
M2610	Sierran Forest	8	4.45	5	4.42
3130	Intermountain Sagebrush	107	4.38	58	4.32
2410	Willamette-Puget Forest	15	4.33	10	4.20
M2410	Pacific Forest	94	4.27	60	4.20
3120	Palouse Grassland	22	4.27	9	4.26
M2620	California Chaparral	59	4.23	25	4.08
17	Mexican Pine-Oak	15	4.19	3	3.97
M3110	Rocky Mountains Forest	47	4.16	19	4.17
3140	Mexican Shrub Steppe	14	4.16	6	4.10
M2110	Columbia Forest	13	4.15	4	4.13
P3130	Colorado Plateau	0	—	2	4.05
3220	American Desert	25	4.15	13	4.03
M3120	Upper Gila Mountains Forest	8	4.08	5	4.08
A3140	Wyoming Basin	9	4.08	1	4.00

Male and female mean maxilla heights are highly correlated ($r = 0.92$, $P < 0.001$).

When means of maxilla heights of adjacent Ecoregion Provinces are compared, significant differences are noted as follows: Southeastern Mixed Forest > Eastern Deciduous Forest (♂, ♀); Alaska Range (Aleutian) > Pacific Forest (♂, ♀); California Grassland > Sierran Forest (♂); California Grassland > California Chaparral (♂); Intermountain Sagebrush > Rocky Mountain Forest (♂, ♀); Intermountain Sagebrush > American Desert (♂, ♀); Short-grass Prairie > Wyoming Basin (♂); Palouse Grassland > Rocky Mountain Forest (♂); Sierran Forest > Pacific Forest (♂, ♀); Sierran Forest > American Desert (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 5, 6).—Significant differences between mean maxilla heights representative of adjoining Ecoregion Section/Life Area units are: 8-2214 Appalachian Oak (deciduous) > 8-2211 Mixed Mesophytic Forest (♂); 9-2610 California Grassland (valley) > 6-M2610 Sierran Forest (♂); 9-2610 California Grassland (valley) > 9-M2610 California Chaparral (grass) (♂); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (chaparral) (♂, ♀); 14-M3111 Oregon Montane (Piñon-Juniper) > 6-M3112 Northern Rockies (montane) (♂); 14-M3111 Oregon Montane (Piñon-Juniper) > 11-M3112 Northern Rockies (sagebrush) (♂, ♀); 14-3131 Sagebrush-Wheatgrass (Piñon) > 14-3132 Lahontan Saltbush (Piñon) (♂); 1-M1310 Alaska Range

(Aleutians) > 7-M2416 Alaska Pacific Forest (♂, ♀); 7-M2415 Cascades Forest > 6-M2111 Columbia Forest (montane) (♂); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂); 4-2113 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂); 4-2113 N. Hardwoods (New York-Wisconsin) > 4-2114 N. Hardwoods-Spruce (New England) (♂); 9-3111 Short-grass Prairie (west) > 6-M3112 N. Rockies (Montane Forest) (♂); 8-2320 Southeastern Mixed Forest > 8-2211 Mixed Mesophytic Forest (♂); 11-3131 Sagebrush-Wheatgrass > 6-M3112 Rocky Mountains (montane) (♂); 13-3140N Mexican Shrub Steppe (north) > 12-3222 Sonoran Desert (♀).

Cases of significant differences between Life Belts within single Ecoregion Sections are: 8-2214 Appalachian Oak Forest (deciduous) > 4-2214 Appalachian Oak (Northern Hardwood-Conifer) (♂); 8A-2320A Atlantic Coastal Marsh (south) > 8-2320 Southeastern Mixed Forest (♂, ♀); 9-M2620 California Chaparral (grassland) > 9-M2620B San Francisco Bay Marsh (south) (♂); 15-M2620 California Chaparral (Chaparral-Oak) > 9-M2620B San Francisco Bay Marsh (south) (♂, ♀); 14-3131 Sagebrush-Wheatgrass (Piñon-Juniper-Oak) > 11-3131 Sagebrush-Wheatgrass (Northern Desert Scrub) (♂).

Relative heights of maxillae of males in different Ecoregion Sections are shown in Figure 17.

North-south transects. A transect along the Pacific Coast (Figs. 3, 18, transect A) shows an initial significant decrease in maxilla height between the Alaska Range (Aleutians) and the Alaska Pacific Forest in both sexes. From there, maxilla heights fluctuate slightly, southward along the coast, but with no significant change to the California Chaparral. The maximum height for both sexes is in the Alaska Range (Aleutians), and the minimum, in the Alaska Pacific Forest for males, and in the Redwood Forest for females.

The Alaska-Cascades-Sierra Transect (Figs. 3, 18, transect B) shows an overall increase in both sexes from the Alaska Pacific Forest to the California Grassland. The increase is significant in males, from the Columbia Forest (montane) to the Cascades, and from the Sierra Forest to the California Grassland. A significant decrease occurs in both sexes from that section to the California Chaparral. Maxima for both sexes are in the California Grassland, and minima in the Columbia Forest (montane) for males, and Alaska Pacific, for females.

A transect from the Central Boreal through the interior basins (Figs. 3, 18, transect C) shows an initial significant decrease in maxilla height to the Palouse Grassland in both sexes, then a steady increase to the Lahontan Saltbush-Greasewood, followed by another decrease, significant in females, to the Sonoran Desert. Maxima are in the Central Boreal and minima in the Sonoran Desert for both sexes.

The Rocky Mountains transect (Figs. 3, 18, transect D) shows a fairly pronounced and steady decrease in maxilla height from the Central Boreal south to the Upper Gila Mountains Forest of middle Arizona and New Mexico, then an increase, significant in females, to the Mexican Shrub Steppe. Maxima are in the Central Boreal, and minima in the Upper Gila Mountains Forest for both sexes.

A transect through the central plains (Figs. 3, 18, transect E) shows very little change from the Central Boreal to the Short-grass Prairie. Maxima are in the Central Boreal for males, and Short-grass Prairie for females. Minima are in the Short-grass Prairie for males, and Aspen Parkland for females.

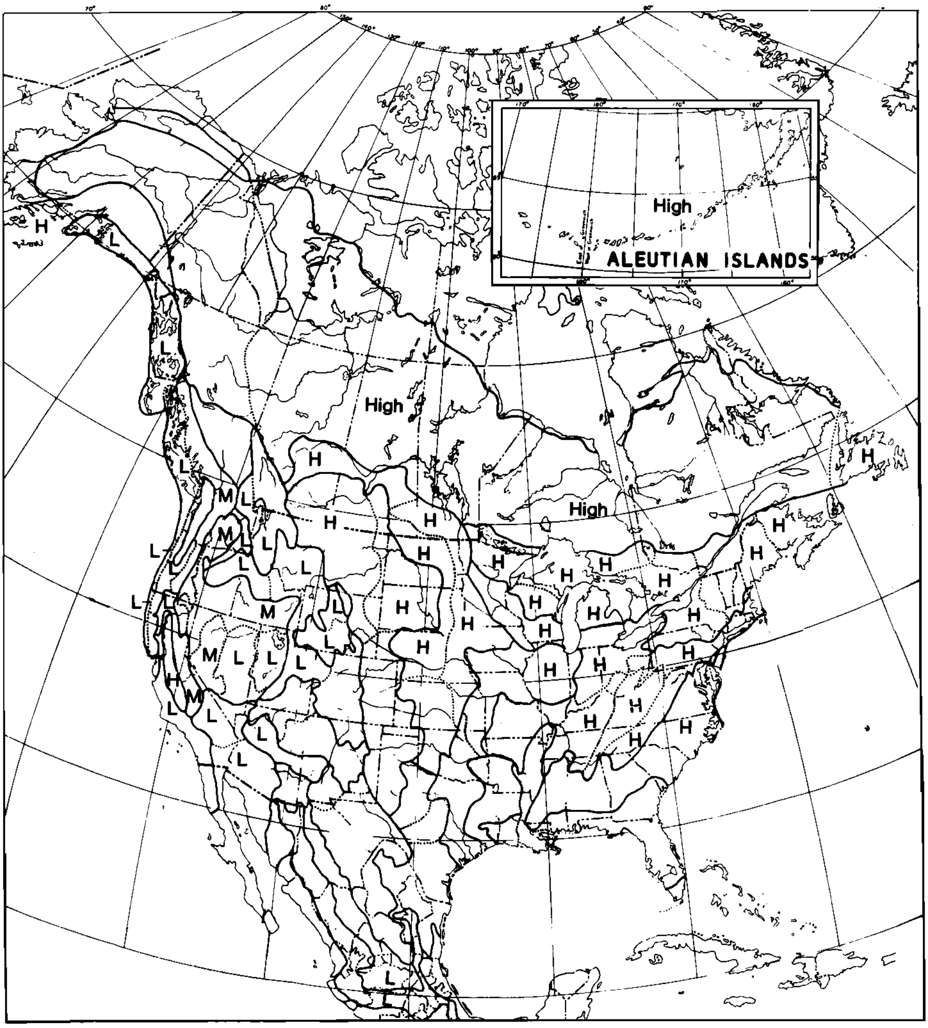

FIG. 17. Relative heights of maxillae of males in different Ecoregion Sections. H = higher; L = lower; M = middle one-third of means.

A transect through the central forests (Figs. 3, 18, transect F) shows an alternating decrease and increase in maxilla heights in both sexes without any particular trend, from the Central Boreal to the Oak-Hickory Forest, with a significant increase, in males, from the Spruce-Fir (Minnesota) to the Northern Hardwoods (Wisconsin). Maxima are in the Northern Hardwoods for males and Central Boreal for females. Minima are in the Spruce-Fir (Minnesota) for both sexes.

Along the Eastern forests transect (Figs. 3, 18, transect G) maxilla heights increase and decrease differently in the two sexes, but show a slight increase from Newfoundland Boreal to Southeastern Mixed Forest. The maximum height is for males in the Appalachian Oak (deciduous), and for females in the Southeastern Mixed Forest. Minima are in the Newfoundland Boreal for females, and Northern Hardwoods-Spruce for males.

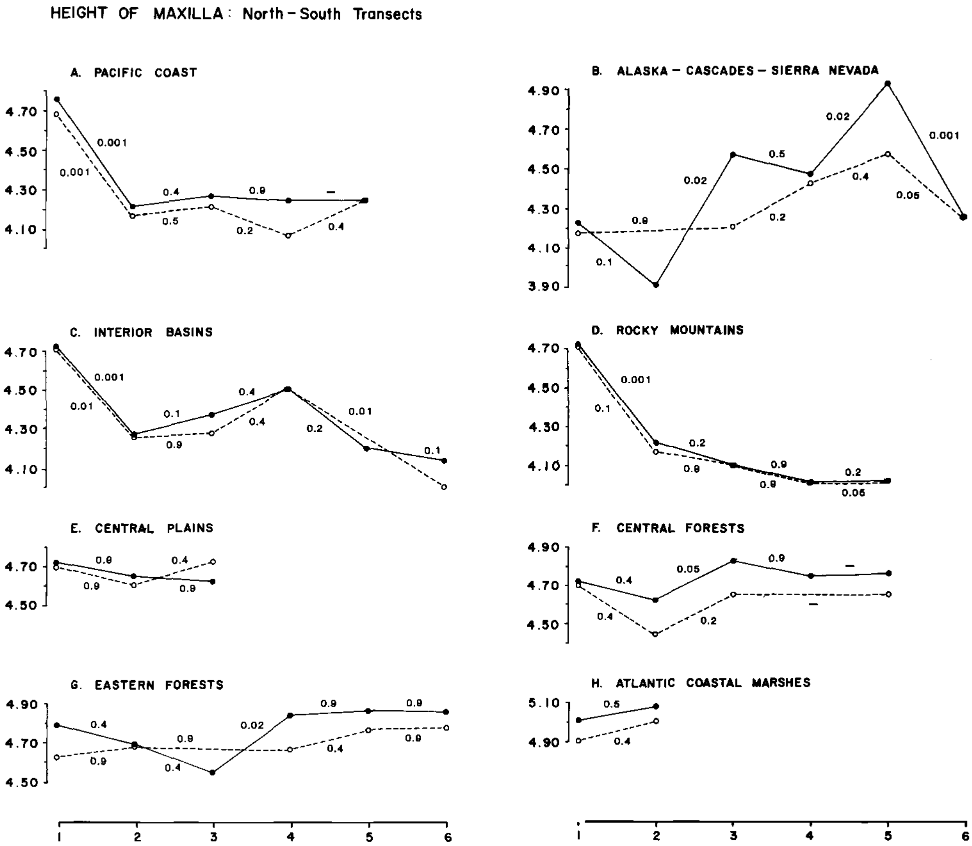

FIG. 18. North-south transects of mean heights of maxillae. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

Along the Atlantic Coastal Marshes (Figs. 3, 18, transect H), no differences in maxilla height from north to south are apparent in either sex.

East-west transects. Along the northernmost east to west transects (Figs. 4, 19, transect A) maxilla height decreases slightly for both sexes from Newfoundland Boreal to Spruce-Fir (Minnesota), followed by a slight increase to the Central Boreal. Then a significant decrease occurs in both sexes to the Alaska Pacific Forest followed by a significant increase to the Alaska Range (Aleutians). The maximum for males is in the Newfoundland Boreal, and for females in the Central Boreal. Minima are in the Alaska Pacific Forest for both sexes.

Maxilla heights of birds along the median transect (Figs. 4, 19, transect B) are variable among populations, frequently with marked differences between the sexes. Height in males increases significantly within the Laurentian Forest from New England to New York-Wisconsin, then decreases significantly from the Short-grass Prairie to the Rocky Mountain Forest, then increases significantly from the Columbia Forest (moist) to the Silver Fir-Douglas-fir of the Cascades, then decreases significantly to the Sitka Spruce-Cedar-Hemlock of the Pacific Coast. The only significant change in females is a decrease within the Short-grass Prairie from

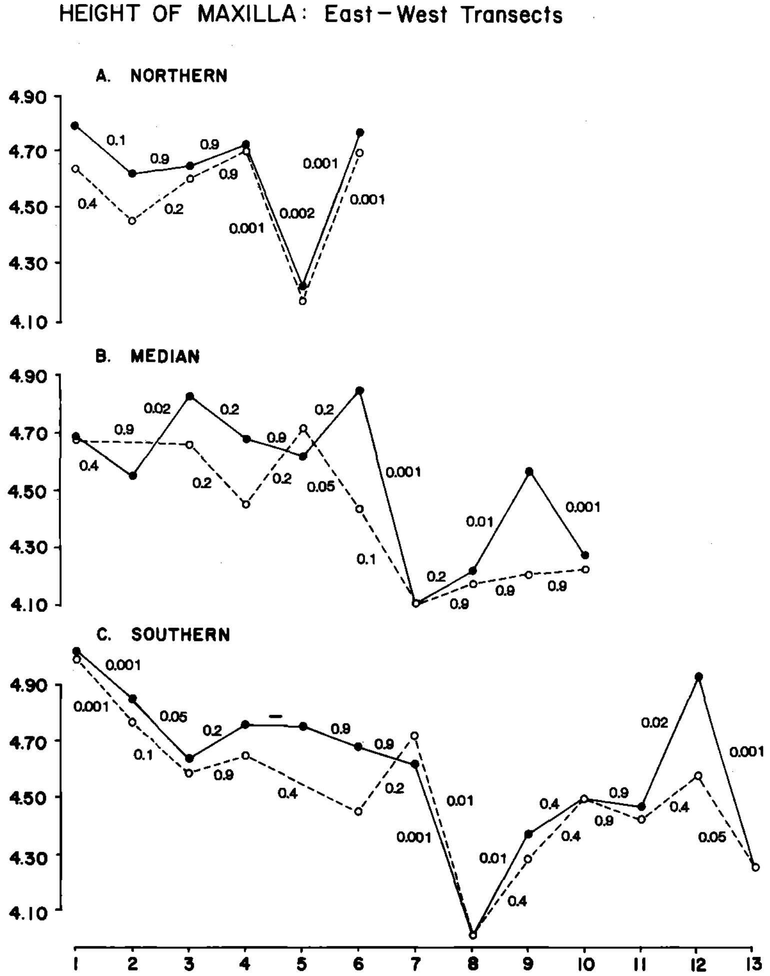

FIG. 19. East-west transects of mean heights of maxillae. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

east to west. Maxima are in the western Short-grass Prairie for males, and eastern Short-grass Prairie for females. Minima are in the Rocky Mountain Forest for both sexes.

The southernmost transect (Figs. 4, 19, transect C) begins with significant decreases in maxilla height in both sexes from the Atlantic Coastal Marsh (south) to the Southeastern Mixed Forest, and again from that section to the Mixed Mesophytic Forest. Following a slight increase in both sexes to the Oak-Hickory Forest there is a progressive decrease in both sexes to the middle Rockies, significantly from the Short-grass Prairie to the Rockies. Males increase significantly to the Lahontan Saltbush-Greasewood of the western Great Basin, decrease slightly to the Sierran Forest, and increase significantly to the California Grassland;

then maxilla height in both sexes decreases significantly to the California Chaparral. Maxima are in the Atlantic Coastal Marshes, and minima in the Middle Rocky Mountains for both sexes.

Discussion.—Lower maxillae, contributing to thinner bills, are found on the Pacific Coast, particularly in the Pacific Rain Forest areas, the Rocky Mountain forests, southwestern deserts, and Mexican mountains and shrub steppes. Higher maxillae, indicating thicker bills, are found west of the Rocky Mountains in grassland, northern desert scrub, and Aleutian tundra populations, and east of the Rockies in grassland and forest populations, particularly in the Southeastern Mixed Forest and its included Atlantic Coastal Marshes. Except for the high maxillae in the birds of the Aleutian tundra, there is little indication of a north to south trend. A strong east to west trend is evident with higher maxillae in eastern forest and grassland populations and lower maxillae in western mountain and rain forest populations; exceptions to the east-west decline in height are populations in western grasslands and northern deserts, in which birds have higher maxillae than other western birds.

Males tend to have higher maxillae than females, and male maxillae are higher in all instances in which differences are significant.

Ratio of Height of Maxilla to Culmen Length

Sex differences.—In 22 (45%) of the 49 samples males have a higher ratio of maxilla height to total culmen length than females, and in 25 (51%) females have a higher ratio. In two samples ratios are equal. None of the differences in which male ratios are greater is significant, but in two cases (15-M2620, California Chaparral; 9-M3111, Grasslands of the Northern Rocky Mountains) female ratios are significantly greater.

Differences by Life Area (Fig. 1, Table 7).—Ratios of height of maxilla to length of culmen arranged in order of decreasing magnitude for males are:

		♂ N	Mean	♀ N	Mean
8	Eastern Deciduous Forest	112	.352	47	.351
3	Boreal	20	.347	6	.349
10	Oak-Savannah	2	.345	0	.0
5	Aspen Parkland	6	.340	3	.330
4	Northern Hardwood-Conifer	111	.339	39	.342
9	Grasslands	49	.318	31	.321
11	Northern Desert Scrub	94	.311	41	.311
14	Piñon-Juniper-Oak	50	.310	29	.312
6	Montane Woodland-Brush	26	.307	16	.306
15	Chaparral-Oak Woodland	32	.304	12	.316
12	Southern Desert Scrub	25	.300	13	.299
17	Mexican Pine-Oak	19	.292	3	.275
7	Pacific Rain Forest	112	.285	70	.282
13	Mesquite-Grassland	14	.283	6	.288
1	Arctic-Alpine (Aleutian)	57	.261	31	.262

Male and female ratios are highly correlated ($r = 0.97$, $P < 0.001$).

Adjacent Life Areas whose ratios of maxilla height to culmen length differ significantly are: Boreal > Arctic-Alpine (Aleutians) (♂, ♀); Eastern Deciduous Forest > Northern Hardwood Conifer (♂); Eastern Deciduous Forest > Grasslands (♂, ♀); Grasslands > Northern Desert Scrub (♀); Montane Woodland-Brush > Pacific Rain Forest (♂, ♀); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Southern Desert Scrub > Mesquite-Grassland (♂); Grasslands > Mesquite-Grassland (♂, ♀); Grasslands > Chaparral-Oak Woodland (♂); Grasslands > Montane Woodland-Brush (♀); Grasslands > Northern Desert Scrub (♂).

Means of ratios of height of maxilla to culmen length representing Life Areas occurring within different Ecoregion Sections differ significantly from each other as follows:

Pacific Rain Forest

7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2416 Alaska Pacific Forest (♂, ♀)
7-M2415 Cascades Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂)

Eastern Deciduous Forest

8A-2320A Atlantic Coastal Marsh (south) > 8-2320 Southeastern Mixed Forest (♀)
8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♀)

Grasslands

9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂)
9-3111 Short-grass Prairie (west) > 9-M2620 California Chaparral (grassland) (♂)
9-3111 Short-grass Prairie (west) > 9-M3111 Oregon Montane (grassland) (♂)
9-3112 Short-grass Prairie (east) > 9-3120 Palouse Grassland (♂)
9-2610 California Grassland (valley) > 9-M3111 Oregon Montane (grassland) (♀)
9-3111 Short-grass Prairie (west) > 9-3120 Palouse Grassland (♀)

Differences by Ecoregion Province (Fig. 2, Table 8).—Means of ratios of height of maxilla to total culmen length arranged in order of decreasing values for males are:

		♂ N	Mean	♀ N	Mean
2320	Southeastern Mixed Forest	83	.361	45	.354
3110	Short-grass Prairie	7	.350	11	.337
2210	Eastern Deciduous Forest	146	.348	49	.348
2510	Prairie-Parkland	2	.345	0	—
2610	California Grassland	3	.345	4	.334
3120	Boreal Forest	20	.334	6	.349
2530	Tall-grass Prairie	13	.342	6	.333
2110	Laurentian Forest	45	.338	21	.349
M2610	Sierran Forest	8	.318	5	.317
3130	Intermountain Sagebrush	104	.314	56	.316
3120	Palouse Grassland	21	.307	9	.299

M2620	California Chaparral	59	.306	25	.307
M3120	Upper Gila Mountains Forest	8	.303	5	.302
A3140	Wyoming Basin	9	.303	1	.305
M3110	Rocky Mountains Forest	46	.301	19	.305
P3130	Colorado Plateau	0	—	2	.294
8220	American Desert	25	.300	13	.299
M2110	Columbia Forest	12	.298	4	.291
2410	Willamette-Puget Forest	15	.293	10	.286
M2410	Pacific Forest	89	.283	60	.282
3140	Mexican Shrub Steppe	13	.283	6	.288
17	Mexican Pine-Oak	15	.283	3	.275
M1310	Alaska Range (Aleutian)	57	.261	37	.262

Male and female ratios are highly correlated ($r = 0.97$, $P < 0.001$).

Adjacent Ecoregion Provinces whose ratios of maxilla height to culmen length differ significantly are: Yukon Forest (Boreal) > Alaska Range (Aleutians) (♂, ♀); Eastern Deciduous Forest > Laurentian Forest (♂); Southeastern Mixed Forest > Eastern Deciduous Forest (♂); Pacific Forest > Alaska Range (Aleutians) (♂, ♀); California Grassland > Sierran Forest (♂); California Grassland > California Chaparral (♂, ♀); Yukon Forest (Boreal) > Columbia Forest (♀); Upper Gila Mountains Forest > Mexican Highlands Shrub Steppe (♂); Intermountain Sagebrush > Rocky Mountains Forest (♂, ♀); Intermountain Sagebrush > American Desert (♂, ♀); Short-grass Prairie > Wyoming Basin (♂); Sierran Forest > Pacific Forest (♂, ♀); Sierran Forest > American Desert (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2, Table 9).—Significant differences between mean ratios of maxilla height to culmen length in adjoining Ecoregion/Life Area units are found in: 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2416 Alaska Pacific (♂, ♀); 9-2610 California Grassland (valley) > 6-M2610 Sierran Forest (♂); 9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (chaparral) (♂); 9-3111 Short-grass Prairie (west) > 6-M3112 N. Rockies (montane) (♂); 9-3111 Short-grass Prairie (west) > 11-M3112 N. Rockies (sagebrush) (♂); 7-M2415 Cascades Forest > 6-M2111 Columbia Forest (montane) (♂, ♀); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂); 9-3112 Short-grass Prairie (east) > 5-2530E Aspen Parklands (east) (♂); 11-3131 Sagebrush-Wheatgrass > 6-M3112 Middle Rockies (montane) (♂); 8-2214 Appalachian Oak (deciduous) > 8-2320 Southeastern Mixed Forest (♀).

Within Ecoregion Sections, mean ratios of different Life Belts (Life Areas) are different in the following cases: 8-2214 Appalachian Oak (deciduous) > 4-2214 Appalachian Oak (Northern Hardwoods) (♂, ♀); 8A-2320A Southeastern Mixed Forest (Atlantic Coastal Marshes-S) > 8-2320 Southeastern Mixed Forest (forest) (♀).

Relative ratios of height of maxilla to culmen length of males in different Ecoregion Sections are shown in Figure 20.

North-south transects. A north-south transect along the Pacific Coast (Figs. 3,

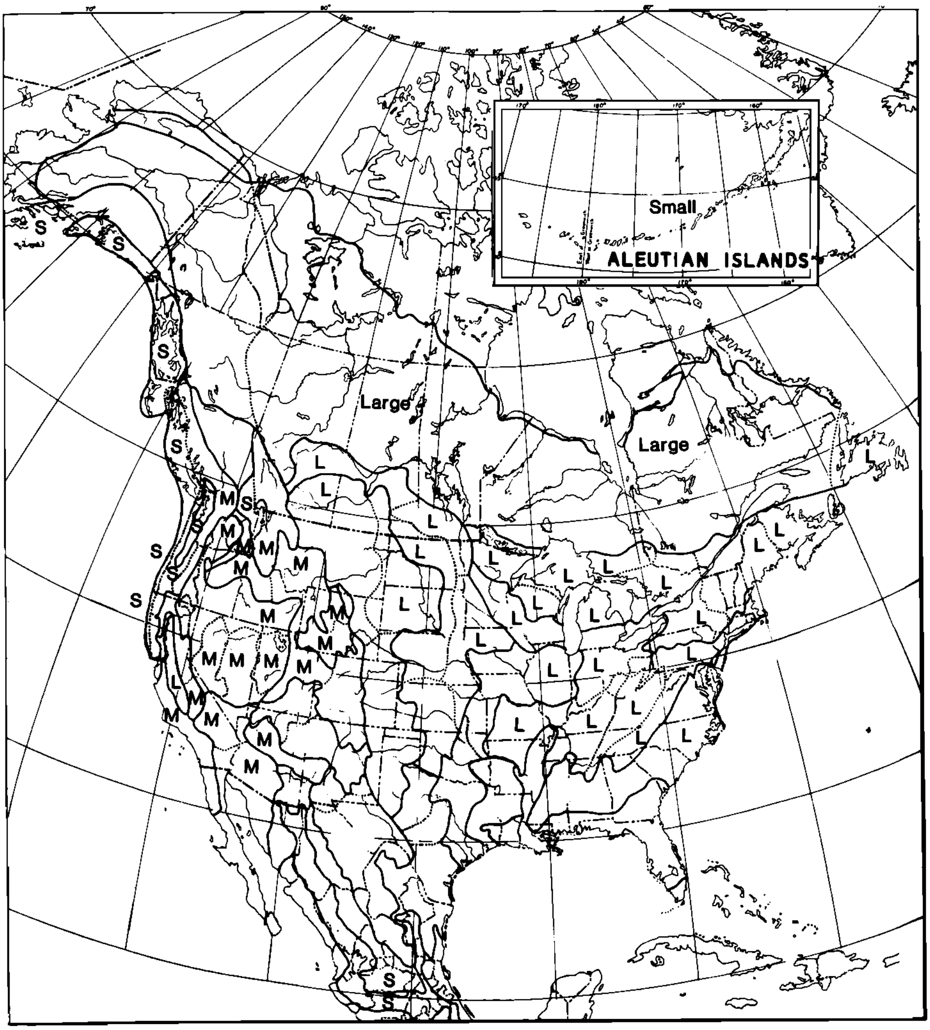

FIG. 20. Relative ratios of height of maxilla to total culmen of males in different Ecoregion Sections. L = larger; S = smaller; M = middle one-third of means.

21, transect A) shows marked and continuous increases in ratios from the Aleutians, to maxima in both sexes in the California Chaparral, with the increase in both sexes significant from the Alaska Pacific to the Sitka Spruce-Cedar-Hemlock. Females show a significant increase from the Redwood Forest to the California Chaparral.

In the Alaska-Cascades-Sierra Nevada transect (Figs. 3, 21, transect B) increases occur from the Alaska Pacific to the California Grassland, followed by a decrease, significant in males, to the California Chaparral. Significant changes also occur from Columbia Montane to Cascades, and from the Sierras to California Grassland in males. In both sexes maxima are in the California Grassland, and minima in Alaska Pacific.

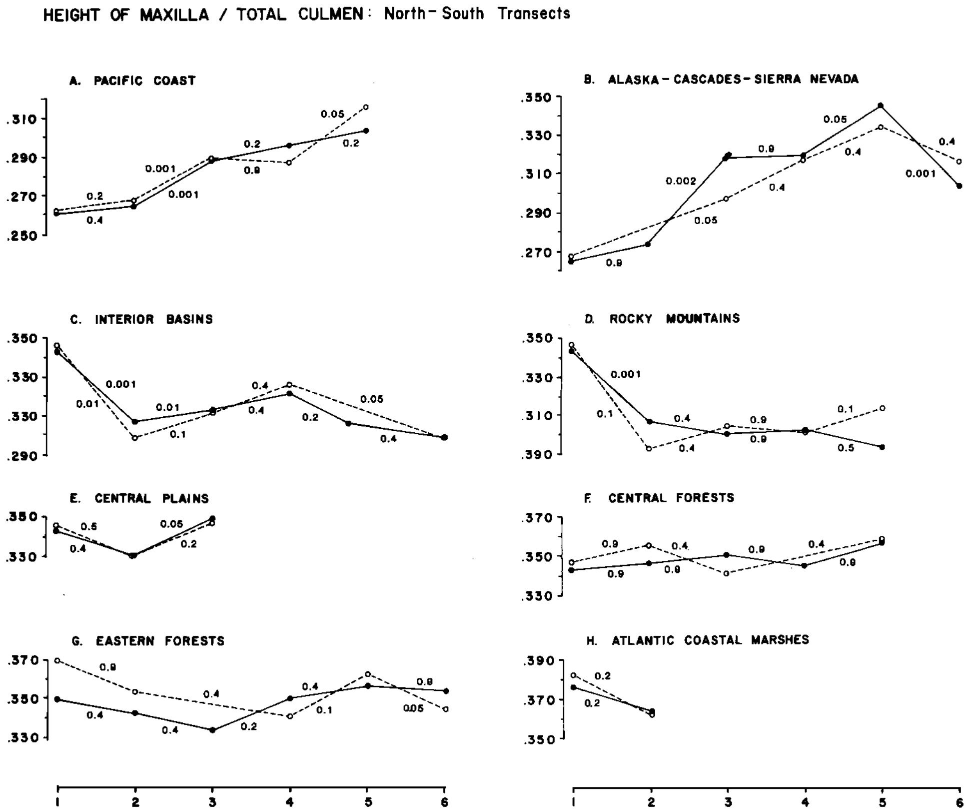

FIG. 21. North-south transects of mean height of maxilla to culmen ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

Along the interior basins transect (Figs. 3, 21, transect C), after significant decreases from the Central Boreal to the Palouse Grassland in both sexes, there is a slight increase to the Lahontan Saltbush-Greasewood. Then ratios decrease, significantly in females, to the Sonoran Desert. Maxima in both sexes are in the Central Boreal, and minima in the Sonoran Desert.

Along the Rocky Mountains transect (Figs. 3, 21, transect D), decreases and increases occur irregularly, and differently in males and females, from the Central Boreal to the Mexican Highlands Shrub Steppe. The only significant change is a decrease in males from the Central Boreal to the moist Columbia Forest. Maxima in both sexes are in the Central Boreal, and minima in the Mexican Highlands Shrub Steppe for males, and moist Columbia Forest for females.

The central plains transect (Figs. 3, 21, transect E) shows no overall trend, but a significant increase does occur in males from the Aspen Parklands to the Short-grass Prairie. Maxima for both sexes are in the Short-grass Prairie, and minima in the Aspen Parklands.

In the central forests (Figs. 3, 21, transect F), slight increases and decreases in ratios occur irregularly with an increasing trend. Maxima are in the Oak-Hickory

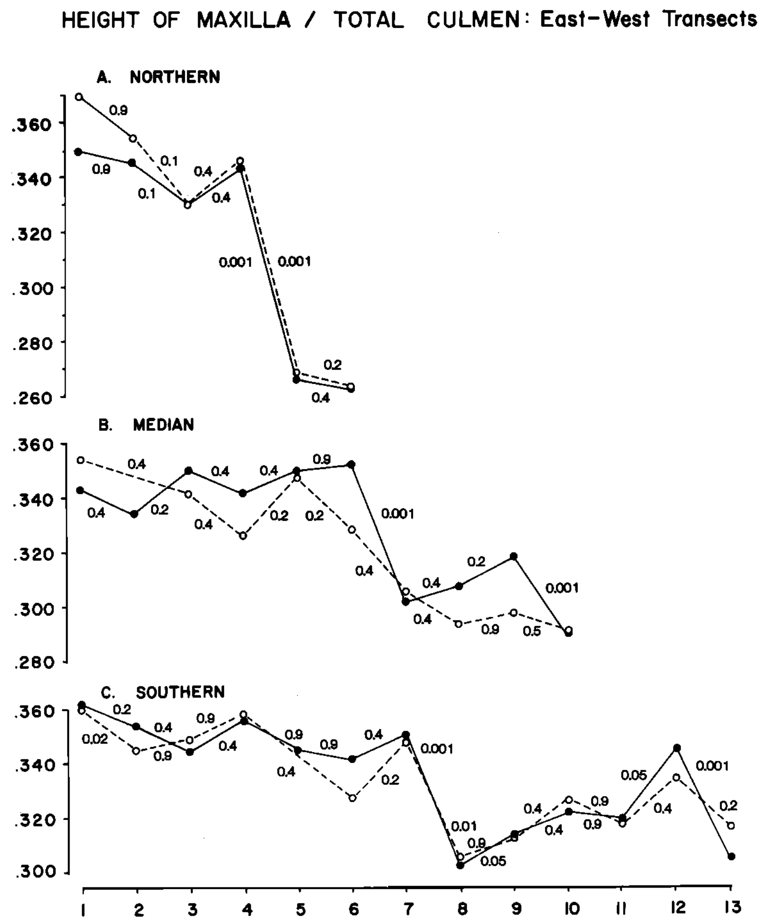

FIG. 22. East-west transects of mean height of maxilla to culmen ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

Forest for both sexes, and minima in the Central Boreal for males, and Northern Hardwoods (Wisconsin) for females.

In the Eastern forests (Figs. 3, 21, transect G), there is no pronounced trend in either sex, but the maximum for males is in the Appalachian Oak (deciduous), and for females in the Newfoundland Boreal. Minimum for males is in the Northern Hardwoods-Spruce of New England, and for females in the Northern Hardwoods of New York.

In the Atlantic Coastal Marshes (Figs. 3, 21, transect H), ratios decrease slightly in both sexes from the northern to the southern marshes.

East-west transect. In the northern east to west transect (Figs. 4, 22, transect A), the ratios of maxilla height to culmen length in both sexes generally decrease from maxima in the Newfoundland Boreal to minima in the Aleutian Islands, broken only by insignificant increases from the Aspen Parklands to the Central

Boreal. Significant decreases occur in both sexes from the Central Boreal to the Alaska Pacific.

Along the median transect (Figs. 4, 22, transect B), progression is irregular, sometimes in opposite directions in the two sexes, but with an overall decreasing trend, from the Northern Hardwoods-Spruce (Maritime) to the Sitka Spruce-Cedar-Hemlock of the Pacific Coast. Decreases in male ratios from the Short-grass Prairie to the Rocky Mountains Forest, and from the Silver Fir-Douglas-fir of the Cascades to the Stika Spruce-Cedar-Hemlock on the coast are significant. Maxima are in the Short-grass Prairie (west) for males, and the northern Hardwoods-Spruce (Maritime) for females. Minima are in the Sitka Spruce-Cedar-Hemlock for both sexes.

In the southern east-west transect (Figs. 4, 22, transect C), ratios fluctuate, but gradually decrease in both sexes from the Atlantic to the Pacific coast, with a significant decrease in both sexes from the Short-grass Prairie to the middle Rocky Mountains Forest, a significant increase in males from the Rockies to the Sagebrush-Wheatgrass of the Great Basin and from the Sierran Forest to the California Grassland, and a signficant decrease in males to the California Chaparral. Maxima are in the Atlantic Coastal Marsh, and minima in the Douglas-fir of the Middle Rockies for both sexes.

Discussion.—Females tend to have a higher ratio of height of maxilla to culmen length (thicker bills) than males, particularly on the Pacific Coast and in the Rocky Mountains. Both sexes tend to have higher ratios in eastern coastal marshes and eastern forests, western woodlands, and all grasslands, and lower ratios (thinner bills) in Aleutian tundra, Pacific Rain Forests, Rocky Mountains, southern deserts, and Mexican areas. Birds from northern deserts and Sierran Forest are intermediate with respect to these ratios.

Width of Maxilla

Sex differences.—Of the total 49 samples, males in 40 samples have wider maxillae, females in 8 samples have wider maxillae, and in one sample widths are equal in males and females. Significant differences occur in only four cases, 1-M1310, 3-1320A, 8-2214 and 15-M2620, in all of which male maxillae are wider.

Differences by Life Area (Fig. 1; Tables 1, 2).—Mean maxilla widths arranged in decreasing order for males are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutian)	59	6.78	38	6.53
10	Oak-Savannah	2	6.70	0	—
5	Aspen Parkland	5	6.62	3	6.47
8	Eastern Deciduous Forest	117	6.60	48	6.44
4	Northern Hardwood Conifer	114	6.54	41	6.45
3	Boreal	21	6.48	6	6.07
9	Grassland	51	6.27	31	6.32
6	Montane Woodland-Brush	26	6.23	16	6.21
14	Piñon-Juniper-Oak	51	6.23	30	6.15
11	Northern Desert Scrub	96	6.21	42	6.15

7	Pacific Rain Forest	114	6.15	70	6.10
15	Chaparral-Oak Woodland	32	6.13	12	6.14
17	Mexican Pine-Oak	19	6.08	3	5.93
13	Mesquite-Grassland	14	5.88	6	5.90
12	Southern Desert Scrub	25	5.86	13	5.81

Male and female mean maxilla widths are highly correlated ($r = 0.90$, $P < 0.001$).

The order of decreasing maxilla widths is similar to the decreasing order found in height of maxilla.

Significant differences between maxilla widths in adjoining Life Areas are: Northern Hardwood-Conifer > Boreal (♀); Eastern Deciduous Forest > Grasslands (♂); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Aspen Parkland > Grasslands (♂); Grasslands > Mesquite-Grassland (♂, ♀).

Mean maxilla widths representing Life Areas within different Ecoregion Sections are:

Pacific Rain Forest

7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀)
7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂, ♀)

Eastern Deciduous Forest

8A-2320A Atlantic Coastal Marsh (south) > 8A-2214A Atlantic Coastal Marsh (north) (♂, ♀)

Grasslands

9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂)
9-3111 Short-grass Prairie (west) > 9-3120 Palouse Grassland (♂)
9-3112 Short-grass Prairie (east) > 9-3120 Palouse Grassland (♂)
9-2532 Tall-grass Prairie (west) > 9-3120 Palouse Grassland (♂)

Northern Desert Scrub

11-3131 Sagebrush-Wheatgrass > 11-M3112 N. Rockies (sagebrush) (♂)

Piñon-Juniper-Oak

14-3131 Sagebrush-Wheatgrass (Piñon) > 14-3132 Lahontan Saltbush-Greasewood (Piñon) (♂)
14-3131 Sagebrush-Wheatgrass (Piñon) > 14-M3120 Upper Gila Mts. Forest (Piñon) (♀)

Differences by Ecoregion Province (Fig. 2, Tables 3, 4).—Mean maxilla widths in order of decreasing male values are:

		♂ N	Mean	♀ N	Mean
2320	Southeastern Mixed Forest	87	6.82	46	6.77
M1310	Alaska Range (Aleutian)	59	6.78	38	6.53
2510	Prairie Parkland	2	6.70	0	—
2610	California Grassland	3	6.70	4	6.15
3110	Short-grass Prairie	8	6.60	11	6.39
2210	Eastern Deciduous Forest	152	6.57	52	6.43
M2610	Sierran Forest	8	6.54	5	6.22
2530	Tall-grass Prairie	13	6.53	6	6.52
2110	Laurentian Forest	47	6.51	21	6.40
1320	Boreal Forest	21	6.48	6	6.07
3130	Intermountain Sagebrush	107	6.29	58	6.23
2410	Willamette-Puget Forest	16	6.28	10	6.20
M2410	Pacific Forest	89	6.17	60	6.09
M3110	Rocky Mountains Forest	47	6.12	19	6.05
M2620	California Chaparral	59	6.09	25	5.89
3120	Palouse Grassland	22	6.07	9	6.14
17	Mexican Pine-Oak	15	6.07	3	5.93
P3130	Colorado Plateau	0	—	2	5.90
M2110	Columbia Forest	13	6.06	4	6.05
A3140	Wyoming Basin	9	5.96	1	6.30
M3120	Upper Gila Mountains Forest	8	5.89	5	5.78
3140	Mexican Shrub Steppe	14	5.88	6	5.90
3220	American Desert	25	5.86	13	5.81

Male and female mean maxilla widths are highly correlated ($r = 0.81$, $P < 0.001$).

Significant differences between maxilla widths of adjoining Ecoregion Provinces are: Laurentian Forest > Boreal Forest (♀); Southeastern Mixed Forest > Deciduous Forest (♂, ♀); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); California Grassland > California Chaparral (♂); Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂); Intermountain Sagebrush > Rocky Mountains Forest (♂); Intermountain Sagebrush > American Desert (♂, ♀); Short-grass Prairie > Wyoming Basin (♂); Sierran Forest > Pacific Forest (♂); Sierran Forest > American Desert (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 5, 6).—Significant differences in mean maxilla widths between adjoining Ecoregion Section/Life Area units are: 3-1320B Central Boreal > 6-M2111 Columbia Forest (montane) (♂); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀); 9-2610 California Grassland (valley) > 9-M2620 California Chaparral (grassland) (♂); 14-M3111 Sagebrush-Wheatgrass (Piñon) > 6-M3112 N. Rockies (montane) (♂); 11-3131 Sagebrush-Wheatgrass > 11-M3112 N. Rockies (sagebrush) (♂); 14-3131 Sagebrush-Wheatgrass (Piñon) > 14-3132 Lahontan Saltbush-Greasewood (Piñon) (♂); 7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂, ♀); 1-M1310 Alaska Range (Aleutians) > 7-M2416 Alaska Pacific Forest (♂, ♀); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (♂, ♀); 11-3131

TABLE 1

MEAN LINEAR MEASUREMENTS OF MALE SONG SPARROWS BY LIFE AREA[1]

Life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
1. Arctic-Alpine (Aleutian)	59	81.43 (2.59)	58	9.92 (1.44)	58	18.29 (0.72)	59	4.76 (0.29)	59	6.78 (0.49)	51	78.96 (3.82)	59	27.49 (1.00)	59	19.07 (0.96)
3. Boreal (Open and closed)	22	66.30 (2.12)	22	10.44 (1.46)	21	13.70 (0.37)	21	4.70 (0.26)	21	6.48 (0.20)	22	66.44 (2.98)	22	21.67 (0.65)	22	15.09 (0.65)
4. Northern Hardwood-Conifer	112	65.96 (1.70)	111	9.26 (1.38)	111	13.73 (0.53)	114	4.68 (0.21)	114	6.54 (0.25)	109	66.19 (2.81)	116	21.30 (0.66)	115	15.05 (0.57)
5. Aspen Parkland	6	67.32 (0.52)	6	10.52 (1.19)	6	13.65 (0.89)	6	4.68 (0.10)	5	6.62 (0.18)	6	69.20 (2.09)	6	21.25 (0.60)	6	14.72 (0.98)
6. Montane Woodland-Brush	26	67.53 (2.27)	26	9.51 (1.19)	26	13.98 (0.56)	26	4.29 (0.33)	26	6.23 (0.37)	26	68.42 (3.54)	26	22.45 (0.59)	26	15.39 (0.54)
7. Pacific Rain Forest	107	67.62 (3.31)	104	9.62 (7.81)	113	15.02 (0.99)	113	4.23 (0.34)	114	6.15 (0.44)	110	65.63 (3.62)	115	23.49 (2.51)	114	16.39 (0.91)
8. Eastern Deciduous Forest	115	65.45 (1.65)	114	9.10 (1.33)	114	13.55 (1.39)	117	4.81 (0.26)	117	6.60 (0.30)	113	65.73 (2.49)	117	21.52 (0.66)	118	15.00 (0.60)
9. Grasslands	49	67.72 (1.82)	50	9.82 (0.98)	50	13.90 (0.61)	50	4.40 (0.30)	51	6.27 (0.33)	47	67.89 (2.31)	51	22.20 (0.78)	51	15.11 (0.64)
10. Oak-Savannah	2	67.90 (0.57)	2	9.50 (1.84)	2	13.80 (1.13)	2	4.75 (0.21)	2	6.70 (0.14)	2	68.35 (1.48)	2	21.50 (1.13)	2	14.75 (0.49)
11. Northern Desert Scrub	96	68.56 (2.01)	97	9.08 (1.17)	94	13.87 (0.60)	98	4.31 (0.24)	96	6.21 (0.36)	96	69.34 (3.00)	93	22.33 (0.60)	96	15.19 (0.56)
12. Southern Desert Scrub	25	65.97 (1.55)	26	8.82 (1.21)	25	13.84 (0.43)	25	4.15 (0.14)	25	5.86 (0.26)	25	68.78 (2.00)	25	21.87 (0.73)	25	14.34 (0.66)
13. Mesquite-Grassland	14	66.06 (1.78)	14	7.20 (0.94)	14	14.73 (0.51)	14	4.16 (0.13)	14	5.88 (0.27)	12	63.18 (4.05)	13	22.96 (0.95)	14	15.46 (0.63)
14. Piñon-Juniper-Oak	50	68.19 (2.00)	49	8.45 (1.55)	51	13.92 (0.51)	53	4.30 (0.22)	51	6.23 (0.38)	50	68.94 (2.58)	50	22.31 (0.58)	51	15.05 (0.65)
15. Chaparral-Oak Woodland	31	62.47 (1.80)	30	7.35 (0.90)	32	13.99 (0.61)	32	4.24 (0.26)	32	6.13 (0.38)	31	62.07 (2.38)	31	21.92 (0.64)	32	15.03 (0.60)
17. Mexican Pine and Pine-Oak	18	67.79 (2.09)	18	8.32 (1.44)	18	14.47 (0.71)	18	4.19 (0.16)	19	6.08 (0.21)	18	63.41 (3.23)	19	23.78 (1.40)	18	15.85 (0.85)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 2

MEAN LINEAR MEASUREMENTS OF FEMALE SONG SPARROWS BY LIFE AREA[1]

Life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
1. Arctic-Alpine (Aleutian)	38	78.27 (2.34)	37	10.10 (1.22)	37	17.88 (0.80)	38	4.69 (0.31)	38	6.53 (0.46)	37	73.77 (12.72)	38	27.03 (0.98)	38	18.46 (0.97)
3. Boreal (Open and closed)	6	63.85 (2.02)	6	9.92 (0.98)	6	13.18 (0.90)	6	4.57 (0.28)	6	6.07 (0.38)	6	63.63 (4.10)	6	21.15 (0.77)	6	14.95 (0.27)
4. Northern Hardwood-Conifer	40	69.92 (2.17)	40	9.04 (1.64)	40	14.74 (7.73)	41	4.66 (0.19)	41	6.45 (0.25)	35	62.99 (2.86)	41	21.03 (0.72)	41	14.75 (0.62)
5. Aspen Parkland	3	64.67 (0.45)	3	11.03 (1.47)	3	13.93 (0.45)	3	4.60 (0.10)	3	6.47 (0.15)	3	63.40 (2.59)	3	21.43 (1.20)	3	15.95 (0.64)
6. Montane Woodland-Brush	16	63.85 (1.86)	15	8.66 (1.21)	16	13.86 (0.48)	16	4.24 (0.27)	16	6.21 (0.32)	16	64.62 (2.54)	16	21.71 (0.56)	16	14.98 (0.55)
7. Pacific Rain Forest	71	63.83 (8.48)	71	8.51 (1.52)	70	14.92 (0.84)	70	4.19 (0.21)	70	6.10 (0.34)	71	61.90 (3.54)	72	23.11 (0.96)	71	15.95 (0.76)
8. Eastern Deciduous Forest	46	62.36 (2.07)	46	8.91 (1.55)	47	13.48 (0.60)	48	4.71 (0.23)	48	6.44 (0.37)	42	62.43 (2.83)	48	20.68 (3.11)	48	14.85 (0.67)
9. Grasslands	31	64.18 (1.68)	31	9.06 (1.38)	31	13.82 (0.57)	31	4.43 (0.24)	31	6.32 (0.32)	30	63.98 (2.42)	31	21.92 (1.06)	31	14.94 (0.51)
10. Oak-Savannah	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
11. Northern Desert Scrub	40	64.64 (1.78)	41	8.43 (1.25)	42	13.68 (0.43)	42	4.26 (0.25)	42	6.15 (0.40)	39	65.56 (2.72)	42	21.75 (0.53)	42	14.81 (0.62)
12. Southern Desert Scrub	12	62.32 (1.37)	12	8.10 (1.37)	13	13.49 (0.47)	13	4.05 (0.15)	13	5.81 (0.27)	12	64.38 (2.56)	13	20.92 (0.51)	13	14.11 (0.46)
13. Mesquite Grassland	6	61.95 (0.82)	6	6.42 (0.90)	6	14.32 (0.76)	6	4.10 (0.09)	6	5.90 (0.27)	6	59.10 (2.53)	6	22.48 (1.05)	6	14.82 (0.57)
14. Piñon-Juniper-Oak	30	64.14 (1.73)	30	7.79 (1.41)	29	13.82 (0.43)	30	4.30 (0.24)	30	6.15 (0.35)	29	64.69 (2.65)	30	21.88 (0.49)	30	14.70 (0.42)
15. Chaparral-Oak Woodland	12	58.55 (2.05)	12	6.42 (1.26)	12	13.62 (0.57)	12	4.25 (0.27)	12	6.14 (0.43)	11	57.41 (3.14)	12	21.30 (0.86)	12	14.26 (0.53)
17. Mexican Pine and Pine-Oak	3	63.87 (1.55)	3	8.43 (1.19)	3	14.43 (0.74)	3	3.97 (0.32)	3	5.93 (0.32)	3	59.23 (2.75)	3	22.13 (0.65)	3	15.27 (0.72)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 3

MEAN LINEAR MEASUREMENTS OF MALE SONG SPARROWS BY ECOREGION PROVINCE[1]

	Ecoregion province	Wing		Wing-tip		Culmen		Ht. max.		Width max.		Tail		Tarsus		Toe	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
M1310	Alaska Range (Aleutians)	59	81.43 (2.59)	58	9.92 (1.44)	58	18.29 (0.72)	59	4.76 (0.29)	59	6.78 (0.49)	51	78.96 (3.82)	59	27.49 (1.00)	59	19.07 (0.96)
1320	Yukon Forest (Boreal)	22	66.30 (2.12)	22	10.44 (1.46)	21	13.70 (0.37)	21	4.70 (0.26)	21	6.48 (0.20)	22	66.44 (2.98)	22	21.67 (0.65)	22	15.09 (0.65)
2110	Laurentian Mixed Forest	47	66.39 (1.38)	47	9.89 (1.27)	46	13.78 (0.59)	47	4.71 (0.22)	47	6.51 (0.25)	47	65.13 (9.09)	48	21.43 (0.72)	47	15.02 (0.56)
M2110	Columbia Forest	13	66.23 (1.79)	11	8.93 (1.51)	13	13.93 (0.56)	13	4.15 (0.30)	13	6.06 (0.30)	12	65.31 (3.69)	13	22.34 (0.37)	13	15.32 (0.51)
2210	Eastern Deciduous Forest	149	65.73 (1.75)	151	9.22 (1.39)	148	13.66 (0.51)	152	4.74 (0.24)	152	6.57 (0.28)	141	65.95 (2.71)	148	21.36 (0.62)	152	15.05 (0.57)
2320	Southeastern Mixed Forest	84	65.29 (1.71)	85	8.94 (1.33)	84	13.93 (0.64)	87	4.97 (0.26)	87	6.82 (0.34)	77	65.67 (2.30)	87	21.83 (0.72)	88	15.06 (0.63)
2410	Willamette-Puget Forest	16	66.69 (1.54)	16	8.23 (0.67)	16	14.79 (0.49)	15	4.33 (0.14)	16	6.28 (0.25)	16	64.81 (2.94)	16	23.64 (0.71)	16	16.73 (0.93)
M2410	Pacific Forest	93	67.91 (3.70)	93	9.09 (1.54)	92	15.15 (0.99)	94	4.27 (0.24)	89	6.17 (0.36)	90	65.69 (3.64)	93	23.76 (1.28)	93	16.40 (0.87)
2510	Prairie Parkland	2	67.90 (0.57)	2	9.50 (1.84)	2	13.80 (1.13)	2	4.75 (0.21)	2	6.70 (0.14)	2	68.35 (1.48)	2	21.50 (1.13)	2	14.75 (0.49)
2530	Tall-grass Prairie	13	67.37 (1.07)	13	10.35 (1.05)	13	13.72 (0.48)	13	4.68 (0.13)	13	6.53 (0.20)	12	68.18 (2.46)	13	21.46 (0.54)	13	14.92 (0.79)
2610	California Grassland	3	67.10 (0.40)	3	9.80 (0.72)	3	14.30 (0.26)	3	4.93 (0.06)	3	6.70 (0.10)	3	66.57 (1.42)	3	21.93 (0.47)	3	15.00 (0.74)

TABLE 3

CONTINUED

	Ecoregion province	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
M2610	Sierra Forest	8	66.05 (1.46)	8	9.23 (1.67)	8	13.99 (0.45)	8	4.45 (0.23)	8	6.54 (0.16)	8	66.75 (1.89)	8	22.70 (0.48)	8	15.28 (0.48)
M2620	California Chaparral	57	61.37 (2.51)	56	7.07 (0.98)	57	13.83 (0.60)	59	4.23 (0.23)	59	6.09 (0.40)	56	60.76 (3.16)	57	21.61 (0.71)	59	14.99 (0.65)
3110	Great Plains Short-grass Prairie	7	67.71 (1.77)	8	10.28 (0.76)	8	13.45 (0.49)	7	4.69 (0.18)	8	6.60 (0.27)	7	68.34 (1.76)	8	21.25 (0.39)	8	14.93 (0.57)
M3110	Rocky Mountain Forest	47	68.62 (1.91)	47	9.46 (1.06)	46	13.81 (0.57)	47	4.16 (0.18)	47	6.12 (0.26)	46	70.30 (2.81)	47	22.18 (0.59)	47	15.10 (0.65)
3120	Palouse Grassland	21	67.08 (1.78)	21	9.51 (0.87)	21	13.99 (0.67)	22	4.27 (0.17)	22	6.07 (0.26)	20	66.97 (2.02)	22	22.69 (0.64)	22	15.23 (0.66)
M3120	Upper Gila Mts. Forest	6	65.42 (1.48)	6	7.02 (0.95)	8	13.45 (0.42)	8	4.08 (0.10)	8	5.89 (0.24)	6	69.45 (1.84)	8	22.19 (0.83)	8	14.53 (0.46)
3130	Intermountain Sagebrush	108	68.55 (1.98)	107	8.99 (1.23)	104	13.99 (0.56)	107	4.38 (0.22)	107	6.29 (0.38)	108	68.90 (2.86)	106	22.40 (0.55)	108	15.20 (0.56)
P3130	Colorado Plateau	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
3140	Mexican Highlands Shrub Steppe	14	66.09 (1.78)	14	7.20 (0.94)	14	14.73 (0.51)	14	4.16 (0.13)	14	5.88 (0.27)	12	63.27 (4.05)	14	22.81 (1.08)	14	15.46 (0.63)
A3140	Wyoming Basin	9	69.43 (1.66)	9	9.21 (0.99)	9	13.46 (0.41)	9	4.08 (0.15)	9	5.96 (0.30)	9	69.91 (2.92)	9	22.09 (0.81)	9	14.94 (0.44)
3220	American Desert	25	65.97 (1.55)	25	8.84 (1.23)	25	13.84 (0.43)	25	4.15 (0.14)	25	5.86 (0.26)	25	68.78 (2.00)	25	21.87 (0.73)	25	14.34 (0.66)
17	Mexican Pine-Oak	15	68.25 (1.87)	15	8.75 (0.95)	15	14.79 (0.40)	15	4.19 (0.17)	15	6.07 (0.22)	15	63.27 (3.52)	15	24.38 (0.80)	15	16.15 (0.72)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 4
Mean Linear Measurements of Female Song Sparrows by Ecoregion Province[1]

	Ecoregion province	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
M1310	Alaska Range (Aleutians)	38	78.27 (2.34)	37	10.10 (1.22)	37	17.88 (0.80)	38	4.69 (0.31)	38	6.53 (0.46)	37	73.77 (12.72)	38	27.03 (0.98)	38	18.46 (0.97)
1320	Yukon Forest (Boreal)	6	63.85 (2.02)	6	9.92 (0.98)	6	13.18 (0.90)	6	4.57 (0.28)	6	6.07 (0.38)	6	63.63 (4.10)	6	21.15 (0.77)	6	14.95 (0.27)
2110	Laurentian Mixed Forest	20	62.90 (1.48)	20	9.85 (1.69)	21	13.39 (0.53)	21	4.66 (0.19)	21	6.40 (0.27)	18	62.69 (3.22)	21	21.19 (0.69)	21	14.66 (0.56)
M2110	Columbia Forest	5	63.46 (0.92)	5	8.26 (1.68)	4	14.18 (0.21)	4	4.13 (0.13)	4	6.05 (0.24)	5	63.22 (3.21)	5	22.54 (0.55)	5	15.06 (0.40)
2210	Eastern Deciduous Forest	52	62.33 (1.96)	51	8.57 (1.50)	48	13.40 (0.59)	52	4.68 (0.22)	52	6.43 (0.37)	48	62.92 (2.99)	52	21.01 (0.66)	52	14.92 (0.65)
2320	Southeastern Mixed Forest	44	62.13 (1.73)	45	8.78 (1.51)	45	13.85 (0.52)	46	4.90 (0.19)	46	6.77 (0.39)	40	61.97 (2.63)	46	21.37 (0.66)	46	14.54 (0.29)
2410	Willamette-Puget Forest	10	62.35 (1.12)	10	7.96 (0.98)	10	14.71 (0.49)	10	4.20 (0.16)	10	6.20 (0.44)	10	59.54 (3.05)	10	22.84 (0.53)	10	16.08 (0.45)
M2410	Pacific Forest	60	65.08 (3.96)	60	8.53 (1.64)	60	14.94 (0.91)	60	4.20 (0.22)	60	6.09 (0.32)	60	61.98 (3.80)	60	23.11 (1.08)	60	15.91 (0.90)
2510	Prairie Parkland	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
2530	Tall-grass Prairie	6	64.47 (0.99)	6	10.02 (1.94)	6	13.70 (0.56)	6	4.55 (0.10)	6	6.52 (0.29)	6	63.97 (2.11)	6	21.05 (0.96)	6	14.93 (0.64)
2610	California Grassland	4	61.80 (2.16)	4	8.18 (0.50)	4	13.93 (0.59)	4	4.40 (0.22)	4	6.15 (0.24)	4	62.65 (1.23)	4	21.40 (0.35)	4	14.65 (0.55)
M2610	Sierran Forest	5	62.90 (1.87)	5	8.12 (1.16)	5	13.94 (0.51)	5	4.42 (0.19)	5	6.22 (0.26)	5	62.76 (1.09)	5	21.70 (0.61)	5	14.94 (0.38)

TABLE 4

CONTINUED

Ecoregion province	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
M2620 California Chaparral	25	56.39 (2.65)	25	6.30 (1.19)	25	13.44 (0.67)	25	4.08 (0.30)	25	5.89 (0.49)	23	55.13 (3.32)	25	20.95 (0.76)	25	14.08 (0.56)
3110 Great Plains Short-grass Prairie	11	64.46 (1.44)	11	9.87 (1.43)	11	13.55 (0.52)	11	4.56 (0.25)	11	6.39 (0.28)	11	63.77 (2.43)	11	21.45 (0.72)	11	14.79 (0.27)
M3110 Rocky Mountain Forest	19	64.76 (1.66)	19	8.78 (1.44)	19	13.69 (0.47)	19	4.17 (0.21)	19	6.05 (0.35)	19	65.37 (2.36)	19	21.85 (0.57)	19	14.94 (0.48)
3120 Palouse Grassland	9	64.14 (0.96)	9	8.36 (1.11)	9	14.23 (0.49)	9	4.26 (0.13)	9	6.14 (0.33)	9	64.49 (2.18)	9	22.71 (1.16)	9	15.30 (0.58)
M3120 Upper Gila Mts. Forest	5	62.62 (1.49)	5	6.98 (0.60)	5	13.52 (0.40)	5	4.08 (0.08)	5	5.78 (0.08)	5	64.22 (2.42)	5	21.54 (0.50)	5	14.16 (0.19)
3130 Intermountain Sagebrush	56	64.56 (1.67)	57	8.35 (1.19)	56	13.80 (0.43)	58	4.32 (0.25)	58	6.23 (0.37)	54	65.12 (2.67)	58	21.86 (0.52)	58	14.76 (0.55)
P3130 Colorado Plateau	2	63.10 (0.85)	2	7.50 (0.57)	2	13.80 (0.00)	2	4.05 (0.21)	2	5.90 (0.28)	2	65.05 (0.49)	2	21.25 (0.21)	2	14.85 (0.07)
3140 Mexican Highlands Shrub Steppe	6	61.95 (0.82)	6	6.42 (0.90)	6	14.32 (0.76)	6	4.10 (0.09)	6	5.90 (0.27)	6	59.10 (2.53)	6	22.48 (1.05)	6	14.82 (0.57)
A3140 Wyoming Basin	1	68.50 —	1	10.10 —	1	13.10 —	1	4.00 —	1	6.30 —	1	71.60 —	1	21.00 —	1	15.10 —
3220 American Desert	12	62.32 (1.37)	12	8.10 (1.37)	13	13.49 (0.47)	13	4.03 (0.11)	13	5.81 (0.27)	12	64.38 (2.56)	13	20.92 (0.51)	13	14.11 (0.46)
17 Mexican Pine-Oak	3	63.87 (1.55)	3	8.43 (1.19)	3	14.43 (0.74)	3	3.97 (0.32)	3	5.93 (0.32)	3	59.23 (2.75)	3	22.13 (0.65)	3	15.27 (0.72)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 5

MEAN LINEAR MEASUREMENTS OF MALE SONG SPARROWS BY ECOREGION SECTION/LIFE AREA[1]

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
13-3140	Mexican Highlands Shrub Steppe (Mesquite-Grasslands)[2]	11	66.05 (1.61)	11	7.05 (0.93)	11	14.85 (0.42)	11	4.17 (0.13)	11	5.86 (0.27)	9	61.40 (1.74)	11	23.31 (0.50)	11	15.50 (0.71)
17	Mexican Pine-Oak	14	68.04 (1.75)	14	8.67 (1.00)	14	14.78 (0.41)	14	4.16 (0.13)	14	6.06 (0.23)	14	62.70 (2.84)	14	24.39 (0.83)	14	16.11 (0.73)
1-M1310	Alaska Range (Arctic-Alpine, Aleutian Tundra)	59	81.43 (2.59)	58	9.92 (1.44)	58	18.29 (0.72)	59	4.76 (0.29)	59	6.78 (0.49)	51	78.96 (3.82)	59	27.49 (1.00)	59	19.07 (0.96)
3-1320B	Yukon Forest (Central Boreal)	9	67.59 (1.48)	9	11.22 (1.18)	9	13.80 (0.43)	9	4.72 (0.19)	9	6.51 (0.14)	9	67.73 (2.21)	9	21.43 (0.47)	9	14.70 (0.65)
3-1320A	Yukon Forest (Newfoundland Boreal)	8	64.45 (1.69)	8	9.16 (1.26)	7	13.66 (0.27)	7	4.79 (0.11)	7	6.47 (0.10)	8	65.09 (3.98)	8	21.90 (0.57)	8	15.33 (0.50)
4-2111	Spruce-fir Forest (N. Hardwood-Conifer, Minnesota)	7	66.26 (1.16)	7	10.04 (0.78)	6	13.87 (1.12)	6	4.62 (0.17)	6	6.42 (0.20)	7	66.53 (1.87)	7	20.93 (0.75)	7	14.63 (0.37)
4-2112	Northern Hardwoods-Fir (N. Hardwood-Conifer, Upper Peninsula)	5	67.30 (1.12)	5	9.48 (1.38)	5	13.74 (0.72)	5	4.52 (0.04)	5	6.68 (0.29)	4	66.80 (0.73)	5	20.92 (0.60)	5	15.02 (0.31)
4-2113	Northern Hardwoods Forest (N. Hardwood-Conifer, New York–Wisconsin)	19	66.08 (1.41)	18	9.32 (1.15)	18	13.92 (0.48)	19	4.83 (0.20)	19	6.61 (0.24)	19	65.76 (1.85)	19	21.63 (0.59)	19	14.99 (0.59)
3-2114	Northern Hardwoods-Spruce (Subalpine Boreal, New England)	3	67.27 (2.42)	3	11.03 (0.76)	3	13.47 (0.46)	3	4.77 (0.15)	3	6.63 (0.15)	3	66.40 (1.78)	3	21.50 (0.70)	3	15.13 (0.65)
4-2114	Northern Hardwoods-Spruce (N. Hardwoods-Conifer, New England)	4	65.75 (1.26)	4	10.50 (2.35)	4	13.63 (0.44)	4	4.55 (0.17)	4	6.35 (0.17)	4	66.68 (1.55)	4	21.35 (0.87)	4	15.25 (0.88)
4-2114A	N. Hardwoods-Spruce (N. Hardwood-Conifer, Maritime)	10	66.66 (1.22)	10	10.42 (0.92)	10	13.63 (0.44)	10	4.69 (0.26)	10	6.32 (0.21)	10	67.09 (4.36)	10	21.68 (0.78)	10	15.29 (0.59)
6-M2111	Douglas-fir Forest (Montane Woodland-Brush)	3	66.13 (1.48)	3	9.13 (0.21)	3	14.27 (0.15)	3	3.90 (0.53)	3	5.87 (0.21)	3	65.03 (3.86)	3	22.57 (0.31)	3	15.27 (0.21)
7-M2112	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest)	9	66.30 (2.06)	8	8.85 (1.79)	9	13.76 (0.58)	9	4.21 (0.16)	9	6.11 (0.32)	8	65.56 (4.10)	9	22.22 (0.37)	9	15.38 (0.60)

TABLE 5
CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
6-M2120	Intermontane, British Columbia (Montane Woodland-Brush)	1	66.50 (–)	1	11.70 (–)	1	14.00 (–)	1	3.80 (–)	1	5.80 (–)	1	65.60 (–)	1	23.20 (–)	1	16.10 (–)
4-2211	Mixed Mesophytic Forest (N. Hardwood-Conifer)	1	68.70 (–)	1	9.80 (–)	0	– (–)	1	4.80 (–)	1	6.70 (–)	1	69.50 (–)	1	21.10 (–)	1	15.10 (–)
8-2211	Mixed Mesophytic Forest (Eastern Deciduous)	11	65.10 (1.65)	11	8.85 (1.02)	11	13.51 (0.40)	11	4.64 (0.19)	11	6.53 (0.25)	11	66.17 (2.02)	11	21.44 (0.63)	11	15.20 (0.43)
8-2212	Beech-Maple Forest (Eastern Deciduous)	6	65.78 (1.27)	6	10.00 (0.74)	6	13.47 (0.50)	6	4.63 (0.10)	6	6.52 (0.10)	5	65.82 (0.82)	6	21.58 (0.25)	6	14.93 (0.71)
8-2213	Maple-Basswood Forest (Eastern Deciduous)	11	65.20 (1.69)	10	9.12 (1.09)	11	13.96 (0.46)	11	4.77 (0.20)	11	6.59 (0.28)	11	65.68 (2.81)	11	20.91 (0.48)	11	14.83 (0.61)
4-2214	Appalachian-Oak Forest (N. Hardwood-Conifer)	69	65.68 (1.85)	69	8.93 (1.35)	68	13.69 (0.49)	69	4.66 (0.20)	69	6.57 (0.24)	64	66.02 (2.98)	69	21.24 (0.61)	69	15.07 (0.57)
8-2214	Appalachian-Oak Forest (Eastern Deciduous)	36	66.04 (1.68)	37	9.50 (1.46)	36	13.68 (0.49)	37	4.86 (0.28)	37	6.64 (0.36)	36	65.76 (2.86)	37	21.63 (0.64)	37	14.99 (0.66)
8A-2214A	Appalachian-Oak (Atlantic Coastal Marsh, north)	9	66.82 (2.01)	9	10.48 (1.46)	9	13.51 (0.84)	9	5.03 (0.19)	9	6.40 (0.36)	8	67.71 (2.32)	9	20.29 (2.79)	9	15.24 (0.34)
8-2215	Oak-Hickory Forest (Eastern Deciduous)	8	65.34 (1.41)	8	8.96 (1.62)	8	13.44 (0.48)	7	4.76 (0.14)	7	6.47 (0.20)	8	65.85 (2.12)	8	21.28 (0.56)	8	15.09 (0.49)
8-2320	Southeastern Mixed Forest (Eastern Deciduous)	40	65.30 (1.47)	43	8.73 (1.25)	41	13.71 (0.62)	44	4.85 (0.28)	44	6.64 (0.30)	41	65.68 (2.44)	44	21.64 (0.70)	44	15.00 (0.60)
8A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, south)	33	65.45 (1.81)	34	9.13 (1.31)	34	14.08 (0.60)	34	5.08 (0.18)	34	6.99 (0.28)	29	65.45 (1.77)	34	22.09 (0.72)	34	15.08 (0.68)
16A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, North Carolina)	8	65.76 (1.68)	8	9.30 (1.74)	8	14.46 (0.57)	8	5.11 (0.23)	8	7.10 (0.18)	7	66.81 (3.03)	8	21.75 (0.59)	8	15.19 (0.65)
7-2410	Willamette-Puget Forest (Pacific Rain Forest)	16	66.69 (1.54)	16	8.23 (0.67)	16	14.79 (0.49)	15	4.33 (0.14)	16	6.28 (0.25)	16	64.81 (2.94)	16	23.64 (0.71)	16	16.73 (0.93)
7-M2416	Alaska Pacific Forest (Pacific Rain Forest)	37	71.01 (2.26)	37	9.88 (1.46)	36	15.95 (0.96)	37	4.22 (0.29)	37	6.12 (0.35)	36	67.83 (2.71)	37	24.64 (1.17)	37	16.54 (0.88)
7-M2411	Sitka Spruce-Cedar-Hemlock (Pacific Rain Forest)	32	66.99 (1.88)	32	8.95 (1.27)	32	14.79 (0.46)	32	4.27 (0.17)	32	6.25 (0.32)	32	64.78 (3.28)	32	23.44 (0.78)	32	16.44 (0.77)

TABLE 5

CONTINUED

Ecoregion section/life area		Wing		Wing-tip		Culmen		Ht. max.		Width max.		Tail		Tarsus		Toe	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
7-M2412	Redwood Forest (Pacific Rain Forest)	11	61.83 (2.69)	11	7.39 (0.68)	11	14.34 (0.71)	11	4.25 (0.20)	11	6.00 (0.35)	10	59.96 (2.00)	11	22.65 (0.87)	11	15.92 (0.73)
7-M2413	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest, inland)	4	67.40 (1.99)	4	7.50 (1.12)	4	15.08 (0.54)	4	4.28 (0.17)	4	6.55 (0.62)	4	66.25 (1.91)	4	23.98 (0.49)	4	17.18 (0.54)
9-M2414-A	California Mixed Evergreen Forest (Grasslands, San Francisco Bay Marsh, north)	1	60.40 (–)	1	8.50 (–)	1	13.30 (–)	1	3.90 (–)	1	5.80 (–)	1	60.90 (–)	1	19.30 (–)	1	14.30 (–)
7-M2415	Silver Fir-Douglas-fir Forest (Pacific Rain Forest, Cascades)	7	65.99 (1.70)	7	8.67 (0.80)	7	14.39 (0.66)	7	4.57 (0.21)	7	6.33 (0.42)	7	66.41 (2.29)	7	22.76 (0.41)	7	16.17 (1.10)
5-2530W	Tall-grass Prairie (Aspen Parkland, west)	2	67.50 (0.00)	2	10.45 (1.91)	2	13.25 (0.07)	2	4.75 (0.07)	2	6.50 (0.00)	2	68.25 (2.47)	2	21.65 (0.35)	2	14.10 (0.14)
10-2511	Oak-Hickory-Bluestem Parkland (Oak-Savannah)	2	67.90 (0.57)	2	9.50 (1.84)	2	13.80 (1.13)	2	4.75 (0.21)	2	6.70 (0.14)	2	68.35 (1.48)	2	21.50 (1.13)	2	14.75 (0.49)
5-2530E	Tall-grass Prairie (Aspen Parkland, east)	4	67.23 (0.64)	4	10.55 (1.07)	4	14.10 (0.61)	4	4.65 (0.10)	4	6.68 (0.21)	4	69.68 (2.09)	4	21.05 (0.64)	4	15.03 (1.10)
9-2531	Bluestem-Prairie (Grasslands, Tall-grass, east)	1	66.10 (–)	1	9.20 (–)	1	13.10 (–)	1	4.70 (–)	1	6.30 (–)	1	66.10 (–)	1	20.80 (–)	1	15.60 (–)
9-2532	Wheatgrass-Bluestem-Needlegrass (Grasslands, Tall-grass, west)	6	67.63 (1.44)	6	10.38 (0.97)	6	13.73 (0.24)	6	4.68 (0.17)	6	6.48 (0.20)	5	67.08 (2.82)	6	21.78 (0.28)	6	15.00 (0.64)
6-M2610	Sierran Forest (Montane Woodland-Brush)	6	66.25 (1.31)	6	9.55 (1.64)	6	14.02 (0.52)	6	4.47 (0.23)	6	6.55 (0.18)	6	67.10 (2.07)	6	22.65 (0.55)	6	15.42 (0.48)
9-2610	California Grassland (Grasslands, California Valley)	3	67.10 (0.40)	3	9.80 (0.72)	3	14.30 (0.26)	3	4.93 (0.06)	3	6.70 (0.10)	3	66.57 (1.42)	3	21.93 (0.47)	3	15.37 (0.31)
9-M2610	Sierran Forest (Grasslands, Sierran)	1	63.80 (–)	1	6.90 (–)	1	13.80 (–)	1	4.60 (–)	1	6.60 (–)	1	65.10 (–)	1	22.90 (–)	1	14.90 (–)
14-M2610	Sierran Forest (Piñon-Juniper-Oak, Sierran)	1	67.10 (–)	1	9.60 (–)	1	14.00 (–)	1	4.20 (–)	1	6.40 (–)	1	66.30 (–)	1	22.80 (–)	1	14.80 (–)
9-M2620	California Chaparral (Grasslands, coastal)	11	59.71 (1.51)	11	6.87 (0.88)	11	13.82 (0.45)	11	4.25 (0.18)	11	6.16 (0.37)	11	59.11 (1.84)	11	21.55 (0.44)	11	14.97 (0.81)

TABLE 5

CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
9-M2620-A	California Chaparral (San Francisco Bay Marsh, north)	3	60.73 (1.86)	3	6.80 (0.72)	3	14.30 (0.85)	3	4.47 (0.15)	3	6.67 (0.15)	3	60.00 (4.80)	3	21.57 (0.25)	3	14.83 (0.15)
9-M2620-B	California Chaparral (San Francisco Bay Marsh, south)	9	58.60 (2.35)	9	6.51 (1.28)	9	13.41 (0.40)	9	4.04 (0.11)	9	5.76 (0.37)	8	56.91 (2.91)	8	20.55 (0.37)	9	14.90 (0.85)
15-M2620	California Chaparral (Chaparral-Oak Woodland)	32	62.52 (1.79)	31	7.30 (0.94)	33	14.02 (0.62)	33	4.25 (0.25)	33	6.10 (0.38)	32	62.25 (2.50)	32	21.91 (0.63)	33	15.04 (0.59)
9-3111	Grama-Needlegrass-Wheatgrass (Grasslands, Short-grass, west)	2	67.00 (1.84)	2	10.50 (0.57)	2	13.80 (0.71)	2	4.85 (0.21)	2	6.65 (0.21)	2	67.20 (2.12)	2	21.65 (0.35)	2	14.55 (0.07)
6-M3111	Grand Fir-Douglas-fir (Montane Woodland-Brush, Oregon)	2	68.25 (2.05)	2	10.05 (1.48)	2	14.05 (0.64)	2	4.25 (0.21)	2	6.15 (0.49)	2	70.00 (3.11)	2	23.05 (0.49)	2	15.60 (0.71)
9-M3111	Grand Fir-Douglas-fir (Grasslands, Oregon)	9	69.36 (1.62)	9	9.66 (1.32)	9	14.20 (0.42)	9	4.10 (0.19)	9	6.16 (0.21)	9	69.79 (2.61)	9	22.26 (0.69)	9	14.79 (0.74)
11-M3111	Grand Fir-Douglas-fir (N. Desert Scrub, Oregon)	1	65.30 (–)	1	8.30 (–)	1	13.80 (–)	1	4.00 (–)	1	6.50 (–)	1	68.00 (–)	1	20.90 (–)	1	15.60 (–)
14-M3111	Grand Fir-Douglas-fir (Piñon-Juniper-Oak, Oregon)	11	67.35 (1.90)	11	8.83 (0.80)	11	14.60 (0.38)	11	4.28 (0.22)	11	6.25 (0.23)	11	68.96 (2.35)	11	22.15 (0.63)	11	15.11 (0.88)
6-M3112	Douglas-fir Forest (Montane Woodland-Brush, Rockies)	9	69.66 (1.56)	9	10.16 (0.98)	9	13.62 (0.64)	9	4.10 (0.13)	9	5.98 (0.17)	9	71.24 (3.32)	9	22.10 (0.47)	9	15.21 (0.42)
9-3112	Wheatgrass-Needlegrass (Grasslands, Short-grass, east)	5	68.00 (1.87)	6	10.20 (0.85)	6	13.33 (0.41)	5	4.62 (0.13)	6	6.58 (0.31)	5	68.80 (1.62)	6	21.12 (0.33)	6	15.05 (0.61)
11-M3112	Douglas-fir Forest (N. Desert Scrub)	12	68.28 (1.62)	12	9.18 (0.74)	11	13.57 (0.56)	12	4.12 (0.12)	12	5.98 (0.20)	11	71.09 (3.04)	12	22.09 (0.46)	12	15.10 (0.51)
9-3113	Grama-Buffalo Grass (Grasslands)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
9-M3113	Ponderosa Pine-Douglas-fir (Grasslands)	1	70.50 (–)	1	11.10 (–)	1	12.80 (–)	1	4.40 (–)	1	6.70 (–)	1	70.40 (–)	1	22.60 (–)	1	15.60 (–)
14-M3113	Ponderosa Pine-Douglas-fir (Piñon-Juniper-Oak)	1	70.80 (–)	1	9.90 (–)	1	13.00 (–)	1	4.10 (–)	1	6.50 (–)	1	71.50 (–)	1	22.70 (–)	1	15.40 (–)

TABLE 5
CONTINUED

	Ecoregion section/life area	Wing		Wing-tip		Culmen		Ht. max.		Width max.		Tail		Tarsus		Toe	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
11-M3113	Ponderosa Pine-Douglas-fir (N. Desert Scrub)	1	70.70 (–)	1	9.70 (–)	1	13.20 (–)	1	4.10 (–)	1	5.90 (–)	1	73.80 (–)	1	22.10 (–)	1	14.40 (–)
9-3120	Palouse Grassland (Grasslands)	21	67.13 (1.84)	21	9.51 (0.87)	21	13.99 (0.67)	22	4.27 (0.17)	22	6.07 (0.26)	20	67.22 (2.04)	22	22.69 (0.64)	22	15.23 (0.66)
14-M3120	Upper Gila Mountains Forest (Piñon-Juniper-Oak)	6	65.42 (1.48)	6	7.02 (0.95)	8	13.45 (0.42)	8	4.08 (0.10)	8	5.89 (0.24)	6	69.45 (1.84)	8	22.19 (0.83)	8	14.53 (0.46)
6-3131	Sagebrush-Wheatgrass (Montane Woodland-Brush)	2	67.45 (2.05)	2	8.65 (0.49)	2	14.00 (0.42)	2	4.45 (0.21)	2	6.45 (0.49)	2	68.45 (2.19)	2	21.85 (1.20)	2	14.90 (0.42)
9-3131	Sagebrush-Wheatgrass (Grasslands)	1	67.70 (–)	1	10.30 (–)	1	14.60 (–)	1	4.20 (–)	1	6.00 (–)	1	67.70 (–)	1	22.90 (–)	1	15.50 (–)
11-3131	Sagebrush-Wheatgrass (N. Desert Scrub)	63	68.62 (2.08)	63	9.17 (1.27)	61	13.97 (0.61)	63	4.37 (0.23)	63	6.30 (0.38)	63	69.21 (2.93)	63	22.40 (0.53)	63	15.21 (0.58)
14-3131	Sagebrush-Wheatgrass (Piñon-Juniper-Oak)	16	68.74 (2.03)	16	8.78 (1.41)	16	14.23 (0.42)	16	4.53 (0.16)	16	6.55 (0.39)	16	69.59 (3.04)	15	22.56 (0.39)	16	15.09 (0.61)
6-P3132	Grama-Galleta Steppe (Montane Woodland-Brush)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
11-3132	Lahontan Saltbush-Greasewood (N. Desert Scrub)	5	66.04 (1.41)	5	7.68 (0.35)	5	14.02 (0.44)	5	4.50 (0.26)	5	6.40 (0.10)	5	65.30 (0.91)	5	22.46 (0.81)	5	15.58 (0.39)
14-3132	Lahontan Saltbush-Greasewood (Piñon-Juniper-Oak)	15	68.89 (1.53)	15	8.78 (0.99)	13	13.73 (0.47)	14	4.21 (0.14)	14	6.01 (0.19)	15	68.01 (2.38)	14	22.16 (0.53)	15	15.21 (0.52)
14-P3132	Grama-Galleta Steppe (Piñon-Juniper-Oak)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
11-3133	Great Basin Sagebrush (N. Desert Scrub)	2	69.10 (0.28)	2	7.75 (0.49)	2	14.10 (0.85)	2	4.20 (0.00)	2	5.90 (0.28)	2	69.65 (1.34)	2	22.85 (1.06)	2	14.60 (0.14)

TABLE 5
CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
11-3134	Bonneville Saltbush-Greasewood (N. Desert Scrub)	1	68.20 (–)	1	9.50 (–)	1	13.20 (–)	1	4.10 (–)	1	6.00 (–)	1	71.70 (–)	1	23.20 (–)	1	15.40 (–)
6-3135	Ponderosa Shrub Forest (Montane Woodland-Brush)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
11-3135	Ponderosa Shrub Forest (N. Desert Scrub)	1	68.30 (–)	1	9.20 (–)	1	13.90 (–)	1	4.70 (–)	1	6.10 (–)	1	70.30 (–)	1	21.70 (–)	1	15.90 (–)
14-3135	Ponderosa Shrub Forest (Piñon-Juniper-Oak)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
13-3140	Mexican Highland Shrub Steppe (Mesquite-Grassland)	2	65.60 (3.54)	2	7.90 (1.27)	2	14.35 (0.92)	2	4.20 (0.14)	2	5.90 (0.42)	2	69.00 (6.36)	2	21.10 (0.28)	2	15.40 (0.14)
11-A3141	Wheatgrass-Needlegrass-Sagebrush (N. Desert Scrub)	5	69.34 (2.16)	5	8.92 (1.08)	5	13.48 (0.50)	5	4.08 (0.04)	5	5.96 (0.26)	5	69.64 (3.83)	5	22.30 (0.45)	5	14.92 (0.51)
11-A3142	Sagebrush-Wheatgrass (N. Desert Scrub)	4	69.55 (1.05)	4	9.58 (0.87)	4	13.43 (0.33)	4	4.08 (0.24)	4	5.95 (0.39)	4	70.25 (1.73)	4	21.83 (1.15)	4	14.98 (0.40)
13-3211	Grama-Tobosa (Mesquite-Grasslands)	1	67.60 (–)	1	7.40 (–)	1	14.20 (–)	1	4.00 (–)	1	6.00 (–)	1	67.60 (–)	1	20.80 (–)	1	15.20 (–)
12-3221	Creosote Bush (S. Desert Scrub)	3	67.50 (1.47)	3	8.33 (1.02)	3	13.67 (0.59)	3	4.20 (0.10)	3	6.07 (0.35)	3	70.00 (3.08)	3	22.33 (0.77)	3	15.03 (0.46)
12-3222	Creosote Bush-Bur Sage (S. Desert Scrub)	22	65.76 (1.47)	22	8.90 (1.27)	22	13.86 (0.42)	22	4.14 (0.14)	22	5.83 (0.24)	22	68.62 (1.86)	22	21.81 (0.72)	22	14.25 (0.63)
17-M2620	California Chaparral (Mexican Pine-Oak)	3	65.37 (0.91)	3	6.83 (0.35)	4	13.38 (0.38)	4	4.33 (0.19)	4	6.10 (0.18)	3	64.07 (0.81)	4	21.53 (0.43)	4	14.93 (0.59)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.
[2] Life area, in parentheses.

TABLE 6
MEAN LINEAR MEASUREMENTS OF FEMALE SONG SPARROWS BY ECOREGION SECTION/LIFE AREA[1]

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
13-3140	Mexican Highlands Shrub Steppe (Mesquite-Grassland)[2]	4	62.13 (0.95)	4	6.40 (0.87)	4	14.78 (0.32)	4	4.05 (0.06)	4	5.88 (0.32)	4	57.85 (0.73)	4	23.08 (0.66)	4	15.08 (0.32)
17	Mexican Pine-Oak	3	63.87 (1.55)	3	8.43 (1.19)	3	14.43 (0.74)	3	3.97 (0.32)	3	5.93 (0.32)	3	59.23 (2.75)	3	22.13 (0.65)	3	15.27 (0.72)
1-M1310	Alaska Range (Arctic-Alpine, Aleutian Tundra)	38	78.27 (2.34)	37	10.10 (1.22)	37	17.88 (0.80)	38	4.69 (0.31)	38	6.53 (0.46)	37	73.77 (12.72)	38	27.03 (0.98)	38	18.46 (0.97)
3-1320B	Yukon Forest (Central Boreal)	2	65.75 (1.48)	2	10.80 (1.27)	2	13.60 (0.42)	2	4.70 (0.28)	2	6.50 (0.00)	2	67.15 (1.20)	2	20.60 (0.57)	2	14.80 (0.14)
3-1320A	Yukon Forest (Newfoundland Boreal)	3	63.43 (1.40)	3	9.67 (0.45)	3	12.60 (0.92)	3	4.63 (0.15)	3	5.90 (0.26)	3	63.67 (1.88)	3	21.33 (0.91)	3	15.03 (0.38)
4-2111	Spruce-Fir Forest (N. Hardwood-Conifer, Minnesota)	2	65.15 (0.21)	2	9.70 (2.55)	2	12.55 (0.07)	2	4.45 (0.07)	2	6.40 (0.28)	2	65.15 (0.21)	2	20.65 (0.92)	2	14.55 (0.21)
6-M2111	Douglas-fir Forest (Montane Woodland-Brush)	1	63.80 (–)	1	9.80 (–)	1	14.00 (–)	1	4.00 (–)	1	6.20 (–)	1	67.00 (–)	1	22.80 (–)	1	14.60 (–)
7-M2112	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest)	3	63.37 (1.27)	3	8.57 (0.60)	3	14.23 (0.21)	3	4.17 (0.12)	3	6.00 (0.26)	3	63.90 (2.31)	3	22.43 (0.74)	3	15.00 (0.10)
4-2112	N. Hardwoods-Fir (N. Hardwood-Conifer, Upper Peninsula)	3	63.27 (0.25)	3	11.33 (2.03)	3	13.53 (0.78)	3	4.63 (0.12)	3	6.50 (0.30)	2	60.90 (0.57)	3	20.83 (0.42)	3	14.50 (0.80)
4-2113	N. Hardwoods Forest (N. Hardwood-Conifer, New York-Wisconsin)	6	62.40 (1.36)	6	8.53 (1.62)	7	13.66 (0.34)	7	4.66 (0.15)	7	6.46 (0.28)	6	62.68 (3.11)	7	21.39 (0.73)	7	14.64 (0.78)
3-2114	N. Hardwoods-Spruce (Subalpine Boreal, New England)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
4-2114	N. Hardwoods-Spruce (N. Hardwoods-Conifer, New England)	4	61.45 (0.48)	3	9.57 (0.12)	4	13.43 (0.29)	4	4.78 (0.13)	4	6.33 (0.21)	4	59.13 (3.01)	4	20.98 (0.53)	4	14.63 (0.48)
4-2114A	N. Hardwoods-Spruce (N. Hardwood-Conifer, Maritime)	5	63.54 (1.52)	5	10.98 (0.61)	5	13.24 (0.59)	5	4.68 (0.29)	5	6.34 (0.34)	5	63.68 (2.97)	5	21.50 (0.74)	5	14.86 (0.26)
6-M2120	Intermontane, British Columbia (Montane Woodland-Brush)	1	61.30 (–)	1	8.90 (–)	1	14.10 (–)	1	4.10 (–)	1	5.70 (–)	1	56.50 (–)	1	21.70 (–)	1	15.00 (–)

TABLE 6
CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
4-2211	Mixed Mesophytic Forest (N. Hardwood-Conifer)	1	62.10 (—)	1	9.10 (—)	0	— (—)	1	4.90 (—)	1	6.00 (—)	1	62.30 (—)	1	19.40 (—)	1	14.90 (—)
8-2211	Mixed Mesophytic Forest (Eastern Deciduous)	10	62.22 (1.72)	9	7.42 (0.61)	10	13.16 (0.40)	10	4.59 (0.24)	10	6.45 (0.21)	9	62.84 (2.47)	10	20.85 (0.45)	10	14.72 (0.65)
8-2212	Beech-Maple Forest (Eastern Deciduous)	3	63.03 (1.70)	3	9.90 (0.10)	3	13.37 (0.93)	3	4.63 (0.23)	3	6.47 (0.25)	3	63.57 (2.06)	3	20.50 (0.82)	3	15.03 (0.23)
8-2213	Maple-Basswood Forest (Eastern Deciduous)	3	61.90 (1.71)	3	8.33 (1.64)	3	13.57 (0.06)	3	4.70 (0.17)	3	6.70 (0.30)	3	60.57 (1.78)	3	21.00 (0.10)	3	15.40 (0.40)
4-2214	Appalachian-Oak Forest (N. Hardwood-Conifer)	19	62.46 (2.47)	19	8.18 (1.15)	17	13.70 (0.51)	19	4.65 (0.20)	19	6.52 (0.21)	16	62.99 3.71)	19	20.95 (0.67)	19	14.84 (0.70)
8-2214	Appalachian-Oak Forest (Eastern Deciduous)	12	62.46 (1.82)	12	9.67 (1.91)	11	13.27 (0.76)	12	4.76 (0.25)	12	6.28 (0.57)	12	63.48 (3.15)	12	21.46 (0.55)	12	15.05 (0.78)
8A-2214A	Appalachian-Oak (Atlantic Coastal Marsh, north)	2	62.10 (0.14)	2	9.55 (1.06)	2	12.90 (0.00)	2	4.90 (0.14)	2	6.15 (0.92)	2	64.40 (0.71)	2	21.65 (0.49)	2	15.00 (0.00)
8-2215	Oak-Hickory Forest (Eastern Deciduous)	2	60.65 (0.64)	2	8.00 (1.27)	2	13.00 (0.28)	2	4.65 (0.21)	2	6.30 (0.14)	2	60.65 (2.19)	2	20.55 (0.07)	2	14.85 (0.49)
8-2320	Southeastern Mixed Forest (Eastern Deciduous)	16	61.93 (1.94)	17	9.21 (1.23)	18	13.79 (0.50)	18	4.77 (0.22)	18	6.50 (0.29)	13	61.62 (2.99)	18	21.24 (0.59)	18	14.66 (0.68)
8A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, south)	24	62.26 (1.55)	24	8.46 (1.55)	23	13.87 (0.59)	24	4.99 (0.10)	24	6.96 (0.37)	23	62.02 (2.60)	24	21.53 (0.72)	24	14.96 (0.65)
16A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, North Carolina)	4	62.20 (2.34)	4	8.90 (2.27)	4	13.73 (0.59)	4	4.95 (0.06)	4	6.88 (0.15)	4	62.80 (1.73)	4	21.23 (0.71)	4	14.80 (0.88)
7-2410	Willamette-Puget Forest (Pacific Rain Forest)	10	62.35 (1.12)	10	7.96 (0.98)	10	14.71 (0.49)	10	4.20 (0.16)	10	6.20 (0.44)	9	59.41 (3.21)	10	22.84 (0.53)	10	16.08 (0.45)
7-M2416	Alaska Pacific Forest (Pacific Rain Forest)	25	67.75 (2.63)	25	9.40 (1.50)	25	15.58 (0.91)	25	4.17 (0.27)	25	6.01 (0.37)	25	63.93 (3.64)	25	23.83 (1.00)	25	16.07 (0.89)
7-M2411	Sitka Spruce-Cedar-Hemlock (Pacific Rain Forest)	24	63.80 (1.54)	24	8.10 (1.12)	24	14.56 (0.50)	24	4.22 (0.18)	24	6.19 (0.26)	24	61.20 (2.70)	24	22.97 (0.55)	24	15.97 (0.71)
7-M2412	Redwood Forest (Pacific Rain Forest)	3	56.80 (2.55)	3	6.33 (0.99)	3	14.20 (0.35)	3	4.07 (0.15)	3	5.87 (0.06)	3	55.25 (0.49)	3	21.43 (0.40)	3	15.73 (0.42)
7-M2413	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest, inland)	3	64.07 (1.43)	3	9.47 (1.87)	3	15.03 (0.31)	3	4.33 (0.15)	3	6.30 (0.26)	3	62.17 (2.82)	3	22.60 (0.60)	3	16.37 (0.61)

TABLE 6

CONTINUED

	Ecoregion section/life area	Wing		Wing-tip		Culmen		Ht. max.		Width max.		Tail		Tarsus		Toe	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
9-M2414	California Mixed Evergreen Forest (Grasslands, San Francisco Bay Marsh, north)	1	57.00 (—)	1	6.30 (—)	1	12.80 (—)	1	4.20 (—)	1	6.00 (—)	1	55.80 (—)	1	20.80 (—)	1	14.00 (—)
7-M2415	Silver Fir-Douglas-fir Forest (Pacific Rain Forest, Cascades)	3	61.60 (0.46)	3	8.77 (1.04)	3	14.17 (0.71)	3	4.20 (0.10)	3	6.10 (0.36)	3	62.17 (1.60)	3	21.87 (0.67)	3	15.30 (0.96)
5-2530W	Tall-grass Prairie (Aspen Parkland, west)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
10-2511	Oak-Hickory-Bluestem Parkland (Oak-Savannah)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
5-2530E	Tall-grass Prairie (Aspen Parkland, east)	3	64.67 (0.45)	3	11.03 (1.47)	3	13.93 (0.45)	3	4.60 (0.10)	3	6.47 (0.15)	3	63.40 (2.59)	3	21.43 (1.20)	3	15.07 (0.64)
9-2531	Bluestem Prairie (Grasslands-Tall-grass, east)	1	65.70 (—)	1	11.30 (—)	1	13.00 (—)	1	4.60 (—)	1	6.90 (—)	1	64.30 (—)	1	21.00 (—)	1	15.50 (—)
9-2532	Wheatgrass-Bluestem-Needlegrass (Grasslands, Tall-grass, west)	2	63.55 (1.06)	2	7.85 (0.49)	2	13.70 (0.71)	2	4.45 (0.07)	2	6.40 (0.42)	2	64.65 (2.62)	2	20.50 (0.85)	2	14.40 (0.42)
6-M2610	Sierran Forest (Montane Woodland-Brush)	5	62.90 (1.87)	5	8.12 (1.16)	5	13.94 (0.51)	5	4.42 (0.19)	5	6.22 (0.26)	5	62.76 (1.09)	5	21.70 (0.61)	5	14.94 (0.38)
9-2610	California Grassland (Grasslands, California Valley)	4	61.80 (2.16)	4	8.18 (0.50)	4	13.70 (0.42)	4	4.58 (0.21)	4	6.50 (0.24)	3	60.93 (2.46)	4	21.65 (0.55)	4	14.65 (0.55)
9-M2610	Sierran Forest (Grasslands, Sierran)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
14-M2610	Sierran Forest (Piñon-Juniper-Oak, Sierran)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
9-M2620A	California Chaparral (Grasslands, coastal)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
9-M2620A	California Chaparral (San Francisco Bay Marsh, north)	3	55.27 (1.99)	3	6.13 (1.38)	3	14.23 (0.12)	3	4.07 (0.29)	3	6.33 (0.21)	3	55.43 (1.36)	3	20.50 (0.50)	3	13.87 (0.76)
9-M2620B	California Chaparral (San Francisco Bay Marsh, south)	10	54.14 (0.68)	10	6.21 (1.17)	10	12.99 (0.57)	10	3.88 (0.23)	10	5.45 (0.16)	9	52.26 (1.03)	10	20.67 (0.52)	10	13.93 (0.52)
15-M2620	California Chaparral (Chaparral-Oak Woodland)	12	58.55 (2.05)	12	6.42 (1.26)	12	13.62 (0.57)	12	4.25 (0.27)	12	5.14 (0.43)	11	57.41 (3.14)	12	21.30 (0.86)	12	14.26 (0.53)

TABLE 6

CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
9-3111	Grama-Needlegrass-Wheatgrass (Grasslands, Short-grass, west)	4	64.60 (1.02)	4	10.40 (1.22)	4	13.55 (0.69)	4	4.43 (0.17)	4	6.30 (0.22)	4	63.78 (1.48)	4	21.48 (0.68)	4	14.73 (0.21)
6-M3111	Grand Fir-Douglas-fir (Montane Woodland-Brush, Oregon)	4	64.53 (1.36)	4	9.30 (1.56)	4	13.83 (0.57)	4	4.13 (0.33)	4	6.20 (0.29)	4	65.63 (2.55)	4	21.73 (0.29)	4	14.53 (0.41)
9-M3111	Grand Fir-Douglas-fir (Grasslands, Oregon)	4	65.75 (1.31)	4	9.35 (0.97)	4	14.05 (0.53)	4	4.28 (0.17)	4	6.13 (0.22)	4	65.23 (2.15)	4	22.63 (0.49)	4	14.93 (0.48)
11-M3111	Grand Fir-Douglas-fir (N. Desert Scrub, Oregon)	1	63.20 (–)	1	6.50 (–)	1	13.50 (–)	1	4.50 (–)	1	6.10 (–)	1	62.90 (–)	1	21.90 (–)	1	14.30 (–)
14-M3111	Grand Fir-Douglas-fir (Piñon-Juniper-Oak, Oregon)	3	63.83 (1.71)	3	9.23 (1.89)	3	13.83 (0.40)	3	4.23 (0.06)	3	6.03 (0.15)	3	64.00 (3.70)	3	21.37 (0.31)	3	14.80 (0.17)
6-M3112	Douglas-fir Forest (Montane Woodland-Brush, N. Rockies)	3	66.13 (1.21)	3	8.73 (0.75)	3	13.47 (0.12)	3	4.10 (0.26)	3	6.10 (0.66)	3	67.03 (2.17)	3	21.33 (0.58)	3	15.27 (0.35)
9-3112	Wheatgrass-Needlegrass (Grasslands, Short-grass, east)	6	64.45 (1.84)	6	9.50 (1.67)	6	13.62 (0.46)	6	4.72 (0.19)	6	6.50 (0.30)	6	65.65 (3.16)	6	21.30 (0.76)	6	14.90 (0.28)
11-M3112	Douglas-fir Forest (N. Desert Scrub)	3	63.33 (1.86)	2	8.00 (1.70)	3	13.13 (0.06)	3	4.03 (0.06)	3	5.83 (0.45)	3	65.93 (2.11)	3	21.93 (0.12)	3	15.33 (0.42)
9-3113	Grama-Buffalo Grass (Grasslands, Short-grass, south)	1	64.20 (–)	1	10.00 (–)	1	13.10 (–)	1	4.20 (–)	1	6.10 (–)	1	63.10 (–)	1	22.30 (–)	1	14.40 (–)
9-M3113	Ponderosa Pine-Douglas-fir (Grasslands, Short-grass, S. Rockies)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
14-M3113	Ponderosa Pine-Douglas-fir (Piñon-Juniper-Oak, S. Rockies)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
11-M3113	Ponderosa Pine-Douglas-fir (N. Desert Scrub)	0	–	0	–	0	–	0	–	0	–	0	–	0	–	0	–
9-3120	Palouse Grassland (Grasslands)	9	64.14 (0.96)	9	8.36 (1.11)	9	14.23 (0.49)	9	4.26 (0.13)	9	6.14 (0.33)	9	64.49 (2.18)	9	22.71 (1.16)	9	15.30 (0.58)
14-M3120	Upper Gila Mountains Forest (Piñon-Juniper-Oak)	5	62.62 (1.49)	5	6.98 (0.60)	5	13.52 (0.40)	5	4.08 (0.08)	5	5.78 (0.08)	5	64.22 (2.42)	5	21.54 (0.50)	5	14.10 (0.16)

TABLE 6
CONTINUED

	Ecoregion section/life area	Wing		Wing-tip		Culmen		Ht. max.		Width max.		Tail		Tarsus		Toe	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
6-3131	Sagebrush-Wheatgrass (Montane Woodland-Brush)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
9-3131	Sagebrush-Wheatgrass (Grasslands)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
11-3131	Sagebrush-Wheatgrass (N. Desert Scrub)	31	64.76 (1.64)	32	8.59 (1.20)	32	13.75 (0.43)	33	4.28 (0.23)	33	6.17 (0.40)	30	65.52 (2.61)	33	21.71 (0.47)	33	14.66 (0.56)
14-3131	Sagebrush-Wheatgrass (Piñon-Juniper-Oak)	16	64.17 (1.63)	16	8.04 (1.18)	16	13.93 (0.48)	16	4.38 (0.19)	16	6.29 (0.28)	15	64.49 (2.80)	16	22.10 (0.47)	16	14.78 (0.36)
6-P3132	Grama-Galleta Steppe (Montane Woodland-Brush)	1	62.50 (—)	1	7.10 (—)	1	13.80 (—)	1	4.20 (—)	1	6.10 (—)	1	65.40 (—)	1	21.10 (—)	1	14.90 (—)
11-3132	Lahontan Saltbush-Greasewood (N. Desert Scrub)	2	63.00 (1.56)	2	8.15 (0.21)	2	13.80 (0.57)	2	4.50 (0.57)	2	6.40 (0.57)	2	62.30 (1.56)	2	21.60 (1.41)	2	15.65 (0.92)
14-3132	Lahontan Saltbush-Greasewood (Piñon-Juniper-Oak)	3	65.90 (1.61)	3	7.83 (1.17)	3	13.73 (0.06)	3	4.33 (0.12)	3	6.20 (0.10)	3	66.37 (3.18)	3	21.83 (0.25)	3	14.67 (0.55)
14-P3132	Grama-Galleta Steppe (Piñon-Juniper-Oak)	1	63.70 (—)	1	7.90 (—)	1	13.80 (—)	1	3.90 (—)	1	5.70 (—)	1	64.70 (—)	1	21.40 (—)	1	14.80 (—)
11-3133	Great Basin Sagebrush (N. Desert Scrub)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
11-3134	Bonneville Saltbush-Greasewood (Northern Desert Scrub)	2	65.05 (2.19)	2	7.80 (1.27)	2	13.65 (0.21)	2	4.05 (0.07)	2	5.95 (0.07)	2	67.25 (0.78)	2	22.60 (0.42)	2	15.30 (0.99)
6-3135	Ponderosa Shrub Forest (Montane Woodland-Brush)	1	62.30 (—)	1	9.90 (—)	1	13.80 (—)	1	4.60 (—)	1	6.50 (—)	1	63.60 (—)	1	21.80 (—)	1	15.10 (—)

TABLE 6
CONTINUED

	Ecoregion section/life area	Wing N	Wing M (s.d.)	Wing-tip N	Wing-tip M (s.d.)	Culmen N	Culmen M (s.d.)	Ht. max. N	Ht. max. M (s.d.)	Width max. N	Width max. M (s.d.)	Tail N	Tail M (s.d.)	Tarsus N	Tarsus M (s.d.)	Toe N	Toe M (s.d.)
11-3135	Ponderosa Shrub Forest (N. Desert Scrub)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
14-3135	Ponderosa Shrub Forest (Piñon-Juniper-Oak)	1	65.20 (—)	1	7.00 (—)	1	14.10 (—)	1	5.00 (—)	1	7.00 (—)	1	66.70 (—)	1	22.10 (—)	1	14.90 (—)
13-3140	Mexican Highland Shrub Steppe (Mesquite-Grassland)	2	61.60 (0.57)	2	6.45 (1.34)	2	13.40 (0.28)	2	4.20 (0.00)	2	5.95 (0.21)	2	61.60 (3.39)	2	21.30 (0.14)	2	14.30 (0.71)
11-A3141	Wheatgrass-Needlegrass-Sagebrush (N. Desert Scrub)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
11-A3142	Sagebrush-Wheatgrass (N. Desert Scrub)	1	68.50 (—)	1	10.10 (—)	1	13.10 (—)	1	4.00 (—)	1	6.30 (—)	1	71.60 (—)	1	21.00 (—)	1	15.10 (—)
13-3211	Grama-Tobosa (Mesquite-Grassland)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
12-3221	Creosote Bush (S. Desert Scrub)	1	61.10 (—)	1	5.90 (—)	1	13.90 (—)	1	4.20 (—)	1	6.00 (—)	1	64.50 (—)	1	21.90 (—)	1	13.30 (—)
12-3222	Creosote Bush-Bur Sage (S. Desert Scrub)	11	62.43 (1.38)	11	8.30 (1.24)	12	13.46 (0.48)	12	4.02 (0.10)	12	5.79 (0.27)	11	64.37 (2.68)	12	20.84 (0.43)	12	14.18 (0.41)
17-M2620	California Chaparral (Mexican Pine-Oak)	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.
[2] Life area, in parentheses.

TABLE 7

MEAN RATIOS OF SONG SPARROW LINEAR MEASUREMENTS BY LIFE AREA[1]

	Males								Females							
	Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
Life area	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
1. Arctic-Alpine (Aleutian)	57	.122 (.0180)	58	.337 (.0113)	57	.261 (.0147)	57	.371 (.0235)	37	.129 (.0158)	38	.346 (.0124)	37	.262 (.0134)	37	.365 (.0230)
3. Boreal (Open and Closed)	21	.156 (.0187)	21	.328 (.0163)	20	.347 (.0173)	20	.473 (.0210)	6	.155 (.0105)	6	.329 (.0222)	6	.349 (.0413)	6	.462 (.0432)
4. Northern Hardwood-Conifer	113	.140 (.0203)	114	.324 (.0121)	111	.339 (.0348)	110	.477 (.0233)	40	.144 (.0249)	41	.336 (.0144)	39	.342 (.0256)	39	.477 (.0232)
5. Aspen Parkland	6	.156 (.0177)	6	.316 (.0103)	6	.340 (.0183)	6	.480 (.0246)	3	.171 (.0218)	3	.331 (.0178)	3	.330 (.0093)	3	.464 (.0053)
6. Montane Woodland-Brush	26	.141 (.0157)	26	.333 (.0156)	26	.307 (.0222)	26	.446 (.0298)	16	.137 (.0194)	16	.340 (.0119)	16	.306 (.0218)	16	.448 (.0237)
7. Pacific Rain Forest	112	.132 (.0191)	114	.350 (.0146)	112	.285 (.0219)	113	.412 (.0334)	71	.132 (.0189)	71	.358 (0.150)	70	.282 (.0201)	70	.410 (.0318)
8. Eastern Deciduous Forest	112	.139 (.0197)	114	.329 (.0122)	112	.352 (.0243)	112	.484 (.0259)	45	.143 (.0232)	46	.340 (.0137)	47	.351 (.0222)	47	.478 (.0290)
9. Grasslands	49	.145 (.0146)	49	.328 (.0147)	49	.318 (.0275)	50	.453 (.0331)	31	.141 (.0198)	31	.342 (.0184)	31	.321 (.0238)	31	.458 (.0288)
10. Oak-Savannah	2	.140 (.0283)	2	.312 (.0127)	2	.345 (.0127)	2	.487 (.0297)	0	—	0	—	0	—	0	—
11. Northern Desert Scrub	97	.132 (.0163)	97	.326 (.0123)	94	.311 (.0148)	94	.449 (.0242)	40	.131 (0.182)	40	.337 (.0116)	41	.311 (.0168)	40	.449 (.0264)
12. Southern Desert Scrub	25	.134 (.0181)	25	.332 (.0123)	25	.300 (.0125)	25	.424 (.0179)	12	.130 (.0210)	12	.336 (.0126)	13	.299 (.0111)	13	.431 (.0210)
13. Mesquite-Grassland	14	.109 (.0139)	14	.346 (.0205)	14	.283 (.0152)	14	.399 (.0157)	6	.104 (.0149)	6	.363 (.0141)	6	.288 (.0217)	6	.413 (.0296)
14. Piñon-Juniper-Oak	50	.127 (.0165)	47	.329 (.0129)	50	.310 (.0128)	49	.448 (.0232)	30	.124 (.0183)	30	.341 (.0114)	29	.312 (.0186)	29	.444 (.0245)
15. Chaparral-Oak Woodland	30	.118 (.0137)	30	.352 (.0132)	32	.304 (.0157)	32	.437 (.0302)	12	.109 (.0199)	12	.364 (.0202)	12	.316 (.0214)	12	.452 (.0345)
17. Mexican Pine and Pine-Oak	18	.124 (.0162)	18	.352 (.0155)	19	.292 (.0214)	19	.420 (.0239)	3	.132 (.0182)	3	.340 (.0093)	3	.275 (.0084)	3	.411 (.0204)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 8

MEAN RATIOS OF SONG SPARROW LINEAR MEASUREMENTS BY ECOREGION PROVINCE[1]

		Males								Females							
		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
	Ecoregion province	N	M (s.d.)	N	M (s.d.	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
M1310	Alaska Range (Aleutians)	57	.122 (.0180)	58	.337 (.0113)	57	.261 (.0147)	57	.371 (.0235)	38	.128 (.0164)	38	.346 (.0124)	37	.262 (.0134)	37	.365 (.0230)
1320	Yukon Forest (Boreal)	21	.157 (.0192)	21	.328 (.0163)	20	.344 (.0241)	20	.473 (.0210)	6	.155 (.0105)	6	.329 (.0222)	6	.349 (.0413)	6	.462 (.0432)
2110	Laurentian Mixed Forest	43	.148 (.0184)	47	.323 (.0123)	45	.338 (.0344)	45	.472 (.0236)	20	.156 (.0257)	20	.337 (.0130)	21	.349 (.0196)	21	.479 (.0245)
M2110	Columbia Forest	11	.134 (.0215)	13	.338 (.0094)	12	.298 (.0258)	13	.436 (.0308)	5	.140 (.0098)	5	.357 (.0070)	4	.291 (.0074)	4	.427 (.0157)
2210	Eastern Deciduous Forest	147	.140 (.0205)	151	.325 (.0118)	146	.348 (.0221)	148	.482 (.0265)	51	.137 (.0225)	51	.338 (.0147)	49	.348 (.0223)	49	.479 (.0287)
2320	Southeastern Mixed Forest	83	.136 (.0200)	84	.335 (.0136)	83	.361 (.0420)	83	.491 (.0248)	44	.140 (.0228)	44	.345 (.0129)	45	.354 (.0196)	45	.487 (.0355)
2410	Willamette-Puget Forest	16	.124 (.0100)	16	.355 (.0117)	15	.293 (.0121)	16	.425 (.0174)	10	.128 (.0153)	10	.367 (.0074)	10	.286 (.0145)	10	.422 (.0321)
M2410	Pacific Forest	93	.134 (.0195)	93	.350 (.0149)	89	.283 (.0235)	92	.409 (.0353)	60	.132 (.0203)	60	.357 (.0160)	60	.282 (.0218)	60	.409 (.0325)
2510	Prairie Parkland	2	.140 (.0283)	2	.312 (.0127)	2	.345 (.0127)	2	.487 (.0297)	0	—	0	—	0	—	0	—
2530	Tall-grass Prairie	13	.154 (.0161)	13	.319 (.0086)	13	.342 (.0158)	13	.476 (.0190)	6	.155 (.0283)	6	.327 (.0129)	6	.333 (.0157)	6	.476 (.0273)
2610	California Grassland	3	.146 (.0118)	3	.327 (.0055)	3	.345 (.0095)	3	.469 (.0146)	4	.132 (.0089)	4	.351 (.0037)	4	.334 (.0164)	4	.475 (.0103)
M2610	Sierran Forest	8	.139 (.0234)	8	.344 (.0132)	8	.318 (.0161)	8	.468 (.0185)	5	.130 (.0218)	5	.345 (.0060)	5	.317 (.0221)	5	.447 (.0262)

TABLE 8
CONTINUED

		Males								Females							
		Wing-tip/ wing		Tarsus; wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
	Ecoregion province	N	M (s.d.)	N	M (s.d.	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
M2620	California Chaparral	56	.115 (.0144)	55	.353 (.0140)	59	.306 (.0161)	59	.440 (.0280)	25	.112 (.0206)	25	.373 (.0181)	25	.307 (.0232)	25	.439 (.0309)
3110	Great Plains Short-grass Prairie	7	.153 (.0112)	7	.315 (.0129)	7	.350 (.0093)	8	.491 (.0178)	11	.153 (.0201)	11	.333 (.0160)	11	.337 (.0200)	11	.472 (.0189)
M3110	Rocky Mountain Forest	46	.138 (.0148)	47	.323 (.0106)	46	.301 (.0148)	46	.444 (.0255)	19	.135 (.0207)	19	.338 (.0095)	19	.305 (.0160)	19	.442 (.0246)
3120	Palouse Grassland	21	.142 (.0122)	21	.339 (.0128)	21	.307 (.0195)	21	.436 (.0275)	9	.130 (.0169)	9	.354 (.0214)	9	.299 (.0121)	9	.432 (.0200)
M3120	Upper Gila Mts. Forest	6	.107 (.0149)	6	.344 (.0062)	8	.303 (.0110)	8	.438 (.0262)	5	.112 (.0121)	5	.344 (.0140)	5	.302 (.0054)	5	.428 (.0088)
3130	Intermountain Sagebrush	106	.131 (.0173)	106	.328 (.0115)	104	.314 (.0139)	103	.450 (.0245)	56	.130 (.0180)	56	.339 (.0113)	56	.316 (.0202)	56	.453 (.0242)
P3130	Colorado Plateau	0	—	0	—	0	—	0	—	2	.129 (.0178)	2	.337 (.0141)	2	.294 (.0149)	2	.457 (.0205)
3140	Mexican Highlands Shrub Steppe	13	.109 (.0145)	13	.348 (.0181)	13	.283 (.0158)	13	.398 (.0148)	6	.104 (.0149)	6	.363 (.0141)	6	.288 (.0217)	6	.413 (.0296)
A3140	Wyoming Basin	9	.132 (.0121)	9	.318 (.0160)	9	.303 (.0140)	9	.443 (.0248)	1	.147 (—)	1	.307 (—)	1	.305 (—)	1	.447 (—)
3220	American Desert	25	.134 (.0181)	25	.332 (.0123)	25	.300 (.0125)	25	.424 (.0179)	12	.130 (.0210)	12	.336 (.0126)	13	.299 (.0111)	13	.431 (.0210)
17	Mexican Pine-Oak	15	.128 (.0146)	15	.357 (.0112)	15	.283 (.0115)	15	.411 (.0162)	3	.132 (.0182)	3	.340 (.0093)	3	.275 (.0083)	3	.340 (.0093)

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.

TABLE 9

MEAN RATIOS OF SONG SPARROW LINEAR MEASUREMENTS BY ECOREGION SECTION/LIFE AREA[1]

		Males								Females							
		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
	Ecoregion section/life area	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
13-3140	Mexican Highlands Shrub Steppe (Mesquite-Grassland)[2]	11	.107 (.0144)	11	.353 (.0137)	11	.282 (.0138)	11	.395 (.0148)	4	.103 (.0141)	4	.371 (.0062)	4	.275 (.0099)	4	.398 (.0221)
17-	Mexican Pine-Oak	14	.130 (.0142)	14	.358 (.0104)	14	.281 (.0098)	14	.411 (.0168)	3	.132 (.0182)	3	.340 (.0093)	3	.275 (.0048)	3	.411 (.0204)
1-M1310	Alaska Range (Arctic-Alpine, Aleutian Tundra)	57	.122 (.0180)	58	.337 (.0113)	57	.261 (.0147)	57	.371 (.0235)	38	.128 (.0164)	38	.346 (.0124)	37	.262 (.0134)	37	.365 (.0230)
3-1320B	Yukon Forest (Central Boreal)	9	.166 (.0148)	9	.317 (.0126)	9	.343 (.0216)	9	.472 (.0134)	2	.164 (.0156)	2	.306 (.0113)	2	.346 (.0311)	2	.478 (.0149)
3-1320A	Yukon Forest (Newfoundland Boreal)	8	.142 (.0176)	8	.339 (.0110)	7	.350 (.0143)	7	.474 (.0119)	3	.152 (.0038)	3	.336 (.0156)	3	.370 (.0380)	3	.471 (.0499)
4-2111	Spruce-Fir Forest (N. Hardwood-Conifer, Minnesota)	7	.152 (.0111)	7	.316 (.0136)	5	.346 (.0113)	5	.478 (.0074)	2	.149 (.0396)	2	.317 (.0127)	2	.355 (.0078)	2	.510 (.0198)
6-M2111	Douglas-fir Forest (Montane Woodland-Brush)	3	.138 (.0060)	3	.341 (.0042)	3	.274 (.0390)	3	.411 (.0125)	1	.154 (—)	1	.359 (—)	1	.154 (—)	1	.443 (—)
7-M2112	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest)	8	.133 (.0253)	9	.336 (.0107)	9	.307 (.0153)	9	.445 (.0324)	3	.135 (.0078)	3	.357 (.0099)	3	.293 (.0080)	3	.422 (.0142)
4-2112	N. Hardwood-Fir (N. Hardwood-Conifer, Upper Peninsula)	5	.141 (.0227)	5	.311 (.0096)	5	.330 (.0195)	5	.487 (.0161)	3	.179 (.0313)	3	.329 (.0061)	3	.343 (.0146)	3	.482 (.0196)
4-2113	N. Hardwoods Forest (N. Hardwood-Conifer, New York-Wisconsin)	18	.141 (.0168)	19	.328 (.0104)	17	.350 (.0192)	18	.474 (.0240)	6	.137 (.0254)	6	.343 (.0138)	7	.341 (.0158)	7	.473 (.0232)
3-2114	N. Hardwoods-Spruce (Subalpine Boreal, New England)	3	.164 (.0142)	3	.320 (.0139)	3	.354 (.0087)	3	.493 (.0262)	0	—	0	—	0	—	0	—
4-2114	N. Hardwoods-Spruce (N. Hardwood-Conifer, New England)	4	.160 (.0337)	4	.327 (.0071)	4	.334 (.0124)	4	.466 (.0085)	4	.152 (.0067)	4	.341 (.0092)	4	.356 (.0153)	4	.471 (.0192)
4-2114A	N. Hardwoods-Spruce (N. Hardwoods-Conifer, Maritime)	9	.154 (.0096)	9	.327 (.0131)	9	.343 (.0147)	9	.461 (.0169)	5	.173 (.0085)	5	.338 (.0114)	5	.354 (.0319)	5	.479 (.0316)

TABLE 9

CONTINUED

		Males								Females							
		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen	
	Ecoregion section/life area	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
6-M2120	Intermontane, British Columbia (Montane Woodland-Brush)	1	.176 (—)	1	.349 (—)	1	.271 (—)	1	.414 (—)	1	.145 (—)	1	.354 (—)	1	.291 (—)	1	.404 (—)
4-2211	Mixed Mesophytic Forest (N. Hardwood-Conifer, Appalachian)	1	.145 (—)	1	.312 (—)	0	— (—)	0	— (—)	1	.147 (—)	1	.312 (—)	1	.389 (—)	1	.476 (—)
8-2211	Mixed Mesophytic Forest (E. Deciduous, Appalachian)	11	.136 (.0156)	11	.329 (.0114)	11	.344 (.0191)	11	.484 (.0225)	9	.120 (.0104)	10	.335 (.0143)	10	.349 (.0235)	10	.491 (.0268)
8-2212	Beech-Maple Forest (E. Deciduous)	6	.152 (.0126)	6	.328 (.0070)	6	.344 (.0118)	6	.485 (.0164)	3	.157 (.0046)	3	.325 (.0174)	3	.347 (.0201)	3	.485 (.0172)
8-2213	Maple-Basswood Forest (E. Deciduous)	9	.142 (.0144)	11	.321 (.0115)	11	.342 (.0169)	11	.472 (.0253)	3	.134 (.0235)	3	.340 (.0112)	3	.346 (.0144)	3	.494 (.0240)
4-2214	Appalachian Oak Forest (N. Hardwood-Conifer)	69	.136 (.0207)	69	.324 (.0120)	68	.341 (.0176)	68	.480 (.0229)	19	.131 (.0172)	19	.336 (.0155)	17	.338 (.0178)	17	.475 (.0226)
8-2214	Appalachian-Oak Forest (E. Deciduous)	36	.144 (.0210)	36	.328 (.0116)	36	.357 (.0252)	36	.486 (.0310)	12	.154 (.0280)	12	.344 (.0148)	11	.363 (.0261)	11	.470 (.0376)
8A-2214A	Appalachian Oak (Atlantic Coastal Marsh, north)	9	.157 (.0201)	9	.325 (.0143)	9	.374 (.0254)	9	.474 (.0228)	2	.154 (.0177)	2	.349 (.0071)	2	.380 (.0113)	2	.477 (.0714)
8-2215	Oak-Hickory Forest (E. Deciduous)	8	.138 (.0226)	8	.326 (.0110)	7	.356 (.0208)	7	.484 (.0231)	2	.132 (.0198)	2	.339 (.0042)	2	.358 (.0240)	2	.485 (.0212)
8-2320	Southeastern Mixed Forest (Eastern Deciduous)	42	.134 (.0194)	42	.332 (.0128)	41	.354 (.0276)	40	.485 (.0245)	16	.147 (.0183)	16	.344 (.0117)	18	.345 (.0197)	18	.470 (.0258)
8A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, south)	34	.140 (.0197)	34	.338 (.0144)	34	.362 (.0201)	34	.498 (.0251)	24	.135 (.0238)	24	.346 (.0148)	23	.360 (.0175)	23	.502 (.0350)
16A-2320A	Southeastern Mixed Forest (Atlantic Coastal Marsh, North Carolina)	8	.132 (.0232)	8	.334 (.0124)	8	.358 (.0157)	8	.494 (.0216)	4	.142 (.0307)	4	.342 (.0047)	4	.362 (.0191)	4	.502 (.0295)
7-2410	Willamette-Puget Forest (Pacific Rain Forest)	16	.124 (.0100)	16	.355 (.0117)	15	.293 (.0121)	16	.425 (.0174)	10	.128 (.0153)	10	.367 (.0074)	10	.286 (.0145)	10	.417 (.0263)

TABLE 9
CONTINUED

	Ecoregion section/life area	Males								Females							
		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
7-M2416	Alaska Pacific Forest (Pacific Rain Forest)	36	.140 (.0206)	36	.347 (.0155)	35	.265 (.0218)	35	.382 (.0232)	25	.138 (.0192)	25	.350 (.0148)	25	.268 (.0221)	25	.387 (.0301)
7-M2411	Sitka Spruce-Cedar-Hemlock (Pacific Rain Forest)	33	.133 (.0174)	35	.350 (.0124)	34	.289 (.0137)	34	.423 (.0263)	24	.127 (.0180)	24	.362 (.0141)	24	.290 (.0155)	24	.425 (.0236)
7-M2412	Redwood Forest (Pacific Rain Forest)	11	.119 (.0125)	11	.367 (.0113)	10	.296 (.0154)	11	.410 (.0319)	3	.112 (.0185)	3	.378 (.0210)	3	.287 (.0071)	3	.413 (.0139)
7-M2413	Cedar-Hemlock-Douglas-fir (Pacific Rain Forest, inland)	4	.112 (.0181)	4	.356 (.0039)	4	.284 (.0071)	4	.435 (.0537)	3	.148 (.0280)	3	.353 (.0070)	3	.288 (.0049)	3	.419 (.0257)
9-M2414A	California Mixed Evergreen Forest (Grasslands, San Francisco Bay Marsh, north)	1	.140 (—)	1	.317 (—)	1	.293 (—)	1	.436 (—)	1	.100 (—)	1	.385 (—)	1	.303 (—)	1	.421 (—)
7-M2415	Silver Fir-Douglas-fir Forest (Pacific Rain Forest, Cascades)	7	.131 (.0112)	7	.345 (.0117)	7	.318 (.0104)	7	.441 (.0306)	3	.142 (.0175)	3	.355 (.0118)	3	.297 (.0206)	3	.431 (.0320)
5-2530W	Tall-grass Prairie, west (Aspen Parklands, west)	2	.155 (.0283)	2	.321 (.0050)	2	.359 (.0078)	2	.491 (.0021)	0	—	0	—	0	—	0	—
10-2511	Oak-Hickory-Bluestem Parkland (Oak-Savannah)	2	.140 (.0283)	2	.312 (.0127)	2	.345 (.0127)	2	.487 (.0297)	0	—	0	—	0	—	0	—
5-2530E	Tall-grass Prairie, east (Aspen Parklands, east)	4	.157 (.0159)	4	.313 (.0120)	4	.330 (.0134)	4	.474 (.0298)	3	.171 (.0218)	3	.331 (.0178)	3	.330 (.0093)	3	.464 (.0053)
9-2531	Bluestem Prairie (Grasslands, Tall-grass, east)	1	.139 (—)	1	.315 (—)	1	.338 (—)	1	.481 (—)	1	.172 (—)	1	.320 (—)	1	.354 (—)	1	.531 (—)
9-2532	Wheatgrass-Bluestem-Needlegrass (Grasslands, Tall-grass, west)	6	.154 (.0161)	6	.322 (.0066)	6	.341 (.0140)	6	.472 (.0149)	2	.124 (.0064)	2	.323 (.0078)	2	.326 (.0219)	2	.467 (.0071)
6-M2610	Sierran Forest (Montane Woodland-Brush)	6	.144 (.0232)	6	.342 (.0138)	6	.319 (.0158)	6	.468 (.0209)	5	.130 (.0218)	5	.345 (.0060)	5	.317 (.0221)	5	.447 (.0262)
9-2610	California Grassland (Grasslands, Valley)	3	.146 (.0118)	3	.327 (.0055)	3	.345 (.0095)	3	.469 (.0146)	4	.132 (.0089)	4	.351 (.0037)	4	.334 (.0164)	4	.475 (.0103)

TABLE 9

CONTINUED

		Males								Females							
		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen	
	Ecoregion section/life area	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
9-M2610	Sierran Forest (Grasslands, Sierran)	1	.108 (—)	1	.359 (—)	1	.333 (—)	1	.478 (—)	0	—	0	—	0	—	0	—
14-2610	Sierran Forest (Piñon-Juniper-Oak, Sierran)	1	.143 (—)	1	.340 (—)	1	.300 (—)	1	.457 (—)	0	—	0	—	0	—	0	—
9-M2620	California Chaparral (Grasslands, California Coastal)	11	.115 (.0159)	11	.361 (.0121)	11	.308 (.0159)	11	.446 (.0195)	0	—	0	—	0	—	0	—
9-M2620A	California Chaparral (San Francisco Bay Marsh, north)	3	.112 (.0098)	3	.355 (.0145)	3	.313 (.0149)	3	.467 (.0257)	3	.111 (.0260)	3	.371 (.0051)	3	.295 (.0353)	3	.445 (.0112)
9-M2620B	California Chaparral (San Francisco Bay Marsh, south)	9	.111 (.0175)	8	.354 (.0106)	9	.302 (.0131)	9	.429 (.0298)	10	.115 (.0219)	10	.384 (.0117)	10	.299 (.0189)	10	.421 (.0222)
15-M2620	California Chaparral (Chaparral-Oak-Woodland)	30	.118 (.0137)	30	.352 (.0132)	32	.304 (.0157)	32	.437 (.0302)	12	.109 (.0199)	12	.364 (.0202)	12	.316 (.0214)	12	.452 (.0345)
9-3111	Grama-Needlegrass-Wheatgrass (Grasslands, Shortgrass, west)	2	.157 (.0042)	2	.323 (.0141)	2	.352 (.0021)	2	.483 (.0092)	4	.161 (.0182)	4	.333 (.0158)	4	.328 (.0241)	4	.466 (.0280)
6-M3111	Grand Fir-Douglas-fir (Montane Woodland-Brush, Oregon)	2	.147 (.0170)	2	.338 (.0028)	2	.302 (.0014)	2	.437 (.0156)	4	.144 (.0227)	4	.337 (.0058)	4	.299 (.0264)	4	.449 (.0147)
9-M3111	Grand Fir-Douglas-fir (Grasslands, Oregon)	9	.139 (.0202)	9	.321 (.0117)	9	.289 (.0106)	9	.434 (.0212)	4	.143 (.0154)	4	.344 (.0051)	4	.305 (.0125)	4	.436 (.0163)
11-M3111	Grand Fir-Douglas-fir (N. Desert Scrub, Oregon)	1	.127 (—)	1	.320 (—)	1	.290 (—)	1	.418 (—)	1	.103 (—)	1	.347 (—)	1	.333 (—)	1	.452 (—)
14-M3111	Grand Fir-Douglas-fir (Piñon-Juniper-Oak, Oregon)	11	.131 (.0125)	11	.329 (.0103)	11	.305 (.0168)	11	.444 (.0172)	3	.144 (.0271)	3	.335 (.0044)	3	.306 (.0131)	3	.436 (.0185)
6-M3112	Douglas-fir Forest (Montane Woodland-Brush, N. Rockies)	9	.146 (.0140)	9	.317 (.0080)	9	.301 (.0132)	9	.440 (.0262)	3	.132 (.0114)	3	.323 (.0031)	3	.305 (.0172)	3	.453 (.0452)

TABLE 9
CONTINUED

	Ecoregion section/life area	Males								Females							
		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen		Wing-tip/ wing		Tarsus/ wing		Ht. max./ culmen		Width max./ culmen	
		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
9-3112	Wheatgrass-Needlegrass (Grasslands, Short-grass, east)	5	.152 (.0132)	5	.311 (.0123)	5	.350 (.0113)	6	.494 (.0197)	6	.147 (.0227)	6	.331 (.0179)	6	.347 (.0149)	6	.477 (.0132)
11-M3112	Douglas-fir Forest (N. Desert Scrub)	12	.134 (.0107)	12	.324 (.0105)	11	.302 (.0105)	11	.441 (.0239)	3	.117 (.0210)	3	.347 (.0087)	3	.307 (.0035)	3	.444 (.0341)
9-3113	Grama-Buffalo Grass (Grasslands, Short-grass, south)	0	—	0	—	0	—	0	—	1	.156 (—)	1	.347 (—)	1	.321 (—)	1	.466 (—)
9-M3113	Ponderosa Pine-Douglas-fir (Grasslands, Short-grass, Rockies)	1	.157 (—)	1	.321 (—)	1	.344 (—)	1	.523 (—)	0	—	0	—	0	—	0	—
11-M3113	Ponderosa Pine-Douglas-fir (N. Desert Scrub)	1	.137 (—)	1	.313 (—)	1	.311 (—)	1	.447 (—)	0	—	0	—	0	—	0	—
14-M3113	Ponderosa Pine-Douglas-fir (Piñon-Juniper-Oak)	1	.140 (—)	1	.321 (—)	1	.315 (—)	1	.500 (—)	1	.136 (—)	1	.332 (—)	1	.295 (—)	1	.403 (—)
9-3120	Palouse Grassland (Grasslands)	21	.142 (.0122)	21	.339 (.0128)	21	.307 (.0195)	21	.436 (.0275)	9	.130 (.0169)	9	.354 (.0214)	9	.299 (.0121)	9	.432 (.0200)
14-M3120	Upper Gila Mountains Forest (Piñon-Juniper-Oak)	6	.107 (.0149)	6	.344 (.0062)	8	.303 (.0110)	8	.438 (.0262)	5	.112 (.0121)	5	.344 (.0140)	5	.302 (.0054)	5	.424 (.0037)
6-3131	Sagebrush-Wheatgrass (Montane Woodland-Brush)	2	.129 (.0035)	2	.324 (.0078)	2	.319 (.0248)	2	.462 (.0488)	0	—	0	—	0	—	0	—
9-3131	Sagebrush-Wheatgrass (Grasslands)	1	.152 (—)	1	.338 (—)	1	.288 (—)	1	.411 (—)	0	—	0	—	0	—	0	—
11-3131	Sagebrush-Wheatgrass (N. Desert Scrub)	65	.134 (.0180)	65	.326 (.0114)	63	.313 (.0146)	63	.451 (.0249)	31	.133 (.0180)	31	.335 (.0103)	32	.311 (.0171)	32	.449 (.0275)
14-3131	Sagebrush-Wheatgrass (Piñon-Juniper-Oak)	16	.128 (.0179)	15	.332 (.0145)	16	.318 (.0078)	16	.460 (.0222)	16	.125 (.0176)	16	.345 (.0116)	15	.315 (.0195)	15	.450 (.0239)
6-P3132	Grama-Galleta Steppe (Montane Woodland-Brush)	0	—	0	—	0	—	0	—	1	.114 (—)	1	.338 (—)	1	.304 (—)	1	.442 (—)
11-3132	Lahontan Saltbush-Greasewood (Northern Desert Scrub)	5	.116 (.0046)	5	.340 (.0115)	5	.321 (.0124)	5	.457 (.0190)	2	.130 (.0064)	2	.343 (.0141)	2	.326 (.0276)	2	.464 (.0219)

TABLE 9

CONTINUED

		Males								Females							
		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen		Wing-tip/wing		Tarsus/wing		Ht. max./culmen		Width max./culmen	
Ecoregion section/life area		N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)	N	M (s.d.)
14-3132	Lahontan Saltbush-Greasewood (Piñon-Juniper-Oak)	15	.128 (.0144)	14	.322 (.0092)	13	.309 (.0116)	12	.438 (.0181)	3	.119 (.0165)	3	.331 (.0096)	3	.316 (.0076)	3	.451 (.0078)
14-P3132	Grama-Galleta Steppe (Piñon-Juniper-Oak)	0	—	0	—	0	—	0	—	1	.124 (—)	1	.336 (—)	1	.283 (—)	1	.413 (—)
11-3133	Great Basin Sagebrush (N. Desert Scrub)	2	.112 (.0071)	2	.331 (.0170)	2	.299 (.0177)	2	.419 (.0050)	0	—	0	—	0	—	0	—
11-3134	Bonneville Saltbush-Greasewood (N. Desert Scrub)	1	.139 (—)	1	.340 (—)	1	.311 (—)	1	.455 (—)	2	.120 (.0156)	2	.348 (.0050)	2	.297 (.0007)	2	.436 (.0014)
6-3135	Ponderosa Shrub Forest (Montane Woodland-Brush)	0	—	0	—	0	—	0	—	1	.159 (—)	1	.350 (—)	1	.333 (—)	1	.471 (—)
11-3135	Ponderosa Shrub Forest (N. Desert Scrub)	1	.135 (—)	1	.318 (—)	1	.338 (—)	1	.439 (—)	0	—	0	—	0	—	0	—
14-3135	Ponderosa Shrub Forest (Piñon-Juniper-Oak)	0	—	0	—	0	—	0	—	1	.107 (—)	1	.339 (—)	1	.355 (—)	1	.496 (—)
13-3140	Mexican Highlands Shrub Steppe (Mesquite-Grasslands)	2	.120 (.0127)	2	.323 (.0219)	2	.294 (.0290)	2	.411 (.0028)	2	.105 (.0226)	2	.346 (.0057)	2	.314 (.0064)	2	.444 (.0071)
11-A3141	Wheatgrass-Needlegrass-Sagebrush (N. Desert Scrub)	5	.128 (.0121)	5	.322 (.0128)	5	.303 (.0092)	5	.443 (.0313)	0	—	0	—	0	—	0	—
11-A3142	Sagebrush-Wheatgrass (N. Desert Scrub)	4	.138 (.0116)	4	.314 (.0204)	4	.304 (.0203)	4	.443 (.0184)	1	.147 (—)	1	.307 (—)	1	.305 (—)	1	.481 (—)
13-3211	Grama-Tobosa (Mesquite-Grassland)	1	.109 (—)	1	.308 (—)	1	.282 (—)	1	.423 (—)	0	—	0	—	0	—	0	—
12-3221	Creosote Bush (S. Desert Scrub)	3	.123 (.0143)	3	.331 (.0113)	3	.307 (.0086)	3	.444 (.0090)	1	.097 (—)	1	.358 (—)	1	.302 (—)	1	.432 (—)
12-3222	Creosote Bush-Bur Sage (S. Desert Scrub)	22	.135 (.0184)	22	.332 (.0127)	22	.299 (.0128)	22	.421 (.0171)	11	.133 (.0192)	11	.334 (.0111)	12	.299 (.0115)	12	.431 (.0219)
17-M2620	California Chaparral (Mexican Pine-Oak)	3	.105 (.0070)	3	.327 (.0070)	4	.324 (.0199)	4	.456 (.0061)	0	—	0	—	0	—	0	—

[1] N = sample size; M = mean; s.d. = standard deviation, in parentheses.
[2] Life area, in parentheses.

Sagebrush-Wheatgrass > 9-3120 Palouse Grassland (♂); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂); 8A-2320A Atlantic Coastal Marshes (south) > 8A-2214A Atlantic Coastal Marshes (north) (♂, ♀); 9-3111 Short-grass Prairie (west) > 6-M3112 N. Rockies (montane) (♂); 11-3131 Sagebrush-Wheatgrass > 6-M3112 N. Rockies (montane) (♂); 6-M2610 Sierran Forest > 15-M2620 California Chaparral (♀).

Two life belts within the same Ecoregion Section differ significantly: 8A-2320A Southeastern Mixed Forest (Atlantic Coastal Marsh south) > 8-2320 Southeastern Mixed Forest (forest) (♂, ♀); 9-M2620 California Chaparral (grassland) > 9-M2620B California Chaparral (San Francisco Bay Marsh south (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B California Chaparral (San Francisco Bay Marsh south) (♂, ♀); 14-3131 Sagebrush-Wheatgrass (Piñon-Juniper) > 11-3131 Sagebrush-Wheatgrass (N. Desert Scrub) (♂); 11-3132 Lahontan Saltbush-Greasewood (N. Desert Scrub) > 14-3132 Lahontan Saltbush-Greasewood (Piñon-Juniper) (♂).

North-south transects. A Pacific Coast transect (Fig. 3, transect A) shows an initial significant decrease in maxilla widths in both sexes from the Alaska Range (Aleutians) to the Alaska Pacific followed by alternating increases and decreases to the California Chaparral. Significant decreases occur in both sexes from the Sitka Spruce-Cedar-Hemlock to the Redwood Forest, then a further significant decrease in females, but not males, to the California Chaparral. Maxima are in the Aleutian Islands and minima in the Redwood Forest for males, and California Chaparral for females.

In the Alaska-Cascades-Sierra Nevada transect (Fig. 3, transect B), there are alternating decreases and increases from the Alaska Pacific Forest to the California Chaparral, with significant decreases in both sexes from the California Grassland to California Chaparral. Maxima are in the California Grassland for both sexes and minima in the Columbia Forest (montane) for males and California Chaparral for females.

A transect through the Interior Basins (Fig. 3, transect C) shows an initial decrease, significant in males, from the Central Boreal to the Palouse Grassland, then an increasing trend to the Lahontan Saltbush-Greasewood of the western Great Basin, followed by a decrease, significant in females, to the Sonoran Desert. Maxima are in the Central Boreal, and minima in the Sonoran Desert in both sexes.

A transect along the Rocky Mountains (Fig. 3, transect D) shows a significant decrease in males from the Central Boreal to the Columbia Forest (moist), then a declining trend to the Mexican Shrub Steppe. Maxima are in the Central Boreal and minima in the Upper Gila Mountains Forest for both sexes.

A transect in the Central Plains (Fig. 3, transect E) shows little change with maxima for males in the Aspen Parkland, and in both Central Boreal and Shortgrass Prairie for females. Minima are in the Central Boreal for males and Aspen Parkland for females.

The Central Forests transect (Fig. 3, transect F) indicates little change. Maxima are in the Oak-Savannah for males and Central Boreal for females, and minima in the Spruce-Fir (Minnesota) for males and Oak-Hickory Forest for females.

The Eastern Forest transect (Fig. 3, transect G) indicates little change with maxima in the Southeastern Mixed Forest for both sexes, and minima in the

Northern Hardwood-Spruce (Maritime) for males, and Newfoundland Boreal for females.

The Atlantic Coastal Marsh transect (Fig. 3, transect H) shows a significant increase in both sexes from the northern to the southern portions.

East-west transects. In the most northern transect (Fig. 4, transect A), there is little change in maxilla width from the Newfoundland Boreal to the Central Boreal. Then there is a decrease, significant in males, to the Alaska Pacific followed by a significant increase in both sexes from there to the Alaska Range (Aleutians). Maxima are in the Aleutians for both sexes, and minima in the Alaska Pacific for males and the Newfoundland Boreal for females.

The median transect (Fig. 4, transect B) shows a slightly increasing trend from the northern Hardwoods-Spruce (Maritime) to the Short-grass Prairie, then a decrease, significant in males, to the Northern Rockies, then little change to the Sitka Spruce-Cedar-Hemlock on the coast. Maxima are in the Short-grass Prairie, and minima in the Northern Rocky Mountains for males and Columbia Forest (moist) for females.

In the most southern transect (Fig. 4, transect C), maxilla width decreases significantly in both sexes between the Southern Atlantic Coastal Marsh and the Southeastern Mixed Forest. Then, after little change to the Short-grass Prairie, there is a decrease, significant in males, to the Rocky Mountains Forest. This is followed by an increase, significant in males, to the Sagebrush-Wheatgrass of the Great Basin. A slightly increasing trend continues to the California Grassland, followed by a significant decrease in both sexes to the California Chaparral. Maxima are in the Atlantic Coastal Marsh (south) for both sexes, and minima in the Rocky Mountains Douglas-fir Forest for males and California Chaparral for females.

Discussion.—Birds with wider maxillae live in Aleutian tundra, grasslands, northern deserts, eastern forests and Atlantic coastal marshes, and birds with narrower maxillae are found in Pacific Rain Forest, western mountain forests, California Chaparral, southern deserts, and Mexican Shrub Steppe. In general, birds with wider maxillae occur east of the Rocky Mountains, except for western grasslands and northern deserts where wide maxillae are also found. Variation in maxilla width is quite similar to that in maxilla height.

There is a strong tendency for males to have wider maxillae than females. The decreasing order of female maxilla widths varies more from that of males between different Ecoregions than is the case with maxilla heights.

Ratio of Width of Maxilla to Culmen Length

Sex differences.—Of the 49 samples, males of 22 (45%) have higher ratios of width of maxilla to culmen length and females of 25 (51%) have higher ratios. In two, ratios do not differ between the sexes. These differences are significant in only one case (Southeastern Mixed Forest), in which males have higher ratios, and three cases (Northern Hardwoods-Conifer, Pacific Rain Forest, and Mesquite-Grassland) in which female ratios are higher. This is similar to the situation in ratios of height of maxilla to culmen length, indicating that females tend to have stouter bills than males.

Differences by Life Area (Fig. 1, Table 7).—Ratios of width of maxilla to length of culmen arranged in decreasing order for males are:

		♂ N	Mean	♀ N	Mean
10	Oak-Savannah	2	.487	0	—
8	Eastern Deciduous Forest	112	.484	47	.478
5	Aspen Parkland	6	.480	3	.464
4	Northern Hardwood-Conifer	110	.477	39	.477
3	Boreal	20	.473	6	.462
9	Grasslands	50	.453	31	.458
11	Northern Desert Scrub	94	.449	40	.449
14	Piñon-Juniper-Oak	49	.448	29	.444
6	Montane Woodland-Brush	26	.446	16	.448
15	Chaparral-Oak Woodland	32	.437	12	.452
12	Southern Desert Scrub	25	.424	13	.431
17	Mexican Pine-Oak	19	.420	3	.411
7	Pacific Rain Forest	113	.412	70	.410
13	Mesquite-Grassland	14	.399	6	.413
1	Arctic-Alpine (Aleutian)	57	.371	37	.365

Male and female mean ratios are highly correlated ($r = 0.96$, $P < 0.001$).

Males and females agree closely in order of magnitude except for the relative positions of Northern Hardwood-Conifer, Chaparral-Oak Woodland, and Mesquite-Grassland which are somewhat different. The decreasing orders of ratios of maxilla widths to culmen length of both males and females agree closely with the decreasing orders of the ratios of height of maxilla to length of culmen.

Statistically significant differences in ratios of width of maxilla to total culmen length representing adjoining Life Areas are: Boreal > Arctic-Alpine (Aleutian) (♂, ♀); Eastern Deciduous Forest > Northern Hardwoods-Conifer (♂); Eastern Deciduous Forest > Grasslands (♂, ♀); Montane Woodland-Brush > Pacific Rain Forest (♂, ♀); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Southern Desert Scrub > Mesquite-Grassland (♂); Mexican Pine-Oak > Mesquite-Grassland (♂); Grasslands > Chaparral-Oak Woodland (♂); Grasslands > Mesquite-Grassland (♂, ♀).

Means of ratios of width of maxilla to culmen length representing Life Areas within different Ecoregion Sections differ significantly from each other as follows:

Pacific Rain Forest

7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2416 Alaska Pacific (♂, ♀)

Grasslands

9-3112 Short-grass Prairie (east) > 9-3120 Palouse Grassland (♂)
9-2610 California Grassland (valley) > 9-M3111 Oregon Montane (grassland) (♂, ♀)
9-3111 Short-grass Prairie (west) > 9-3120 Palouse Grassland (♂, ♀)

Northern Desert Scrub

11-3132 Lahontan Saltbush-Greasewood > 11-3133 Great Basin Sagebrush (♂)

Southern Desert Scrub

12-3221 Mojave Desert > 12-3222 Sonoran Desert (♂)

Piñon-Juniper-Oak

14-3131 Sagebrush-Wheatgrass (Piñon) > 14-M3120 N. Gila Mountains (Piñon) (♂)

Chaparral-Oak-Woodland

17-M2620 California Chaparral (Mexican Pine-Oak-N) > 17 Mexican Pine-Oak (S) (♂)

Differences by Ecoregion Province (Fig. 2, Table 8).—Means of ratios of width of maxilla to culmen length arranged in order of decreasing magnitude for males are:

		♂ N	Mean	♀ N	Mean
2320	Southeastern Mixed Forest	83	.491	45	.487
3110	Short-grass Prairie	8	.491	11	.472
2510	Prairie Parkland	2	.487	0	—
2210	Eastern Deciduous Forest	148	.482	49	.479
2530	Tall-grass Prairie	13	.476	6	.476
1320	Boreal Forest	20	.473	6	.462
2110	Laurentian Forest	45	.472	21	.479
2610	California Grassland	3	.469	4	.475
P3130	Colorado Plateau	0	—	2	.457
M2610	Sierran Forest	8	.468	5	.447
3130	Intermountain Sagebrush	103	.450	56	.453
M3110	Rocky Mountains Forest	46	.444	19	.442
A3140	Wyoming Basin	9	.443	1	.447
M2620	California Chaparral	59	.440	25	.439
M3120	Upper Gila Mountains Forest	8	.438	5	.428
M2110	Columbia Forest	13	.436	4	.427
3120	Palouse Grassland	21	.436	9	.432
2410	Willamette-Puget Forest	16	.425	10	.422
3220	American Desert	25	.424	13	.431
17	Mexican Pine-Oak	15	.411	3	.340
M2410	Pacific Forest	92	.409	60	.409
3140	Mexican Shrub Steppe	13	.398	6	.413
M1310	Alaska Range (Aleutians)	57	.371	37	.365

Some disagreement is shown between the orders in size of ratios for males and females, although correlation of all male and female pairs is highly significant ($r = 0.89$, $P < 0.001$).

Significant differences in mean ratios of width of maxilla to total culmen of adjoining Ecoregion Provinces are: Yukon Forest (boreal) > Alaska Range (Aleutians) (♂, ♀); Eastern Deciduous Forest > Laurentian Forest (♂); Southeastern Mixed Forest > Eastern Deciduous Forest (♂); Pacific Forest > Alaska Range (Aleutians) (♂, ♀); California Grassland > California Chaparral (♀); Colorado Plateau > Upper Gila Mountains Forest (♀); Upper Gila Mountains Forest > Mexican Highlands Shrub Steppe (♂); Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂, ♀); Intermountain Sagebrush > American Desert (♂, ♀); Short-grass Prairie > Wyoming Basin (sagebrush) (♂); Sierran Forest > Pacific Forest (♂, ♀); Sierran Forest > American Desert (♂).

Differences by Ecoregion Section/Life Area (Fig. 2, Table 9).—Significant differences between means of ratios of width of maxilla to culmen length of adjacent Ecoregion Section/Life Area units are: 17 Mexican Pine-Oak (south) > 13-3140 (south) Mexican Shrub Steppe (south) (♂); 7-M2410 Alaska Pacific Forest > 1-M1310 Alaska Range (Aleutians) (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2410 Alaska Pacific Forest (♂, ♀); 8A-2320A Atlantic Coastal Marsh (south) > 8A-2214A Atlantic Coastal Marsh (north) (♂); 9-M2620 California Chaparral (grassland) > 6-M2610 Sierran Forest (♂); 9-3111 Short-grass Prairie (west) > 11-M3112 Northern Rockies (sagebrush) (♂); 11-3132 Lahontan Saltbush-Greasewood > 11-3133 Great Basin Sagebrush (♂); 12-3221 Southern Desert Scrub (Mojave) > 12-3222 S. Desert Scrub (Sonoran) (♂); 11-3131 Sagebrush-Wheatgrass > 9-3120 Palouse Grassland (♂); 3-1320B Central Boreal > 7-M2112 Columbia Forest (moist) (♂, ♀); 13-3140 Mexican Shrub Steppe (north) > 14-M3120 Upper Gila Mts. Forest (♀); 4-2111 Spruce-Fir (Minnesota) > 5-2530 E. Aspen Parkland (east) (♀).

Cases of significant differences between two Life Belts within the same Ecoregion Section are: 8A-2320A Southeastern Mixed Forest (Atlantic Coastal Marsh south) > 8-2320 Southeastern Mixed Forest (forest) (♂, ♀); 15-M2620 California Chaparral (chaparral) > 9-M2620B California Chaparral (San Francisco Bay Marsh south) (♀).

North-south transects. A transect along the Pacific Coast (Fig. 3, transect A) shows significantly increasing ratios of width of maxilla to total culmen in both sexes from the Alaska Range (Aleutians) to the Sitka Spruce-Cedar-Hemlock, then no change to the Redwood Forest, then another significant, in males, increase to the California Chaparral. Maxima are in the California Chaparral, and minima in the Aleutian Tundra in both sexes.

A transect from Coastal Alaska down the Cascades-Sierra Nevada chain (Fig. 3, transect B) shows a gradual increase in ratios to the California Grassland, then an insignificant decrease to the California Chaparral. Maxima are in the California Grassland, and minima in Alaska Pacific in both sexes.

A transect through the Interior Basins (Fig. 3, transect C), after an initial significant decrease in both sexes from the Central Boreal to the Palouse Grassland, shows an increasing trend to the Lahontan Saltbush-Greasewood of the western Great Basin, with a significant increase in male ratios from the Palouse Grassland to the Sagebrush-Wheatgrass of the northern Great Basin, then a decline, with a significant decrease in male ratios, from the Mojave Desert to the Sonoran Desert. Maxima are in the Central Boreal, and minima in the Sonoran Desert for both sexes.

A transect down the Rocky Mountains (Fig. 3, transect D) shows an initial significant decrease in both sexes from the Central Boreal to the Columbia Forest (moist), then a fluctuating pattern, with males differing from females in directions of variation but with an overall declining trend to the Mexican Highlands Shrub Steppe. Maxima are in the Central Boreal for both sexes, and minima in the Mexican Shrub Steppe for males and Columbia Forest (moist) for females.

The Central Plains transect (Fig. 3, transect E) shows no particular trend. Maxima are in the Short-grass Prairie for males, and Central Boreal for females. Minima are in the Central Boreal for males, and Aspen Parkland for females.

The Central Forest transect (Fig. 3, transect F) shows no particular trend. Maxima are in the Oak-Hickory-Bluestem Parkland for males and Spruce-Fir (Minnesota) for females. Minima are in the Central Boreal for males and Northern Hardwoods for females.

The Eastern Forest transect (Fig. 3, transect G) indicates no trend. Maxima are in the Appalachian Oak (deciduous) for males and northern Hardwoods-Spruce (Maritime) for females. Minima are in the northern Hardwoods-Spruce (Maritime) for males, and both Appalachian Oak (deciduous) and Southeastern Mixed Forest for females.

In the Atlantic Coastal Marshes (Fig. 3, transect H), there is an increase, significant in males, from north to south.

East-west transects. The most northern east to west transect (Fig. 4, transect A) shows a decreasing trend in ratios with a significant decrease in females from the Spruce-Fir of Minnesota to the Aspen Parkland, then further significant decreases in both sexes between the Central Boreal and Alaska Pacific and also from that section to the Aleutian Tundra. Maxima are in the Spruce-Fir (Minnesota), and minima in the Aleutian Tundra in both sexes.

The median transect (Fig. 4, transect B), shows a slightly increasing trend in males, but not in females, as far as the Short-grass Prairie, then a slight decline in both sexes, but without significant steps, to the Pacific Coast. Maxima are in the Short-grass Prairie for males and Northern Hardwoods-Spruce (Maritime) for females. Minima are in Sitka Spruce-Cedar-Hemlock of the Pacific Coast for males, and the Cedar-Hemlock-Douglas-fir Columbia Forest for females.

The southernmost transect (Fig. 4, transect C), after a significant decrease in both sexes from the Atlantic Coastal Marshes to the Southeastern Mixed Forest, shows no continuous trends or marked changes as far as the Short-grass Prairie. Then there is a significant decrease in males to the Rocky Mountains Forest. From there the trend is a gradual increase to the California Grassland, then a decline to the California Chaparral.

Discussion.—Ratios of width of maxilla to total culmen length are higher in eastern forests and parklands, particularly deciduous and mixed forests and adjoining coastal marshes. They are also high in grasslands, northern deserts, and Piñon-Juniper. Narrower maxillae compared with culmen lenghts are in Aleutian Tundra, Pacific rain forests, including the moist Columbia Forest, southern deserts, shrub steppe, and southern mountain forests. More northern Rocky Mountains Forest and the California Chaparral are intermediate.

The proportionate size of male to female ratios of maxilla width to total culmen lengths are approximately equal, with possibly a somewhat greater number of higher female than male ratios.

Discussion of All Bill Measurements

Sizes and shapes of bills based on total lengths of culmens, heights and widths of maxillae, and ratios of height and width to length vary differently with respect to ecogeographical distribution. The correlation between height of maxillae and total culmen lengths is poor ($r = 0.12$, $P < 0.1$) for male means in Ecoregion Province pairs. Total length of Song Sparrow bills tends to decrease from north to south in the western part of the continent, contradictory to Allen's rule, but this tendency is reversed south of the southern deserts, with an increase in Mexican areas. There is also an irregular increase southward in the eastern forests. In contrast, bill lengths increase from north to south in accordance with Allen's rule in some other species, including Brown Towhees, *Pipilo fuscus* (Davis 1951), species of *Parus* (Snow 1954), Wrentits, *Chamaea fasciata* (Bowers 1960), House Sparrows, *Passer domesticus* (Packard 1967; Johnston 1969; Johnston and Selander 1971), and Hermit Thrushes, *Catharus guttatus* (Aldrich 1968). Bills of Song Sparrows also tend to increase in length from east to west, particularly in the north. Bill and wing lengths generally agree in relative size from one population to another. The correlation of wing and bill lengths, probably related to overall size of bird, is high. For male means in Ecoregion Provinces, $r = 0.81$, $P < 0.001$. Males have longer bills than females in almost all cases, and the correlation between pairs of means representing different ecogeographical areas is high.

The heights and widths of the maxillae reflect overall size of bird to some extent, but also are indicative of bill shape. Smaller heights and widths of maxillae, and particularly their proportion of culmen lengths (ratios), indicate more slender bills; the reverse indicates stouter bills. Variation in height and width of maxillae is essentially the same from one population to another in both sexes. In fact their variations between Ecoregion Provinces are highly correlated ($r = 0.96$, $P < 0.001$ for males; $r = 0.85$, $P < 0.001$ for females). Ratios of maxilla height and width to culmen length, the best indicators of bill stoutness, also show excellent agreement between populations of Ecoregion Provinces in both sexes (male $r = 0.97$, $P < 0.001$; female $r = 0.88$, $P < 0.001$). More slender as well as longer bills are characteristic of Pacific coastal areas, particularly Aleutian Tundra and Pacific rain forests, including Columbia moist forest. Slender bills are found also in southern deserts, Mexican shrub steppes, and southern mountain forests in the southwestern United States and Mexico. Stouter bills are found in eastern forests and parklands, particularly deciduous forests and their adjoining coastal marshes. Stouter bills are found also in all grasslands. Bills in northern Rocky Mountain and Sierran forests, northern deserts, and western woodlands and chaparral are intermediate in stoutness.

Davis (1951) suggested (without documentation) that stouter bills of Brown Towhees, *Pipilo fuscus,* may be correlated with certain types of food. Boag and Grant (1981) found that more large-billed individuals of a Galapagos finch species survived by eating larger and harder seeds during a period of drought than small-billed individuals. Beecher (1951) demonstrated that size, shape, and degree of angulation of bills have mechanical advantages for handling seeds compared to insects in species of Emberizinae. Dilger (1956) found that, in thrushes (Turdinae), broader and shorter bills are associated with arboreal foraging and longer, narrower bills are associated with ground feeding. Pitelka (1951) with *Aphelocoma* jays and Snow (1954) with species of *Parus,* noted that a long, fine bill is adapted to feeding in conifers and a short, stout bill to feeding in broad-leaf habitats. Newton (1967) noted that differences in size and shape of bills of British finches are related to the size of seeds eaten. Hespenheide (1966) and Willson (1971, 1972) experimented with several species of American sparrows (Emberizinae) in captivity and found that species with stouter bills chose larger seeds and fed more easily on such seeds than did species with more slender bills. Data on Song Sparrow food habits presented in Appendix IV indicate that the slender-billed populations inhabiting the humid northwest coastal areas have a more insectivorous diet than those of the chaparral, grasslands, and deciduous forests. Birds in the latter populations may consume a higher proportion of seeds, particularly in the winter when availability of food is probably limiting to survival. Stouter bills would probably be an advantage for eating seeds at a time when insects are in short supply.

Female Song Sparrows tend to have stouter bills than males, as is particularly indicated by the ratios of maxilla height and width to total bill length, suggesting a possible sexual difference in types of food eaten. However, the possibly slightly stouter female bills are not in accordance with the food analysis shown in Appendix III; females, on average, appear to consume fewer seeds than males. There is some difference in the stoutness of male and female bills in relation to various Life Areas and Ecoregions, suggestive of possible sexual differences in food consumed in different ecological communities. These discrepancies, together with the geographic and seasonal differences discussed in Appendix IV, preclude general conclusions on sexual differences in bill shape as adaptations to types of food eaten.

TARSUS MEASUREMENTS

Tarsus Length

Sex differences.—Males have longer tarsi in 41 (84%) of the 49 samples, 20 of which are significantly longer. These males are in Ecoregion/Life Area Units 17, 1-M1310, 8-2211, 8-2212, 8-2320, 8A-2320A, 7-2410, 7-M2416, 7-M2411, 7-M2412, 7-M2413, 9-2532, 6-M2610, 9-M2620A, 15-M2620, 6-M3111, 6-M3112, 11-3131, 14-3131, and 12-3222. Females have longer tarsi in 8 cases (16%), but none are significantly so.

Differences by Life Areas (Fig. 1; Tables 1, 2).—Means of tarsal length arranged in decreasing order for males are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutian)	59	27.49	38	27.02
17	Mexican Pine-Oak	19	23.78	3	22.13
7	Pacific Rain Forest	115	23.49	72	23.11
13	Mesquite-Grassland	13	22.96	6	22.48
6	Montane Woodland-Brush	26	22.45	16	21.71

11	Northern Desert Scrub	93	22.33	42	21.75
14	Piñon-Juniper-Oak	50	22.31	30	21.88
9	Grasslands	51	22.20	31	21.92
15	Chaparral-Oak Woodland	31	21.92	12	21.30
12	Southern Desert Scrub	25	21.87	13	20.92
3	Boreal	22	21.67	6	21.15
8	Eastern Deciduous Forest	117	21.52	48	20.68
10	Oak-Savannah	2	21.50	0	–
4	Northern Hardwood-Conifer	116	21.30	41	21.03
5	Aspen Parkland	6	21.25	3	21.43

Male and female means are highly correlated ($r = 0.97$, $P < 0.001$).

Significant differences between means of adjoining Life Areas are as follows: Arctic-Alpine (Aleutian) > Boreal (♂, ♀); Boreal > Northern Hardwood-Conifer (♂); Eastern Deciduous Forest > Northern Hardwood-Conifer (♂); Grasslands > Eastern Deciduous Forest (♂, ♀); Pacific Rain Forest > Montane Woodland-Brush (♂, ♀); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Mesquite Grassland > Southern Desert Scrub (♂, ♀); Grasslands > Aspen Parkland (♂); Mesquite-Grassland > Grasslands (♂).

Significant differences in mean tarsal lengths in Life Areas within different Ecoregion Sections are:

Northern Hardwood-Conifer

4-2113 Northern Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂)

Pacific Rain Forest

7-2410 Willamette-Puget Forest > 7-M2412 Redwood Forest (♂, ♀)
7-M2416 Alaska Pacific Forest > 7-2410 Willamette-Puget Forest (♂)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2415 Cascades Forest (♂, ♀)

Eastern Deciduous Forest

8-2211 Mixed Mesophytic Forest > 8-2213 Maple-Basswood-Oak (♂)

Grasslands

9-3120 Palouse Grassland > 9-3112 Short-grass Prairie (east) (♂, ♀)
9-M3111 Oregon Montane (grassland) > 9-3111 Short-grass Prairie (west) (♀)
9-M3111 Oregon Montane (grassland) > 9-2610 California Grassland (valley) (♀)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of tarsal lengths in order of decreasing magnitude for males are:

		♂ N	Mean	♀ N	Mean
M1310	Alaska Range (Aleutians)	59	27.49	38	27.03
17	Mexican Pine-Oak	15	24.38	3	22.13
M2410	Pacific Forest	93	23.76	60	23.11
2410	Willamette-Puget Forest	16	23.64	10	22.84
3140	Mexican Shrub Steppe	14	22.81	6	22.48
M2610	Sierran Forest	8	22.70	5	21.54
3120	Palouse Grassland	22	22.69	9	22.71
3130	Intermountain Sagebrush	106	22.40	58	21.86
M2110	Columbia Forest	13	22.34	5	22.54
M3120	Upper Gila Mountains Forest	8	22.19	5	21.54
M3110	Rocky Mountains Forest	47	22.18	19	21.85
A3140	Wyoming Basin	9	22.09	1	21.00
2610	California Grassland	3	21.93	4	21.40
3220	American Desert	25	21.87	13	20.92
P3130	Colorado Plateau	0	—	2	21.25
2320	Southeastern Mixed Forest	87	21.83	46	21.37
1320	Boreal Forest	22	21.67	6	21.15
M2620	California Chaparral	57	21.61	25	20.95
2510	Prairie Parkland	2	21.50	0	—
2530	Tall-grass Prairie	13	21.46	6	21.05
2110	Laurentian Forest	48	21.43	21	21.19
2210	Eastern Deciduous Forest	148	21.36	52	21.01
3110	Short-grass Prairie	8	21.25	11	21.45

Male and female means are highly correlated ($r = 0.93$, $P < 0.001$).

Significant differences between tarsus means of adjoining Ecoregion Provinces are: Alaska Range (Aleutians) > Yukon Forest (boreal) (♂, ♀); Southeastern Mixed Forest > Eastern Deciduous Forest (♂, ♀); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); Sierran Forest > California Grassland (♂); Columbia Forest > Rocky Mountains Forest (♀); Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂); Intermountain Sagebrush > Rocky Mountains Forest (♂); Intermountain Sagebrush > American Desert (♂, ♀); Wyoming Basin > Short-grass Prairie (♂); Palouse Grassland > Rocky Mountains Forest (♂, ♀); Pacific Forest > Sierran Forest (♂, ♀); Sierran Forest > American Desert (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2, Tables 5, 6).—Mean tarsal lengths of adjacent Ecoregion/Life Area units differ significantly from each other as follows: 17 Mexican Pine-Oak (south) > 13-3140 Mexican Shrub Steppe (south) (♂); 8A-2320A Atlantic Coastal Marsh (south) > 8A-2214A Atlantic Coastal Marsh (north) (♂); 7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀); 6-M2610 Sierran Forest > 9-M2620 California Chaparral (grass) (♂); 9-3120 Palouse Grassland > 14-M3111 Oregon Montane (Piñon-Juniper) (♂); 1-M1310 Alaska Range (Aleutians) > 7-M2416 Alaska Pacific Forest (♂, ♀); 9-3120 Palouse Grassland > 11-3131 Sagebrush-Wheatgrass (♂); 7-M2112 Columbia Forest (moist) > 3-1320B Central Boreal (♂); 4-2113 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂).

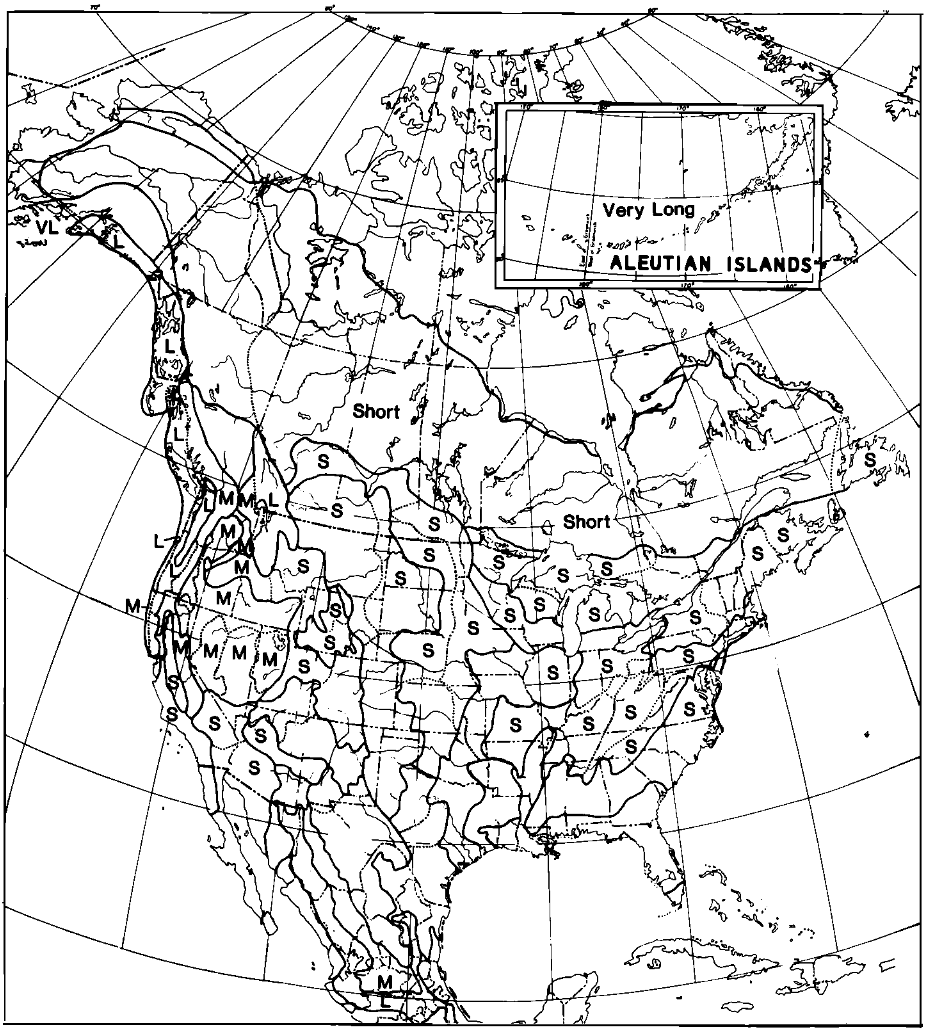

FIG. 23. Relative tarsus lengths of males in different Ecoregion Sections. L = longer; S = shorter; M = middle one-third of means; VL = very long.

Mean tarsal lengths of Life Belts (Life Areas) differing significantly within the same Ecoregion Section are as follows: 8-2214 Appalachian Oak (deciduous) > 4-2214 Appalachian Oak (northern hardwoods) (♂); 8-2214 Appalachian Oak (deciduous) > 8A-2214A Atlantic Coastal Marsh (north) (♂); 9-M2620 California Chaparral (grassland) > 9-M2620B California Chaparral (marsh south) (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B California Chaparral (marsh south) (♂); 9-M3111 Oregon Montane (grassland) > 14-M3111 Oregon Montane (Piñon-Juniper) (♀); 14-3131 Sagebrush-Wheatgrass (Piñon) > 11-3131 Sagebrush-Wheatgrass (sagebrush) (♀).

Relative lengths of tarsi of males in different Ecoregion Sections are shown in Figure 23.

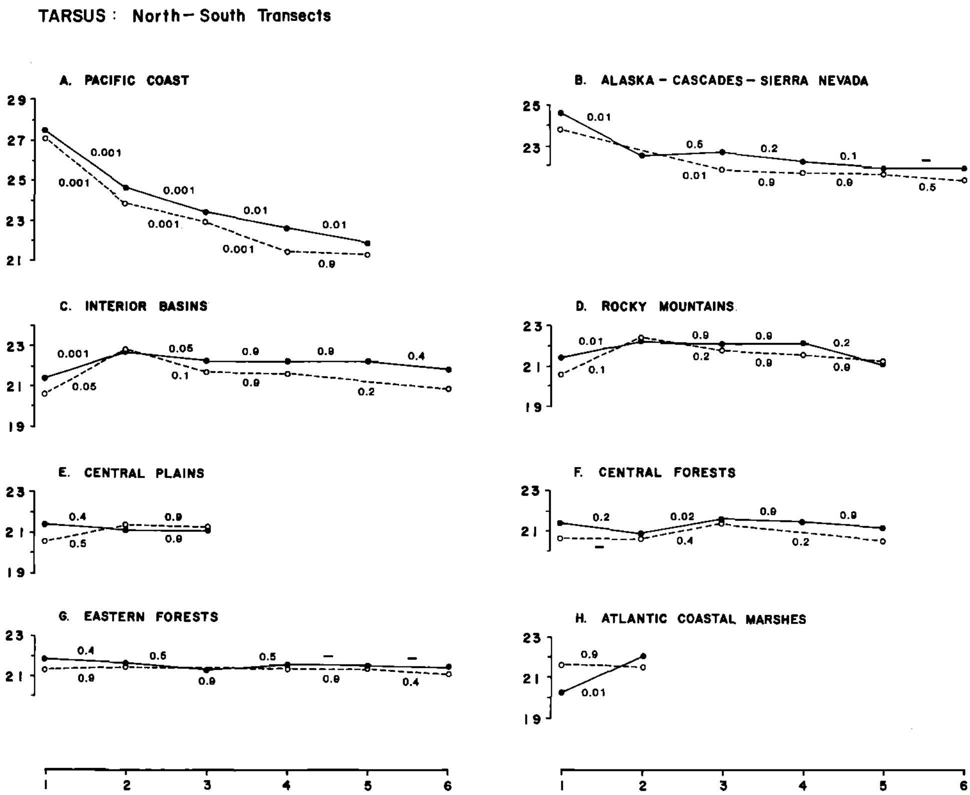

FIG. 24. North-south transects of mean tarsus lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

North to south transects. In a transect along the Pacific Coast (Figs. 3, 24, transect A) tarsal lengths decrease precipitously, with significant differences between each of the 5 sections from the Aleutian Islands to the California Chaparral in males, and as far as the Redwoods in females.

In the Alaska-Cascades-Sierra Nevada transect (Figs. 3, 24, transect B), there is an overall declining trend from coastal Alaska to the California Chaparral, but significant decreases occur only in males from Alaska Pacific to the Columbia Forest (montane), and in females from Alaska Pacific to the Silver Fir-Douglas-fir of the Cascades. In both sexes, maximum tarsal lengths are in the Alaska Pacific, and minimum lengths in the California Chaparral.

In the Interior Basins (Figs. 3, 24, transect C) an initial significant increase in tarsal length in both sexes, from the Central Boreal to the Palouse Grassland, is followed by a progression of slight decreases to the Sonoran Desert, with a significant decrease in males from the Palouse Grassland to the Sagebrush-Wheatgrass. No overall trend is shown. Maxima are in the Palouse Grassland, and minima in the Central Boreal for both sexes.

In the Rocky Mountains transect (Figs. 3, 24, transect D), no overall trend is shown. There is an increase in tarsal length, significant in males, from the Central Boreal to the Columbia Forest (moist), then slight increases and decreases without significant steps to the Mexican Shrub Steppe. Maxima are in the Columbia Forest for both sexes, and minima in the Mexican Shrub Steppe for males and the Central Boreal for females.

In the Central Plains (Figs. 3, 24, transect E), no trend is evident. Maxima are in the Central boreal for males, and Aspen Parkland for females. Minima are in the Aspen Parkland for males, and Central Boreal for females.

In the Central Forests (Figs. 3, 24, transect F), mean tarsal length of males increases significantly from the Spruce-Fir of Minnesota to the Northern Hardwoods of Wisconsin, but no overall trend is evident. Maxima are in the Northern Hardwoods of Wisconsin for both sexes, and minima in the Spruce-Fir of Minnesota for males and Oak-Hickory Forest for females.

In the Eastern Forests (Figs. 3, 24, transect G), no trends are apparent, and no significant differences between sections exist. Maxima are in the Newfoundland Boreal for males, and Northern Hardwoods-Spruce (Maritime) for females. Minima are in the Northern Hardwoods-Spruce (New England) for males, and Southeastern Mixed Forest for females.

The Atlantic Coastal Marsh (Figs, 3, 24, transect H) shows a significant increase from north to south in males but not females.

East-west transects. The most northern transect (Figs. 4, 25, transect A) shows a decrease in tarsal length, significant in males, from the Newfoundland Boreal to the Spruce-Fir forest of Minnesota, then a continuous increasing trend from there to the Aleutian Islands, with significant increases in both sexes from the Central Boreal to Alaska Pacific, and from there to the Aleutian tundra. Maxima are in the Aleutian Islands, and minima in the Spruce-Fir of Minnesota for males, and Central Boreal for females.

The median transect (Figs. 4, 25, transect B) shows hardly any change in tarsal length from the Northern Hardwoods-Spruce to the Tall-grass Prairie, then a significant decrease, in males, but not females, from there to the Short-grass Prairie. From the Short-grass Prairie on there is an increasing trend to the Pacific Coast, with significant increases in male tarsi from the moist Columbia Forest to the Silver Fir-Douglas-fir of the Cascades, and significant increases in both sexes from the Cascades to the Sitka Spruce-Cedar-Hemlock on the coast. Maxima are in the Sitka Spruce-Cedar-Hemlock, and minima in the Short-grass Prairie for both sexes.

In the southernmost transect (Figs. 4, 25, transect C) there is a trend of decreasing tarsal lengths to the Oak-Hickory Forest, with a significant decrease in male tarsi from the Atlantic Coastal Marsh (south) to the Southeastern Mixed Forest. A significant decrease in male, but not female, tarsi occurs from the western Tall-grass to the eastern Short-grass Prairie followed by a significant increase, in males, from there to the Middle Rocky Mountains. Little change in tarsi of either sex takes place from the Rocky Mountains to the California Chaparral.

Discussion.—The longest tarsi are found in birds living in the Aleutian tundra. The next longest are in the Pacific coastal forests, with a sharply decreasing cline southward. Long tarsi are found also in western mountain areas, and Mexican mountains and shrub steppe. The shortest tarsi are in birds of the San Francisco Bay marshes, but also short are those of birds in grasslands (particularly short-

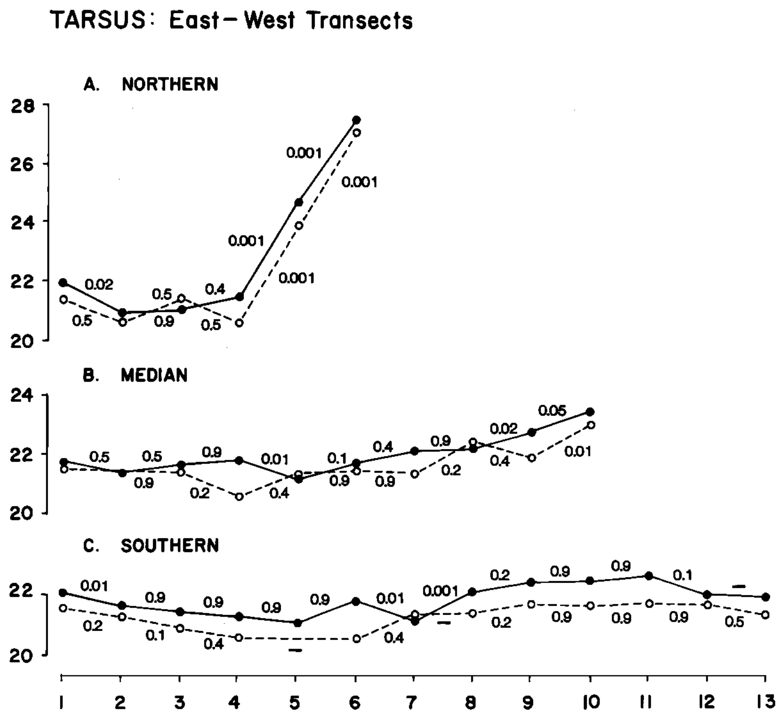

FIG. 25. East-west transects of mean tarsus lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of differences.

grass), eastern forests, and Atlantic coastal marshes, as well as California Chaparral. There is no north-south change in eastern forests.

Males have longer tarsi than females in most populations, and variation in tarsal length in the two sexes is highly correlated ($r = 0.93$, $P < 0.001$).

RATIO OF TARSUS LENGTH TO WING LENGTH

Sex differences.—In 34 (89%) of 38 samples females have a higher ratio of tarsus to wing lengths than males; the difference is significant in 17: 13, 1-M1310, 4-2112, 4-2113, 8-2213, 4-2214, 8-2320, 8-A2320A, 7-2410, 7-M2411, 9-M2620B, 15-M2620, 9-M3111, 11-M-3112, 9-3120, 11-3131, 14-3131. Males have longer tarsus to wing lengths ratios than females in four samples (11%), only one of which, the Mexican Pine-Oak, is significant.

Differences by Life Areas (Fig. 1; Table 7).—Mean ratios of tarsus to wing lengths arranged in order of decreasing values for males are:

		♂ N	Mean	♀ N	Mean
15	Chaparral-Oak Woodland	30	.352	12	.364
17	Mexican Pine-Oak	18	.352	3	.340
7	Pacific Rain Forest	114	.350	71	.358

13	Mesquite-Grassland	14	.346	6	.363
1	Arctic-Alpine (Aleutian)	58	.337	38	.346
6	Montane Woodland-Brush	26	.333	16	.340
12	Southern Desert Scrub	25	.332	12	.336
14	Piñon-Juniper-Oak	47	.329	30	.341
8	Eastern Deciduous Forest	114	.329	46	.340
9	Grasslands	49	.328	31	.342
3	Boreal	21	.328	6	.329
11	Northern Desert Scrub	97	.326	40	.337
4	Northern Hardwood-Conifer	114	.324	41	.336
5	Aspen Parkland	6	.316	3	.331
10	Oak-Savannah	2	.312	0	—

Male and female ratios are significantly correlated ($r = 0.79$, $P < 0.001$).

Significant differences between ratios of tarsus to wing lengths in adjoining Life Areas are: Arctic-Alpine (Aleutian) > Boreal (♂, ♀); Eastern Deciduous Forest > Northern Hardwood-Conifer (♂); Pacific Rain Forest > Montane Woodland-Brush (♂, ♀); Southern Desert Scrub > Northern Desert Scrub (♂); Mesquite-Grassland > Southern Desert Scrub (♂, ♀); Chaparral-Oak Woodland > Grasslands (♂, ♀); Mesquite-Grassland > Mexican Pine-Oak (♀); Mesquite-Grassland > Grasslands (♂, ♀).

Significant differences in means of tarsus to wing ratios representing Life Areas within different Ecoregion Sections are:

Boreal

3-1320A Newfoundland Boreal > 3-1320B Central Boreal (♂)

Northern Hardwood-Conifer

4-2113 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂)

Montane Woodland-Brush

6-M3111 Montane Woodland (Oregon) > 6-M3112 Montane Woodland (N. Rockies) (♀)

Pacific Rain Forest

7-M2412 Redwood Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂)
7-M2412 Redwood Forest > 7-M2415 Cascades Forest (♂)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♀)

Eastern Deciduous Forest

8-2320 Southeastern Mixed Forest > 8-2212 Beech-Maple Forest (♀)

Grassland

9-3120 Palouse Grassland > 9-M3111 Oregon Montane (grassland) (♂)

Northern Desert Scrub

11-3132 Lahontan Saltbush-Greasewood > 11-3131 Sagebrush-Wheatgrass (♂)

Mesquite Grassland

13-3140S Mexican Shrub Steppe (south) > 13-3140N Mexican Shrub Steppe (north) (♂)

14-M3120 N. Gila Mts. Forest (Piñon) > 14-M3111 Sagebrush-Wheatgrass (Piñon) (♂)

Mexican Pine-Oak

17-Mexican Pine-Oak (south) > 17-M2620 California Chaparral (Pine-Oak) (♂)

Differences in Ecoregion Province (Fig. 2, Table 8).—Means of ratio of tarsus to wing in order of decreasing values for males are:

		♂ N	Mean	♀ N	Mean
17	Mexican Pine-Oak	15	.357	3	.340
2410	Willamette-Puget Forest	16	.355	10	.367
M2620	California Chaparral	55	.353	25	.373
M2410	Pacific Forest	93	.350	60	.357
3140	Mexican Shrub Steppe	13	.348	6	.363
M2610	Sierran Forest	8	.344	5	.345
M3120	Upper Gila Mountains Forest	6	.344	5	.344
3120	Palouse Grassland	22	.339	9	.354
M2110	Columbia Forest	13	.338	5	.357
M1310	Alaska Range (Aleutians)	58	.337	38	.346
2320	Southeastern Mixed Forest	84	.335	44	.345
3220	American Desert	25	.332	12	.336
1320	Boreal Forest	21	.328	6	.329
3130	Intermountain Sagebrush	106	.328	56	.339
2610	California Grassland	3	.327	4	.351
2210	Eastern Deciduous Forest	151	.325	51	.338
2110	Laurentian Forest	47	.323	20	.337
P3130	Colorado Plateau	0	—	2	.337
M3110	Rocky Mountains Forest	47	.323	19	.338
2530	Tall-grass Prairie	13	.319	6	.327
A3140	Wyoming Basin	9	.318	1	.307
3110	Short-grass Prairie	7	.315	11	.333
2510	Prairie Parkland	2	.312	0	—

Male and female ratios are significantly correlated ($r = 0.75$, $P < 0.001$).

Significant differences between means of ratios between adjoining Ecoregion Provinces are: Alaska Range (Aleutians) > Yukon Forest (boreal) (♂, ♀); Southeastern Mixed Forest > Eastern Deciduous Forest (♂, ♀); Pacific Forest > Alaska Range (Aleutians) (♂, ♀); California Chaparral > California Grassland (♂, ♀); Columbia Forest > Rocky Mountains Forest (♂, ♀); Columbia Forest > Yukon Forest (boreal) (♀); Mexican Highlands Shrub Steppe > Mexican Pine-Oak (♀); Intermountain Sagebrush > Rocky Mountains Forest (♂); Rocky Mountains Forest >

Wyoming Basin (♀); Palouse Grassland > Rocky Mountains Forest (♂, ♀); Sierran Forest > American Desert (♂).

Differences by Ecoregion Section/Life Area (Fig. 2; Table 9).—Significant differences in means of tarsus to wing ratios of adjoining Ecoregion Section/Life Area units are: 7-M2416 Alaska Pacific Forest > 1-M1310 Alaska Range (Aleutians) (♂); 3-1320A Newfoundland Boreal > 3-1320B Central Boreal (♂); 7-M2412 Redwood Forest > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂); 15-M2620 California Chaparral > 9-2610 California Grassland (valley) (♂); 9-3120 Palouse Grassland > 9-M3111 Oregon Montane (grassland) (♂); 11-3132 Lahontan Saltbush-Greasewood > 11-3131 Sagebrush-Wheatgrass (♂); 13-3140S Mexican Shrub Steppe (south) > 13-3140N Mexican Shrub Steppe (north) (♂); 9-3120 Palouse Grassland > 11-3131 Sagebrush-Wheatgrass (♂); 7-M2112 Columbia Forest (moist) > 3-1320B Central Boreal (♂, ♀); 7-M2112 Columbia Forest (moist) > 6-M3112 N. Rockies (montane) (♂, ♀); 4-2113 N. Hardwoods (New York-Wisconsin) > 4-2111 Spruce-Fir (Minnesota) (♂); 8A-2320A Atlantic Coastal Marsh (south) > 8A-2214A Atlantic Coastal Marsh (north) (♂); 11-3131 Sagebrush-Wheatgrass > 6-M3112 N. Rocky Mts. (montane) (♂); 13-3140S Mexican Shrub Steppe (south) > 17-Mexican Pine-Oak (south) (♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2416 Alaska Pacific Forest (♂, ♀); 6-M3111 Oregon Montane Forest > 6-M3112 N. Rockies Montane Forest (♂, ♀); 14-3131 Sagebrush-Wheatgrass (Piñon) > 6-M3112 N. Rockies Montane Forest (♂, ♀).

Significant differences in tarsus to wing ratios between Life Belts occur in the California Chaparral Ecoregion Section where ratios in the Chaparral Belt (Life Area 15) are higher than in the Mexican Pine-Oak Belt (Life Area 17) of the same Section in northern Baja California (♂), but ratios of the Chaparral Belt are lower than in the San Francisco Bay Marsh Belt (♀); in the Lahontan Saltbush-Greasewood Section the Northern Desert Scrub Life Belt has a higher ratio than the Piñon-Juniper-Oak Life Belt (♂); in the Rocky Mountains Douglas-fir Forest Section the Northern Desert Scrub Belt has a higher ratio than the Montane Woodland-Brush Belt (♀); in the Sagebrush-Wheatgrass Section the Piñon-Juniper Belt has a higher ratio than the Northern Desert Scrub Belt (♀).

Relative ratios of tarsus to wing length of males in different Ecoregion Sections are shown in Figure 26.

North-south transects. A transect along the Pacific Coast (Figs. 3, 27, transect A) shows a sharply increasing trend in tarsus to wing ratios from the Aleutian Islands to the Redwood Forest, with significant increases between all sections in either male or female or both, then a decrease, significant in males, to the California Chaparral. Maxima are in the Redwood Forest, and minima in the Aleutian Islands for both sexes.

A transect from coastal Alaska along the Cascades and Sierra Nevada (Figs. 3, 27, transect B) shows relatively unvarying ratios, without significant differences between sections, except for a significant increase for males from the California grassland to the California Chaparral. Maxima are in the California Chaparral for both sexes. Minima are in the California Grassland for males and Sierran Forest for females.

In the Interior Basins (Figs. 3, 27, transect C) after a significant increase in ratios for both sexes from the Central Boreal to the Palouse Grassland, there is a significant decrease in both sexes to the Sagebrush-Wheatgrass, then a significant,

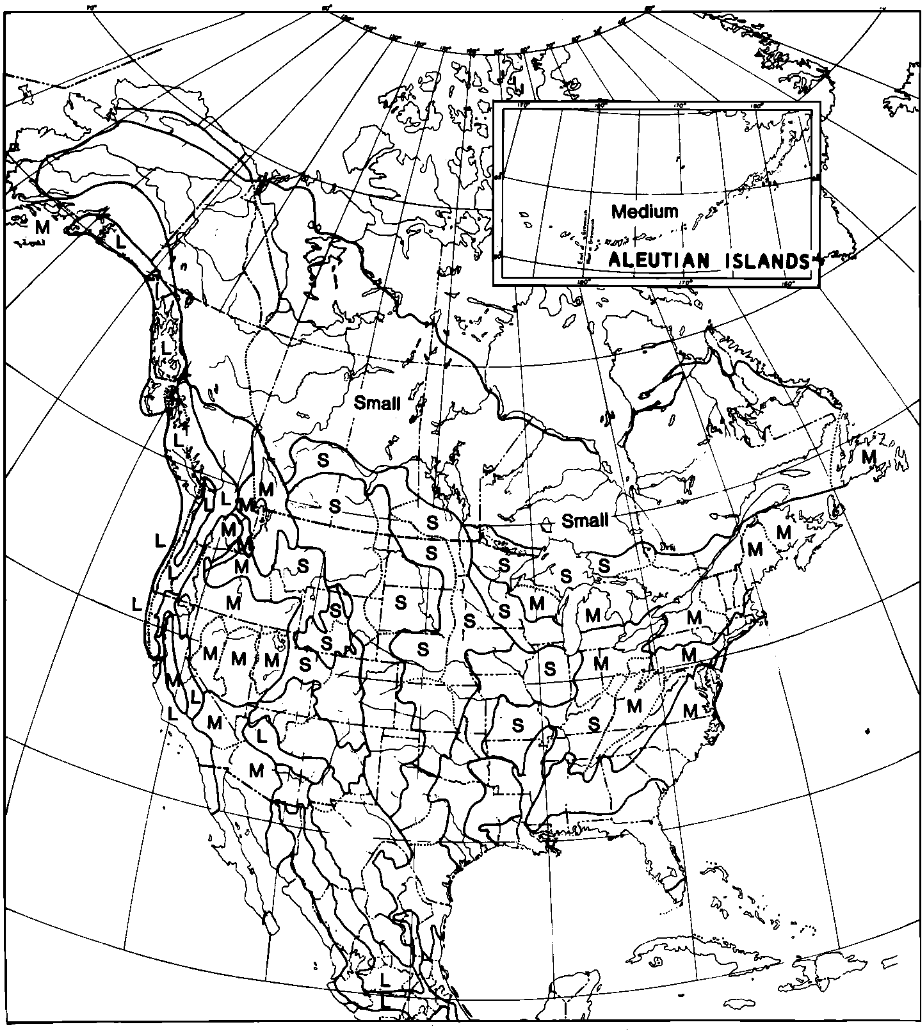

FIG. 26. Relative ratios of tarsus length to wing length of males in different Ecoregion Sections. L = larger; S = smaller; M = middle one-third of means.

in males, increase from the latter section to the Lahontan Saltbush-Greasewood, then little change from there to the Sonoran Desert. Maxima are in the Lahontan Saltbush-Greasewood for males and Palouse Grassland for females. Minima are in the Central Boreal for both sexes.

The Rocky Mountains transect (Figs. 3, 27, transect D) shows an irregular progression, with significant increases in both sexes from the Central Boreal to the moist Columbia Forest, then a significant decrease in both sexes from there to the Rocky Mountain Forest, then significant increase, in both sexes, to the Upper Gila Mountains Forest. Maxima are in the Upper Gila Mountains Forest for males, and moist Columbia Forest for females. Minima are in the Central Boreal and Northern Rockies for males, and Central Boreal for females.

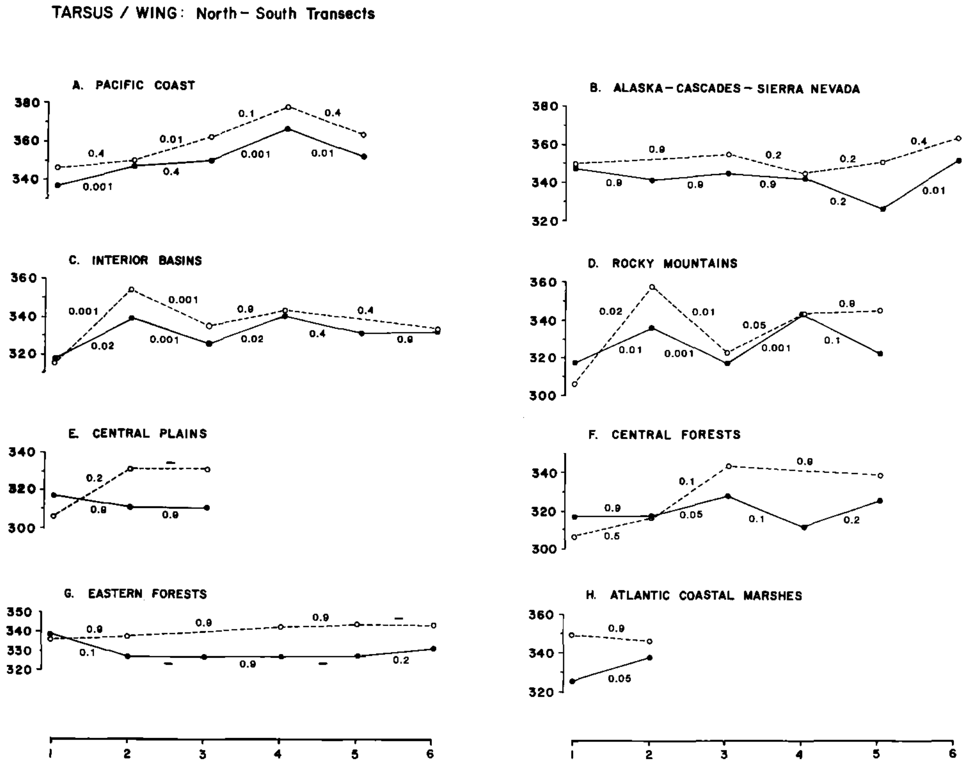

FIG. 27. North-south transects of mean tarsus to wing ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

The Central Plains transect (Figs. 3, 27, transect E) indicates no trend. Maxima are in the Central Boreal for males, and both Aspen Parkland and Short-grass Prairie for females. Minima are in the Short-grass Prairie for males, and Central Boreal for females.

A transect in the Central Forests (Figs. 3, 27, transect F) indicates no sustained trend in either sex but a significant increase in male ratios between the Spruce-Fir (Northern Hardwood-Conifer) of northern Minnesota and the Northern Hardwoods of Wisconsin. Maxima are in the Northern Hardwoods (Wisconsin) for both sexes, and minima in Oak-Hickory-Bluestem Parkland for males, and Central Boreal for females.

In the Eastern Forests (Figs. 3, 27, transect G) little change is indicated from north to south. Maxima are in the Newfoundland Boreal for males, and both Appalachian Oak (deciduous) and Southeastern Mixed Forest for females. Minima are in both Northern Hardwoods-Spruce (New England and Maritime) for males, and in the Newfoundland Boreal for females.

In the Atlantic Coastal Marshes (Figs. 3, 27, transect H) increases from the northern to the southern sections are significant in males, but not in females.

East-west transects. The most northerly transect (Figs. 4, 28, transect A) shows

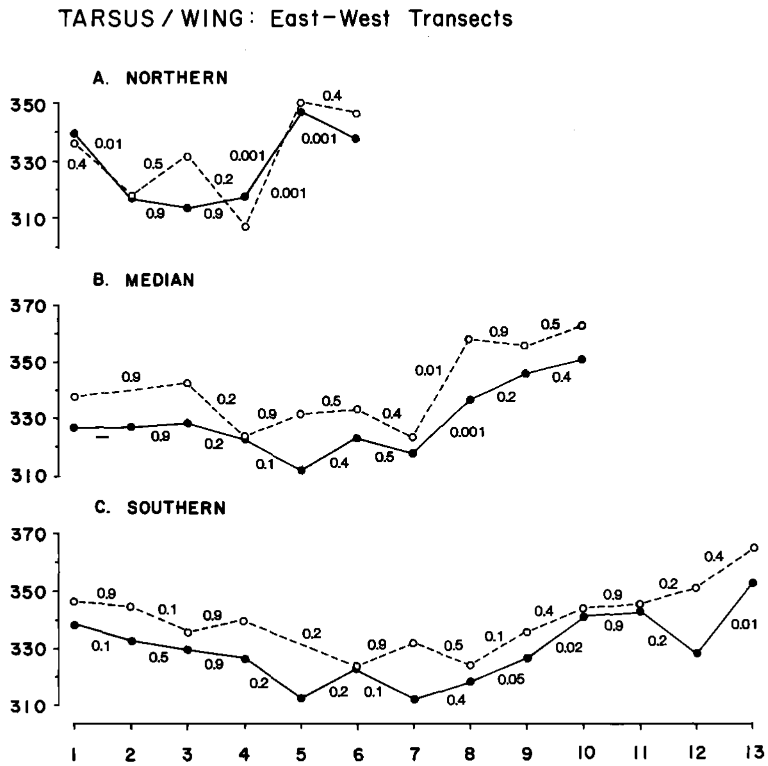

FIG. 28. East-west transects of mean tarsus to wing ratios. Figures on vertical axis are mean ratios. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

an initial decrease in tarsus to wing ratios, significant in males, from the Newfoundland Boreal to the Spruce-Fir of Minnesota, then an increasing trend, significant in both sexes from the Central Boreal to the Alaska Pacific, followed by a significant decrease in males from there to the Aleutian Islands. Maxima are in the Alaska Pacific Forest for both sexes, and minima in the Aspen Parkland for males, and Central Boreal for females.

The median transect (Figs. 4, 28, transect B) shows little change from the northern Hardwoods-Spruce (Maritime) to the Northern Rockies, then a significant increase in both sexes to the Cedar-Hemlock Douglas-fir Columbia Forest, followed by a slight further increase, without significant steps to the Sitka Spruce-Cedar-Hemlock on the coast. Maxima for both sexes are in the Sitka Spruce-Cedar Hemlock, and minima in the Short-grass Prairie (E) for males, and the Tall-grass Prairie (W) and Northern Rockies for females.

In the southernmost transect (Figs. 4, 28, transect C) there is a slight decreasing trend, without significant steps, from the Atlantic Coastal Marsh to the Short-grass Prairie (E), then an increasing trend to the Pacific Coast with significant increasing steps in males from the middle Rocky Mountains to the Sagebrush-Wheatgrass, and again from there to the Lahontan Saltbush-Greasewood. A further significant increase occurs in males from the California Grassland to the California Chaparral.

Discussion.—Ratios of tarsus length to wing length, which may be construed as indicating relatively long- or short-legged birds, are usually greater in females than males. They also show that relatively long legs are characteristic of Aleutian Tundra, Pacific coast rain forests (including the moist Columbia Forest), southern mountain forests and shrub steppes, Palouse Grassland, and California Chaparral. Relatively short legs are characteristic of all grasslands (except Palouse), prairie parklands, savannahs, Northern Rocky Mountains forests (except moist Columbia Forest), and all eastern forests from boreal to deciduous.

Sexual dimorphism in tarsal length and the ratio of tarsus to wing with respect to their differences in the various ecogeographic areas seems to be greater than is the case with other characters. This is especially true in the Mexican Pine-Oak, American Desert, and Short-grass Prairie. However, both paired male and female means for tarsus and paired tarsus-wing means for the various ecogeographical areas are highly correlated.

Discussion of All Tarsus Measurements

Although males exceed females in overall tarsal length in most populations, the reverse is true in proportion of tarsus length to wing length. Assuming that such ratios indicate relatively long or short legs in proportion to body size, females are much more frequently relatively long-legged than are males among Song Sparrows, as was also found with White-crowned Sparrows, *Zonotrichia leucophrys,* by Banks (1964). Banks also pointed out that tarsus/wing ratios show that wings vary in proportion to tarsi to the same degree that tarsi vary in proportion to wings, so in some cases it is the length of the wing and in others the length of the tarsus which is responsible for the proportional difference. However, that fact is immaterial here since, as an indication of possible functional differences, the present objective is to determine relative length of tarsus in proportion to the size of the bird, as indicated by wing length. As noted previously under the discussion of wing measurements, wing length is only an approximate indicator of the volume of a bird's body, but it is the best measure we have among available data.

Actual lengths of tarsi, which presumably reflect the overall size of the bird as in the case of wings, are greatest by far in the Aleutian Tundra, but among the birds with the longer tarsi, are those of the Pacific rain forests, western mountains, Mexican mountains and shrub steppes. Among birds with shorter tarsi, are those in the grasslands (except Palouse), California Chaparral, and both northern and southern eastern forests. Within these broad geographic areas, tarsal lengths show a steady decline in the relatively long Pacific Coast tarsi from the Aleutian tundra southward to the Redwoods; California Chaparral tarsi are longer than those of the San Francisco Bay marshes; there is a decrease in the American Desert from north to south; tarsi of the Eastern Deciduous Forest are longer than those of the adjoining Atlantic Coastal marshes as well as the adjoining Northern Hardwood Conifer Forest.

Relatively long legs are characteristic particularly of the rain forests of the Pacific northwest, but also Aleutian tundra, southern mountain forests, chaparral, Mexican pine-oak forests, and shrub steppes. Relatively short legs are characteristic of all grasslands (except the Palouse), prairie parklands, northern Rocky Mountain forests, and all eastern forests. In the majority of cases the proportional length of tarsus to wing agrees with the total length of tarsus in respect to variation between the same populations. Cases in which this is not true are in the northern deserts and Rocky Mountains Forest in which birds have long tarsi compared with other populations but relatively short as compared to wing length, and in the southern mountain forests, southern deserts and California Chaparral which have short legs but which are relatively long compared with their wing lengths. This would seem to indicate that little correlation exists between leg-length and habitat since long- and short-legged birds are associated with both open and closed vegetation.

There is, however, rough agreement between relatively long and short tarsi and relatively slender and stout bills, respectively, in Song Sparrows, particularly in Aleutian tundra, Pacific Forest, northern and southern eastern forests, grasslands, southern deserts, and Mexican shrub steppes. All pairs of mean ratios of maxilla height to culmen length and tarsus length to wing length for all Ecoregion Province males are significantly correlated ($r = 0.634$, $P < 0.01$). This suggests the possibility that, as in the case of bill shape, tarsal length may be correlated with different food habits in ecogeographic units. The only data supporting this is that presented in Appendix III which shows that long-legged, slender-billed Pacific Forest Song Sparrows consume a significantly larger amount of animal food in the critical winter season than do the short-legged, stout-billed eastern forest birds which subsist on a greater amount of seeds at that time. Observation by Fretwell (1969) that shorter tarsi of different species of Emberizidae, including the Song Sparrow, wintering near Raleigh, North Carolina, are correlated with more perching and scratching, and longer legs with ground feeding suggest some sort of relationship of leg length with feeding habits. The work of Dilger (1956) with thrushes, Newton (1967) with British finches, and Grant (1966) with several groups of birds support the concept that longer legs are associated with ground foraging. To my knowledge no ecogeographical variation in those types of Song Sparrow behavior has ever been determined. Whatever the adaptive functions of short and long legs may be, the difference between males and females in proportion of tarsus length to wing length suggests that longer legs may be more advantageous to females than males. This sexual dimorphism may relate to an apparent greater amount of animal food eaten by females (42.27% of diet compared with 39.27% for males), a difference which is almost significant at $P < 0.1$ (see Appendix V). This might appear to contradict evidence that females eat more seeds in proportion to insects in winter than males, as indicated by the fact that females have relatively stouter bills than males, a character that is correlated with greater winter seed consumption (Appendix V). These apparent discrepancies may result from the seasons when different types of food become critical in survival. Thus, insects may be more critical to females in the breeding season and seeds under adverse winter conditions. There is a possible functional relationship of these morphological differences between the sexes to their different breeding season roles in which males are primarily concerned with defense of territory, mate, and nest, and females with nest building, incubation, and feeding young, the last duty being shared by the male (Nice 1937). The greater amount of time spent by males in perching while singing and patrolling territories may favor shorter tarsi, whereas the greater amount of time spent by females running about on the ground, as compared to perching, in the course of nesting activities, may favor relatively longer tarsi. Both ideas, however, are highly speculative in view of the meager evidence of those morphological and behavioral relationships.

Tarsal lengths of Song Sparrows do not appear to conform to Allen's ecogeographical rule, with the longer ones being found in southern birds, although this rule has been found to apply to members of the genus *Parus* (Snow 1954), Wrentits (Bowers 1960), House Sparrows (Johnston 1969; Packard 1967; Johnston and Selander 1971), and Hermit Thrushes (Aldrich 1968). Investigations that agree with the present study by finding longer tarsi in northern birds, and, thus, conforming to Bergmann's rule as indicative of overall size of bird, are those with Brown Towhees (Davis 1951) and Philadelphia Vireos (Barlow and Power 1970).

TAIL MEASUREMENTS

Tail Length

Sex differences.—In all 49 samples, means of male tail measurements are longer than those of females, and in 31, significantly so (all except: Ecoregion Section/Life Area Units 17, 3-1320, 3-1320A, 4-2111, 7-M2112, 4-2114A, 8-2212, 8A-2214A, 7-M2413, 7-M2415, 9-2532, 9-M2620A, 9-3111, 6-M3111, 6-M3112, 9-3112, 14-3132, 13-3140).

Differences by Life Area (Fig. 1; Tables 1, 2).—Mean tail lengths in decreasing order for males by Life Areas are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutian)	51	78.96	37	73.77
11	Northern Desert Scrub	96	69.34	39	65.56
5	Aspen Parkland	6	69.20	3	63.40
14	Piñon-Juniper-Oak	50	68.94	29	64.69
12	Southern Desert Scrub	25	68.78	12	64.38
6	Montane Woodland-Brush	26	68.42	16	64.62
10	Oak-Savannah	2	68.35	0	—
9	Grasslands	47	67.89	30	63.98
3	Boreal	22	66.44	6	63.63
4	Northern Hardwood-Conifer	109	66.19	35	62.99
8	Eastern Deciduous Forest	113	65.73	42	62.43
7	Pacific Rain Forest	110	65.63	71	61.90
17	Mexican Pine-Oak	18	63.41	3	59.23
13	Mesquite-Grassland	12	63.18	6	59.10
15	Chaparral-Oak Woodland	31	62.07	11	57.41

Male and female means are highly correlated ($r = 0.98$, $P < 0.001$).

Significant differences between mean tail lengths in adjacent Life Areas are: Arctic-Alpine (Aleutian) > Boreal (♂); Grasslands > Eastern Deciduous Forest (♂, ♀); Northern Desert Scrub > Grasslands (♂, ♀); Southern Desert Scrub > Mesquite-Grasslands (♂, ♀); Grasslands > Chaparral-Oak Woodland (♂, ♀); Grasslands > Mesquite-Grassland (♂, ♀).

Significant differences between mean tail lengths representing Life Areas within different Ecoregion Sections are:

Northern Hardwood-Conifer

4-2111 Spruce-Fir (Minnesota) > 4-2112 N. Hardwoods-Fir (Upper Peninsula, Michigan) (♀)

Pacific Rain Forest

7-M2416 Alaska Pacific Forest > 7-2410 Willamette-Puget Forest (♂, ♀)
7-M2416 Alaska Pacific Forest > 7-M2411 Sitka Spruce-Cedar Hemlock (♂, ♀)
7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀)
7-M2415 Cascades Forest > 7-M2412 Redwood Forest (♂)

Northern Desert Scrub

11-A3142 Wyoming Basin > 11-3132 Lahontan Saltbush-Greasewood (♂)
11-3131 Sagebrush-Wheatgrass > 11-3132 Lahontan Saltbush-Greasewood (♂)

Mesquite-Grassland

13-3140N Mexican Shrub Steppe (north) > 13-3140S Mexican Shrub Steppe (south) (♂)

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of tail lengths representing Ecoregion Provinces in order of decreasing length for males are:

		♂ N	Mean	♀ N	Mean
M1310	Alaska Range (Aleutians)	51	78.96	37	73.77
M3110	Rocky Mountains Forest	46	70.30	19	65.37
A3140	Wyoming Basin	9	69.91	1	71.60
M3120	Upper Gila Mountains Forest	6	69.45	5	64.22
3130	Intermountain Sagebrush	108	68.90	54	65.12
3220	American Desert	25	68.78	12	64.38
2510	Prairie Parkland	2	68.35	0	—
3110	Short-grass Prairie	7	68.34	11	63.77
P3130	Colorado Plateau	0	—	2	65.05
2530	Tall-grass Prairie	12	68.18	6	63.97
3120	Palouse Grassland	20	66.97	9	64.49
M2610	Sierran Forest	8	66.75	5	62.76
2610	California Grassland	3	66.57	4	62.65
1320	Boreal Forest	22	66.44	6	63.63
2210	Eastern Deciduous Forest	141	65.95	48	62.92
M2410	Pacific Forest	90	65.69	60	61.98
2320	Southeastern Mixed Forest	77	65.67	40	61.97
M2110	Columbia Forest	12	65.31	5	63.22
2110	Laurentian Forest	47	65.13	18	62.69
2410	Willamette-Puget Forest	16	64.81	10	59.54
3140	Mexican Shrub Steppe	12	63.27	6	59.10
17	Mexican Pine-Oak	15	63.27	3	59.23
M2620	California Chaparral	56	60.76	23	55.13

Male and female means are highly correlated ($r = 0.92$, $P < 0.001$).

Significant differences in mean tail lengths in adjoining Ecoregion Provinces are: Alaska Range (Aleutians) > Boreal Forest (♂); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); California Grassland > California Chaparral (♂, ♀); Rocky Mountains Forest > Columbia Forest (♂); Rocky Mountains Forest > Intermountain Sagebrush (♂); Rocky Mountains Forest > Palouse Grassland (♂); American Desert > Sierran Forest (♂); Upper Gila Mountains Forest > Mexican Shrub Steppe (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 6, 7).—Means of tail lengths in adjoining Ecoregion Section/Life Area units which differ significantly are: 7-M2416 Alaska Pacific > 7-M2411 Sitka Spruce-Cedar-Hemlock (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2412 Redwood Forest (♂, ♀); 7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂, ♀); 13-3140N Mexican Shrub Steppe (north) > 13-3140S Mexican Shrub Steppe (south) (♂, ♀); 1-M1310 Alaska Range (Aleutians) > 7-M2416 Alaska Pacific (♂, ♀); 9-2610 California Grassland (valley) > 15-M2620 California Chaparral (♂); 11-3131 Sagebrush-Wheatgrass > 9-3120 Palouse Grassland (♂); 11-3131 Sagebrush-Wheatgrass > 11-3132 Lahontan Saltbush-Greasewood (♂); 12-3221 Mojave Desert > 11-3132 Lahontan Saltbush-Greasewood (♂); 6-M3112 Northern Rockies (montane) > 7-M2112 Columbia Forest (moist) (♂); 8A-2214A Atlantic Coastal Marsh (north) > 8A-2320A Atlantic Coastal Marsh (south) (♂); 5-2530E Aspen Parkland (east) > 4-2111 Spruce-Fir (Minnesota) (♂); 4-2111 Spruce-Fir (Minnesota) > 4-2112 N. Hardwoods-Fir (Upper Peninsula of Michigan) (♀).

Means of tail lengths in Life Belts of Ecoregion Section/Life Area units that differ significantly from each other are: 15-M2620 California Chaparral (chaparral) > 9-M2620 California Chaparral (grass) (♂); 15-M2620 California Chaparral (chaparral) > 9-M2620B California Chaparral (San Francisco Bay marsh south) (♂, ♀); 14-3132 Lahontan Saltbush (Piñon-Juniper) > 11-3132 Lahontan Saltbush (sagebrush) (♂); 9-M2620B California Chaparral (San Francisco Bay marsh south) > 9-M2620A California Chaparral (San Francisco Bay marsh north) (♂, ♀).

Relative lengths of tails of males in different Ecoregion Sections are shown in Figure 29.

North-south transects. A transect down the Pacific Coast (Figs. 3, 30, transect A) shows a sharply decreasing cline in mean tail length, with significant differences between sections in both sexes, from the Aleutian Islands to the Redwood Forest, then a significant (in males) increase from the Redwoods to the California Chaparral. Maxima are in the Aleutians, and minima in the Redwoods.

A transect from the Alaska Pacific down the Cascades and Sierras (Figs. 3, 30, transect B) shows nonsignificant and alternating increases and decreases with a slight decreasing trend to the California Grassland, then a significant (in males) decrease to the California Chaparral. Maxima are in the Alaska Pacific, and minima are in the California Chaparral for both sexes.

A transect through the Interior Basins (Figs. 3, 30, transect C) shows fluctuating increases and decreases without any overall trend, but with a significant increase from the Palouse Grassland to the Sagebrush-Wheatgrass in males, then a significant decrease from that section to the Lahontan Saltbush-Greasewood in males, followed by a significant increase in males to the Mojave Desert. Maxima are in

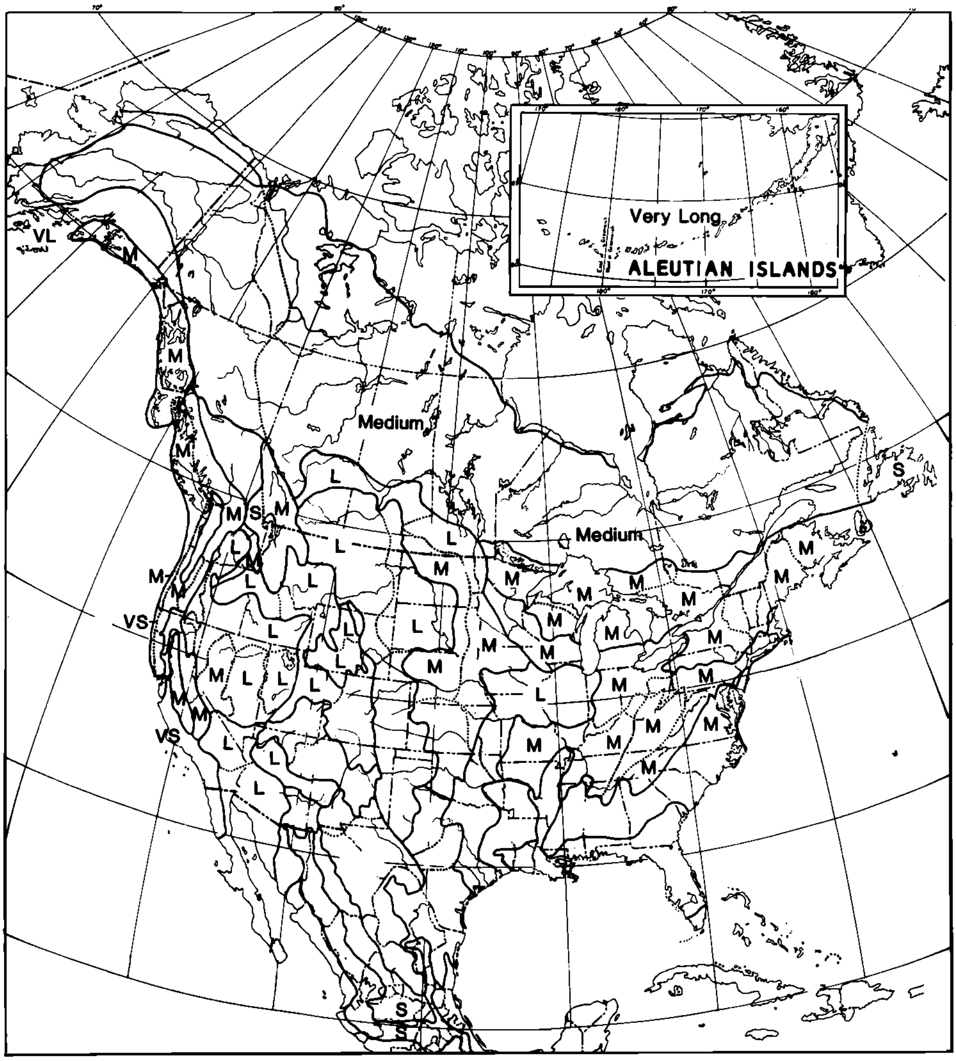

FIG. 29. Relative tail lengths of males in different Ecoregion Sections. L = longer; S = shorter; M = middle one-third of means; VL = very long; VS = very short.

the Mojave Desert for males, and Central Boreal for females. Minima are in the Lahontan Saltbush-Greasewood for both sexes.

A transect down the Rocky Mountains (Figs. 3, 30, transect D) indicates no particular trend. The only significant change is an increase in male tail lengths from the moist Columbia Forest to the Northern Rocky Mountains Forest. Maxima are in the Northern Rocky Mountains Forest for males, and Central Boreal for females. Minima are in the moist Columbia Forest for males, and Mexican Shrub Steppe for females.

A transect in the Central Plains (Figs. 3, 30, transect E) shows no trend. Maxima

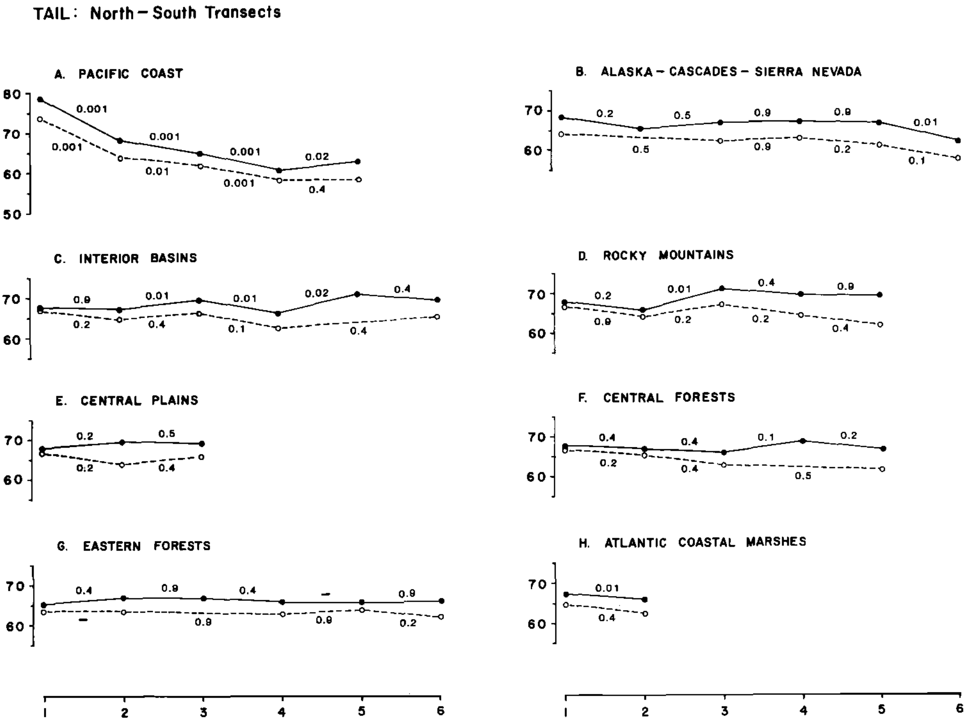

FIG. 30. North-south transects of mean tail lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

are in the Aspen Parkland for males, and Central Boreal for females. Minima are in the Central Boreal for males, and Aspen Parkland for females.

A transect in the Central Forests (Figs. 3, 30, transect F) shows only a slightly decreasing trend in females. Maxima are in the Oak-Hickory-Bluestem Parkland for males, and Central Boreal for females. Minima are in the Northern Hardwoods of Wisconsin for males, and Oak-Hickory for females.

A transect in the Eastern Forests (Figs. 3, 30, transect G) indicates no trend. Maxima are in the Northern Hardwoods-Spruce (Maritime) for both sexes. Minima are in the Newfoundland Boreal for males, and Southeastern Mixed Forest for females.

A transect in the Atlantic Coastal Marshes (Figs. 3, 30, transect H) shows a significant decrease in tail length from the northern to the southern marshes in males, but not in females.

East-west transect. The northern one (Figs. 4, 31, transect A) shows an increase in mean male tail length from Newfoundland Boreal to the Aspen Parkland, significantly from the Minnesota Spruce-Fir to the Aspen Parkland, then little change in either sex to Alaska Pacific, then a significant increase in both sexes to the Aleutian Islands. Maxima are in the Aleutian Islands. Minima are in the Newfoundland Boreal for males, and Aspen Parkland for females.

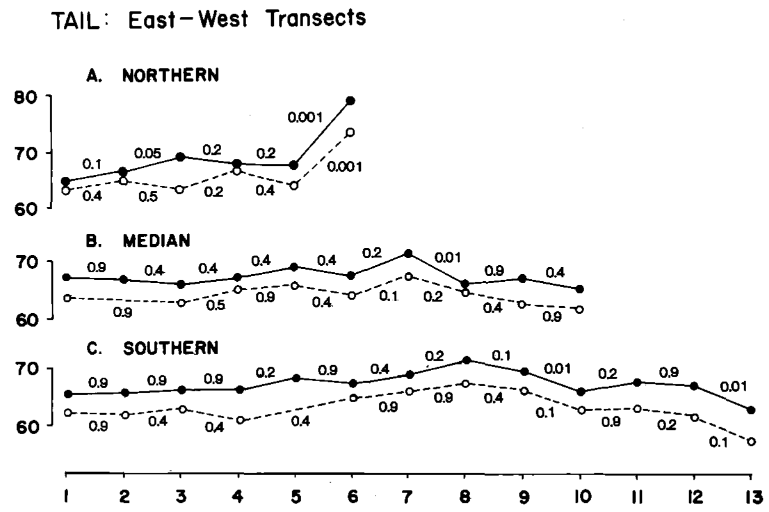

FIG. 31. East-west transects of mean tail lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4). Numbers between sections indicate probabilities of difference.

The median transect (Figs. 4, 31, transect B) shows little change from the Maritime Northern Hardwoods-Spruce to the Northern Rockies, then a significant decrease (in males) to the moist Columbia Forest, but no further change to the Pacific Coast. Maxima are in the Northern Rockies, and minima in the Sitka Spruce-Cedar-Hemlock for both sexes.

In the southernmost transect (Figs. 4, 31, transect C) a slight increase occurs, with no significant differences, between sections from the Atlantic Coastal Marshes to the middle Rocky Mountains, then a decrease to the Pacific Coast with significant decreases in males from the Sagebrush-Wheatgrass to the Lahontan Saltbush-Greasewood, and between the California Grassland and California Chaparral. Maxima are in the Douglas-fir of the middle Rockies, and minima in the California Chaparral for both sexes.

Discussion.—Populations with longer tails are in the Aleutian Tundra, dryer western mountain forests and woodlands (except Sierra Nevada), both northern and southern deserts, Piñon-Juniper, parklands, and Short-grass Prairie. Populations with shorter tails are in Pacific coastal rain forests and moist northwestern mountain forests, eastern forests, California Chaparral, Mexican Highlands Shrub Steppe, and Pine-Oak Forest. Boreal and Sierran Forest, California and Palouse Grasslands, and Tall-grass Prairie are intermediate in tail length. Within these broad categories significant differences occur between populations of different ecological situations. Most pronounced are those in the sharply decreasing tail lengths between components of the Pacific Forest. Also conspicuous are differences in different life belts or edaphic situations in the California Chaparral, Intermountain Sagebrush, and eastern forests.

Males usually have longer tails than females in any given population. There is good agreement in the decreasing order of mean tail length between the two sexes in different Life Areas, but there is more difference in this order of means between the sexes in various Ecoregion Provinces. These differences are particularly pronounced in the Upper Gila Mountains Forest, Palouse Grassland, California Grassland, and Columbia Forest. Reasons for these differences are not apparent. The correlation of male and female tail lengths is high in both Life Areas (r = 0.99, $P < 0.001$) and Ecoregion Provinces ($r = 0.96$, $P < 0.001$).

There is considerable difference between the rank of means of tail and wing lengths in both Life Areas and Ecoregion Provinces. In Life Areas the difference in rank of mean tail and wing are greatest in the Southern Desert Scrub, Pacific Rain Forest, and Mexican Pine-Oak. In Ecoregion Provinces differences in rank of tail and wing lengths are most noticeable in the Pacific Forest, Mexican Pine-Oak, Willamette-Puget Forest, Laurentian Forest, American Desert, Mexican Shrub Steppe, Sierran Forest, and Upper Gila Mountains Forest. In general, tails are relatively longer than wings in southern desert scrub and southern dry mountain forests and are relatively short in northern moist forests, Mexican mountain forests and shrub steppe. In other types of habitats, they are similar to wings in relative length. Despite these noted differences, overall the correlation between wing and tail lengths is high ($r = 0.85$ for males and 0.75 for females in Ecoregion Provinces, and $r = 0.89$ for both sexes in Life Areas, all significant at $P < 0.001$). Tails tend to vary like wings in accordance with Bergmann's rule, with longer tails in the north and high dry situations. Shorter tails are generally in more southern and low moist situations. There may be a general tendency for tails to be longer in dry and shorter in moist environments, irrespective of geographical location.

Ratio of Tail Length to Wing Length

Sex differences.—In 18 samples of Ecoregion Province populations, males had higher ratios of tail lengths to wing lengths in 9 instances, females higher in 3, and in 5 the ratios were equal. The only significant differences were the larger male ratios of tail to wing length in the Eastern Deciduous Forest, Upper Gila Mountains Forest and California Chaparral Ecoregion Provinces. Overall, males tend to have higher tail to wing ratios.

Differences by Ecoregion Province.—Differences in ratios of tail length to wing length in Ecoregion Province samples selected to show the full range of differences are, in order of decreasing magnitude for males:

		♂ N	Mean	♀ N	Mean
M3120	Upper Gila Mountains Forest	6	1.06	5	1.03
3220	American Desert	22	1.04	12	1.03
M3110	Rocky Mountains Forest	32	1.02	19	1.01
2211	Eastern Deciduous Forest	131	1.01	47	1.00
3110	Short-grass Prairie	7	1.01	11	0.99
3130	Intermountain Sagebrush	104	1.01	53	1.01
1320	Boreal Forest	18	1.00	5	1.01
2110	Laurentian Forest	46	1.00	33	0.99
M2620	California Chaparral	30	1.00	11	0.98
M1310	Alaska Range (Aleutians)	49	0.97	36	0.97
M2410	Pacific Forest	82	0.97	59	0.96
3140	Mexican Shrub Steppe	9	0.93	4	0.93
17	Mexican Pine-Oak	14	0.92	3	0.92

This order of relative tail lengths in Ecoregion Provinces agrees fairly closely with the order of tail lengths alone except for the relatively long tails in the Eastern Deciduous Forest and relatively short tails in the Alaska Range (Aleutians).

Male and female mean tail lengths are highly correlated ($r = 0.97$, $P < 0.001$).

Significant differences between mean ratios of tail to wing of selected Ecoregion Provinces are: Yukon Forest (boreal) > Alaska Range (Aleutians) (♂, ♀); Yukon Forest (boreal) > Pacific Forest (♂, ♀); American Desert > Short-grass Prairie (♂, ♀); American Desert > Intermountain Sagebrush (♂, ♀); American Desert > Yukon Forest (boreal) (♂); Rocky Mountain Forest > Pacific Forest (♂, ♀); Rocky Mountain Forest > Mexican Pine-Oak (♂, ♀); Rocky Mountain Forest > Alaska Range (Aleutians) (♂, ♀); Upper Gila Mts. Forest > Rocky Mountain Forest (♂); Upper Gila Mts. Forest > Eastern Deciduous Forest (♂, ♀); Upper Gila Mts. Forest > Yukon Forest (boreal) (♂); Intermountain Sagebrush > Mexican Shrub Steppe (♂, ♀); Intermountain Sagebrush > Pacific Forest (♂, ♀); Intermountain Sagebrush > Alaska Range (Aleutians) (♂, ♀); Short-grass Prairie > Pacific Forest (♂, ♀); Short-grass Prairie > Alaska Range (Aleutians) (♂, ♀); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); Alaska Range (Aleutians) > Mexican Shrub Steppe (♂, ♀); Eastern Deciduous Forest > Pacific Forest (♂, ♀); Eastern Deciduous Forest > Alaska Range (Aleutians) (♂, ♀).

Discussion.—Based on all comparisons it appears that the highest ratios of tail length to wing length are in the Upper Gila Mountains Forest, American Desert, Rocky Mountains Forest, Deciduous Forest, Short-grass Prairie and Intermountain Sagebrush, and the lowest ratios are in the Pacific Forest, Alaska Range (Aleutians), Mexican Pine-Oak, and Mexican Shrub Steppe. Others are intermediate. These values agree in order of size with those for total tail length fairly closely, except for the complete difference in the Alaska Range (Aleutians) birds which have long tails but whose tails are relatively short compared to their wings. Sex differences in tail to wing length ratios are highly correlated and are similar to those differences in total wing length; males have higher values than females in both cases.

Discussion of All Tail Measurements

Both total length of tail and ratio of tail to wing, with few exceptions, agree in rank with wing measurements between ecogeographical units. Overall the correlation is high. Tail measurements conform to Bergmann's ecogeographic rule, reflecting larger overall body size in the colder regions, as do wing measurements. Mean tail lengths both actually and proportionally, are greater in some southern parts of the species range, particularly the Southern Desert Scrub and southern mountain forests, whereas several of the populations with shorter mean tail lengths are in the more northern Pacific rain forests as well as the Mexican areas. There may be a tendency for birds with longer tails to be in dry and those with short tails in moist environments, irrespective of geographical location. However, birds with both long and short tails are found in open, closed, and mixed vegetation types. Also tail length seems not to be related to migration, as long- and short-tailed groups contain birds with migratory, sedentary, and mixed migratory habits. The well known habit of tail "pumping" by Song Sparrows (= "broken-backed flight" of Stone 1937) while flying from one patch of cover to another, may be of survival value in confusing predators. If true, relatively longer tails may be advantageous.

MIDDLE TOE LENGTH

Sex differences.—In the 49 populations sampled mean middle toe lengths of males are greater than those of females in 38 (78%), six significantly so (1-M1310, 7-M2416, 7-M2411, 9-M2620B, 15-M2620, and 11-3131). Female mean toe lengths are greater in 11 cases (22%), none of which is significant.

Differences by Life Area (Fig. 1; Tables 1, 2).—Mean toe lengths in decreasing order are:

		♂ N	Mean	♀ N	Mean
1	Arctic-Alpine (Aleutian)	59	19.07	38	18.46
7	Pacific Rain Forest	114	16.39	71	15.95
17	Mexican Pine-Oak	18	15.85	3	15.27
13	Mesquite-Grassland	14	15.46	6	14.82
6	Montane Woodland-Brush	26	15.39	16	14.98
11	Northern Desert Scrub	96	15.19	42	14.81
9	Grasslands	51	15.11	31	14.94
3	Boreal	22	15.09	6	14.95
4	Northern Hardwood-Conifer	115	15.05	41	14.75
14	Piñon-Juniper-Oak	51	15.05	30	14.70
15	Chaparral-Oak Woodland	32	15.03	12	14.26
8	Eastern Deciduous Forest	118	15.00	48	14.85
10	Oak-Savannah	2	14.75	0	—
5	Aspen Parkland	6	14.72	3	15.07
12	Southern Desert Scrub	25	14.34	13	14.11

Male and female means are highly correlated ($r = 0.97$, $P < 0.001$).

Significant differences between mean middle toe lengths in adjacent Life Areas are: Arctic-Alpine (Aleutian) > Boreal (♂, ♀); Pacific Rain Forest > Montane Woodland-Brush (♂, ♀); Montane Woodland-Brush > Piñon-Juniper (♂); Northern Desert Scrub > Southern Desert Scrub (♂, ♀); Grasslands > Chaparral-Oak Woodland (♀).

Significant differences between toe lengths of birds from different Ecoregion Sections within Life Areas are: 3-1320A Newfoundland Boreal > 3-1320B Central Boreal (♂); 7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂); 14-3132 Lahontan Saltbush (Piñon) > 14-M3120 Gila Mountains (Piñon-Juniper) (♂, ♀); 7-M2411 Sitka Spruce-Cedar-Hemlock > 7-M2415 Cascades Forest (♀); 11-3132 Lahontan Saltbush-Greasewood > 11-3131 Sagebrush-Wheatgrass (♀).

Differences by Ecoregion Province (Fig. 2; Tables 3, 4).—Means of middle toe lengths in order of decreasing values for males are:

		♂ N	Mean	♀ N	Mean
M1310	Alaska Range (Aleutians)	59	19.07	38	18.46
2410	Willamette-Puget Forest	16	16.73	10	16.08
M2410	Pacific Forest	93	16.40	60	15.91
17	Mexican Pine-Oak	15	16.15	3	15.27
3140	Mexican Shrub Steppe	14	15.46	6	14.82
M2110	Columbia Forest	13	15.32	5	15.06

M2610	Sierran Forest	8	15.28	5	14.94
3120	Palouse Grassland	22	15.23	9	15.30
3130	Intermountain Sagebrush	108	15.20	58	14.76
M3110	Rocky Mountain Forest	47	15.10	19	14.94
P3130	Colorado Plateau	0	—	2	14.85
1320	Yukon Forest (boreal)	22	15.09	6	14.95
2320	Southeastern Mixed Forest	88	15.06	46	14.54
2210	Eastern Deciduous Forest	152	15.05	52	14.92
2110	Laurentian Mixed Forest	47	15.02	21	14.66
2610	California Grassland	3	15.00	4	14.65
M2620	California Chaparral	59	14.99	25	14.08
A3140	Wyoming Basin	9	14.94	1	15.10
3110	Short-grass Prairie	8	14.93	11	14.79
2530	Tall-grass Prairie	13	14.92	6	14.93
2510	Prairie Parkland	2	14.75	0	—
M3120	Upper Gila Mountains Forest	8	14.53	5	14.16
3220	American Desert	25	14.34	13	14.11

Male and female means are highly correlated ($r = 0.96$, $P < 0.001$).

Chief sex differences in the order of mean values for middle toe are for the Wyoming Basin, Tall-grass Prairie, Mexican Shrub Steppe, and Intermountain Sagebrush.

Significant differences between mean middle toe lengths for populations in adjacent Ecoregion Provinces are: Alaska Range (Aleutian) > Yukon Forest (boreal) (♂, ♀); Alaska Range (Aleutians) > Pacific Forest (♂, ♀); Mexican Highlands Shrub Steppe > Upper Gila Mountains Forest (♂, ♀); Mexican Pine-Oak > Mexican Highlands Shrub Steppe (♂); Intermountain Sagebrush > American Desert (♂, ♀); Pacific Forest > Sierran Forest (♂, ♀); Sierran Forest > American Desert (♂, ♀).

Differences by Ecoregion Section/Life Area (Fig. 2; Tables 5, 6).—Significant differences between adjacent Ecoregion/Life Area units are: 17 Mexican Pine-Oak (south) > 13-3140S Mexican Shrub Steppe (south) (♂); 3-1320A Newfoundland Boreal > 3-1320B Central Boreal (♂); 7-M2112 Columbia Forest (moist) > 3-1320B Central Boreal (♂); 7-M2413 Pacific Forest (inland) > 7-M2412 Redwood Forest (♂); 1-M1310 Alaska Range (Aleutians) > 7-M2416 Alaska Pacific Forest (♂, ♀); 13-3140N Mexican Shrub Steppe (north) > 14-M3120 Upper Gila Mountains Forest (♂); 9-3120 Palouse Grassland > 11-3131 Sagebrush-Wheatgrass (♀); 11-3132 Lahontan Saltbush-Greasewood > 11-3131 Sagebrush-Wheatgrass (♀); 6-M3112 Rocky Mountain Forest > 9-3111 Short-grass Prairie (west) (♀).

In no instances did mean toe length differ significantly between Life Belts (Life Areas) within the same Ecoregion Section. Differences between Ecoregion Sections within the same Ecoregion Province are found in the Pacific Forest, Boreal Forests, and Intermountain Sagebrush.

Relative lengths of middle toes of males in different Ecoregion Sections are shown in Figure 32.

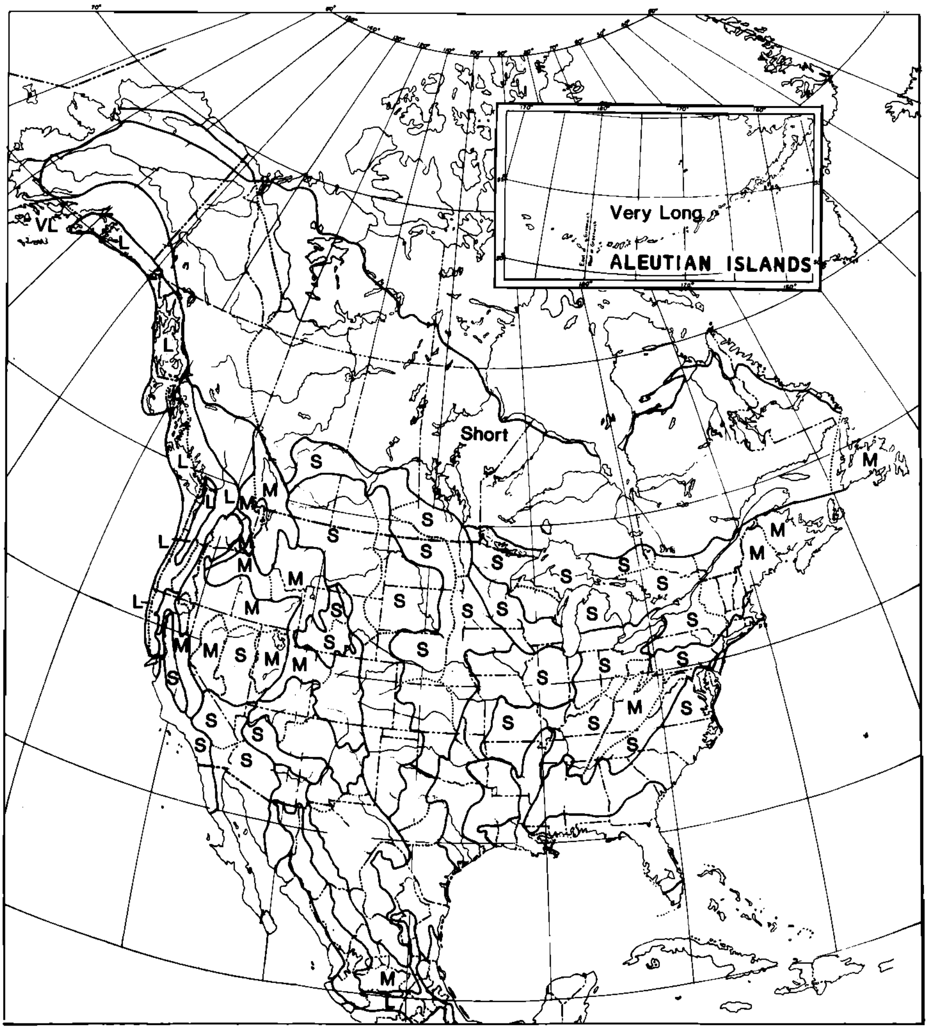

FIG. 32. Relative middle toe lengths of males in different Ecoregion Sections. L = longer; S = shorter; M = middle one-third of means; VL = very long.

North-south transects. A transect along the Pacific Coast (Figs. 3, 33, transect A) indicates a continuous decrease in mean toe length from the Aleutian Tundra to the California Chaparral, with significant decreases in both sexes from the Aleutians to the Alaska Pacific and from the Redwoods to the California Chaparral.

A transect from the Alaska Pacific down the Cascades and Sierra Nevada (Figs. 3, 33, transect B) shows a decreasing trend in both sexes, with significant decrease, in average male toe lengths, to the Columbia Forest (montane), then, after a slight increase to the Cascades, a further slow decrease from there to the California Chaparral. Maxima are in the Alaska Pacific Forest, and minima in the California Chaparral for both sexes.

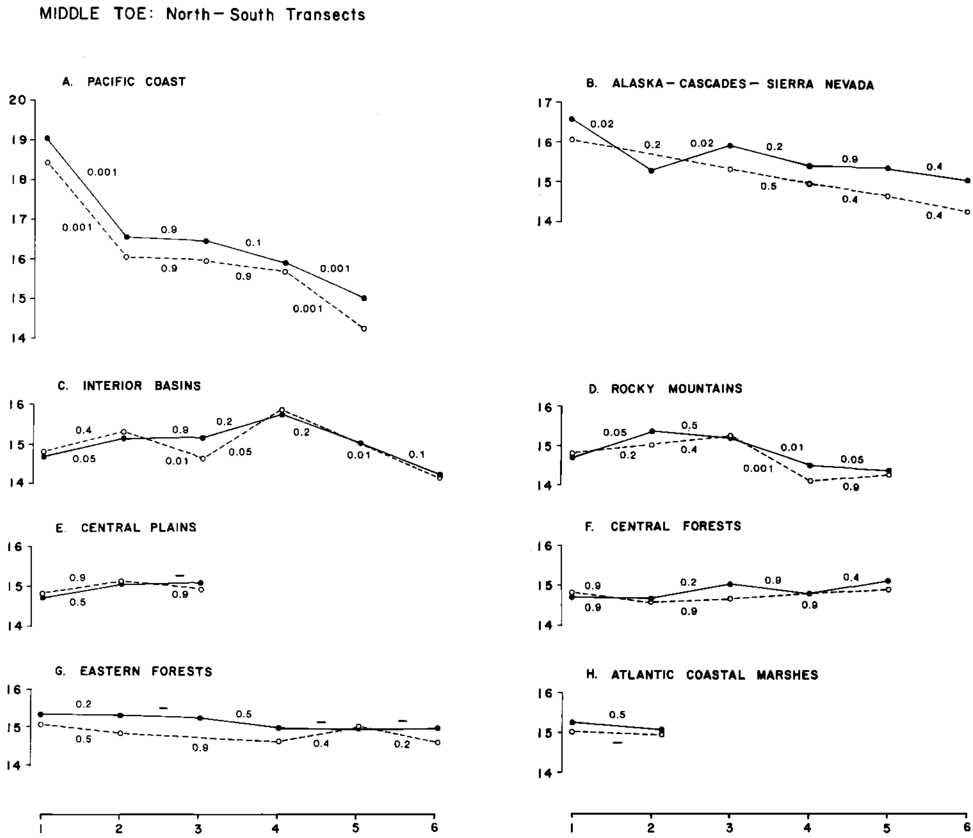

FIG. 33. North-south transects of mean middle toe lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 3). Numbers between sections indicate probabilities of difference.

A transect through the Interior Basins (Figs. 3, 33, transect C) shows a significant decrease in average female toe lengths from the Palouse Grassland to the Sagebrush-Wheatgrass, then a significant increase from there to the Lahontan Saltbush-Greasewood, and finally a significant decrease from there to the Sonoran Desert. No significant differences and only a slight overall decreasing trend are shown for males from the Central Boreal to the Sonoran Desert. Maxima are in the Lahontan Saltbush-Greasewood, and minima in the Sonoran Desert for both sexes.

A transect down the Rocky Mountains (Figs. 3, 33, transect D) shows no overall trend but significant increases, in males, from the Central Boreal to the Columbia Forest (moist), and a significant decrease in both sexes from the Northern Rockies to the Upper Gila Mountains Forest, then a significant increase in males from the Upper Gila Mountains Forest to the Mexican Shrub Steppe. Maxima are in the Mexican Shrub Steppe for males, and northern Rockies for females. Minima are in the Upper Gila Mountains Forest for both sexes.

A transect in the Central Plains (Figs. 3, 33, transect E) shows neither significant differences nor obvious trends. Maxima are in the Short-grass Prairie for males

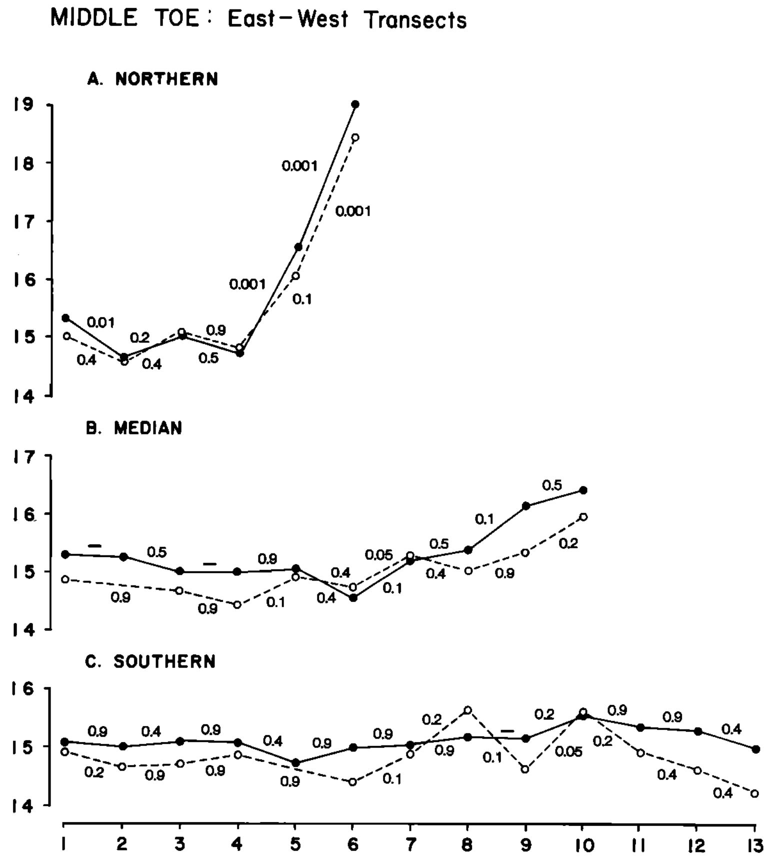

FIG. 34. East-west transects of mean middle toe lengths. Figures on vertical axis are mean measurements. Figures on horizontal axis refer to Ecoregion Sections (Fig. 4).

and Aspen Parklands for females. Minima are in the Central Boreal for both sexes.

A transect in the Central Forests (Figs. 3, 33, transect F) shows no trend nor significant differences. Maxima are in the Oak-Hickory Forest, and minima in the Spruce-Fir of Minnesota for both sexes.

A transect in the Eastern Forests (Figs. 3, 33, transect G) shows no trend nor significant differences between populations. Maxima are in the Newfoundland Boreal for males, and Appalachian Oak (deciduous) for females. Minima are in the Applachian Oak (deciduous) and Northern Hardwoods of New York for males, and Southeastern Mixed Forest for females.

Average toe lengths in northern and southern sections of the Atlantic Coastal Marshes (Figs. 3, 33, transect H) do not differ significantly.

East-west transects. The northernmost (Figs. 4, 34, transect A) shows a significant decrease in mean male, but not mean female, toe lengths from the Newfoundland Boreal to the Spruce-Fir of Minnesota, then little change to the Central Boreal. Increases are significant, for males, from there to the Alaska Pacific and, for both sexes, from that section to the Aleutian Islands. Maxima are in the Aleutian Islands, and minima in the Spruce-Fir (Minnesota) for both sexes.

In the median transect (Figs. 4, 34, transect B), there is a slightly decreasing trend in toe lengths from the northern Hardwoods-Spruce (Maritime) to the Short-grass Prairie, then a steady increase to the Sitka Spruce-Cedar-Hemlock of the Pacific Coast. No significant changes between any sections occur in the transect in males, but there is a significant increase in females from the Short-grass Prairie to the Rocky Mountains Forest. Maxima are in the Sitka Spruce-Cedar-Hemlock, and minima in the Short-grass Prairie for males and Tall-grass Prairie for females.

In the southern transect (Figs. 4, 34, transect C) a progression of insignificant increases and decreases alternates, with no particular trend. The only significant change is an increase in female toe lengths from the Sagebrush-Wheatgrass to the Lahontan Saltbush-Greasewood in the Great Basin. Maxima are in the Lahontan Saltbush-Greasewood for males, and both that section and the middle Rockies for females. Minima are in the Oak-Savannah for males and California Chaparral for females.

Discussion.—In general, longer middle toes are characteristic of the Aleutian Tundra, Pacific coastal rain forests, all western and Mexican mountain forests (both moist and dry except Upper Gila Mountains Forest), northern deserts, Palouse Prairie, and Mexican Highlands Shrub Steppe. Shorter middle toes are characteristic of birds from southern deserts and chaparral, Upper Gila Mountains Forest, all prairie parklands and grasslands (except Palouse), and most eastern forests.

Male middle toes average longer than those of females in the same populations in most instances. This is similar to the situation in tarsal length.

Mean middle toe lengths for the various ecogeographic units vary in approximately the same way as tarsal lengths when arranged by sex in order of decreasing size. Therefore, although ratios of toe length to wing length have not been calculated, it may be assumed that such ratios would be similar to those calculated for tarsus to wing, both between populations and between sexes. This would show relatively little difference between distribution of ratios as compared with actual toe lengths, which are longer in males in both cases. However, if as is assumed, ratios of toe to wing are similar to ratios of tarsus to wing, there is a complete reversal with respect to sex differences, females having relatively longer middle toes compared to wing length than do males.

The same is true with respect to probable ecological and functional adaptations of the middle toe, as noted in the case of the tarsus. There is a tendency for longer toes to be associated with more northern locations, thus conforming to Bergmann's rule as indications of overall greater size of bird in the north, rather than Allen's rule wherein extremities tend to be longer in the south. It seems likely that relative toe length, as well as tarsus length, is related to scratching for food. Fretwell (1969) associated short tarsi of certain fringillid species with more time spent perching and scratching and long tarsi with more time spent feeding on the ground. Since, in the Song Sparrow, toe length varies the same as tarsal length, the same relationship to feeding habits found by Fretwell for tarsi would presumably also apply to toe length, at least in this species. It is not known whether this is the case with different populations of Song Sparrows because no data exist on geographical variation of its behavior. If, as may be the case of tarsus length, there is survival value of longer toes for ground feeding or nesting activities, as opposed to perching for singing and territorial patrol, then females with their relatively long toes would have an advantage over males in that respect.

GENERAL DISCUSSION OF ECOGEOGRAPHICAL VARIATION

The wide range of environmental tolerance of the Song Sparrow is indicated by its extensive geographical breeding distribution, which includes all of North America from the Aleutian tundra and Canadian boreal forests to the southern end of the Mexican Plateau (Dickerman 1963). At present its northward and elevational distributions during the nesting season appear to be limited by the Arctic-Alpine (except Aleutian) and the Open Boreal Life Areas. To the south, in Mexico, its breeding range seems to be limited by Tropical areas and the Chihuahuan Desert section of the Southern Desert Scrub Life Area, and in the eastern United States by the southern Great Plains part of the Grasslands and the Southeast Evergreen Life Areas (Fig. 1). In the Grasslands it is presently restricted in the south to eastern Colorado (Bailey and Niedrach 1965), southern South Dakota, and eastern Nebraska (Johnsgard 1979). It enters the Southeast Evergreen only in the Atlantic Coastal Marshes of South Carolina (American Ornithologists' Union 1983), although extending south in the Eastern Deciduous Forest to northern Georgia (Burleigh 1958), northeastern Alabama (Imhof 1962), and northcentral Arkansas (American Ornithologists' Union 1983). Its occurrence in the southeastern part of its range may be relatively recent since it has extended its distribution farther south there in recent years (Odum and Burleigh 1946).

It seems probable that Song Sparrows will soon expand into currently unoccupied ecogeographical areas. They evidently possess the "genetic plasticity" that permits them to evolve new morphological and physiological characters that preadapt young, pioneering individuals to different environments in unoccupied geographical areas, as suggested by Mayr (1951) and Miller (1956). In this respect they are unlike their congeners, the Lincoln's Sparrow (*Melospiza lincolnii*) and Swamp Sparrow (*Melospiza georgiana*), which have narrow habitat requirements. These species seem to lack sufficient genetic variability to permit the modification of their characters necessary for colonization of new areas. On the other hand, competition with the Song Sparrow may have prevented such expansion. In any case, the Song Sparrow is one of the most highly ecogeographically variable birds of North America, whereas the Lincoln's and Swamp sparrows are much more uniform morphologically and restricted geographically (Miller 1956).

Morphological characters of the Song Sparrow that appear to be adapted differently in different ecogeographic parts of its range are shown in the present study to include wing length and shape, bill shape, and tarsus, tail, and middle toe lengths.

SEXUAL DIMORPHISM

Males and females differ morphologically. Males are larger than females in all linear measurements where the differences are significant, probably reflecting overall differences in body size (McCabe and McCabe 1932; Power 1969). In shape of wing the sexes are essentially equal, but in proportion of height and width of bill to its length, and proportion of tarsus and middle toe to wing length, females exceed males. Thus, on the whole, females have stouter bills than males, but the distribution of the significant differences in stoutness in such diverse ecogeographic areas as Northern Hardwoods, Southeastern Mixed Forest, Pacific Rain Forest, Montane Grassland, California Chaparral, and Mesquite-Grassland gives little basis for suspecting that any of the dimorphism has ecological significance.

In ratio of tarsus to wing, males are significantly relatively longer legged than females in only one population, the Mexican Shrub Steppe. Females are relatively longer legged in 16 populations including such major ecogeographic groups as Aleutian Tundra, eastern forests with adjacent Atlantic salt marshes, Pacific rain forests, California Chaparral with adjacent San Francisco Bay salt marshes, northern Rocky Mountains grasslands, sagebrush and piñon-juniper, and Great Basin sagebrush and piñon-juniper. Thus, it may be advantageous to females to be relatively longer legged than males over a geographically and ecologically wide range. If possession of relatively long legs is an adaptation to more activity on the ground than in flight or perching, such advantage to females would appear to be general rather than related to any particular ecogeographic area.

A problem in correlating morphological characters with habitat and diet is that different factors are important in different seasons. For example, catching insects for feeding young may be critical in the breeding season, whereas opening large or hard seeds may be critical to survival during severe winter conditions. Selection for these factors may sit in opposition, but one factor should be most important under the conditions of one ecogeographic region.

Overall Ecogeographic Variation

When variation in all characters is considered, certain populations of Song Sparrows stand out as being more different from other populations. Among these, the Aleutian tundra birds are the most distinct. They are the largest in linear measurements, have the most slender bills, and one of the most rounded wings of all populations. They are also situated at the extreme northwest end of the range of the species and occupy the most littoral habitat. The large size adapts them to a cold climate, the rounded wings to non-migratory habits, and the slender bill to a highly invertebrate diet (Appendix IV). The slender bill is shared by Pacific Forest, Northern Gila Mountains Forest, American Desert, Mexican Shrub Steppe, and Mexican Pine-Oak populations, indicating winter diets high in insects in those populations also.

Also very distinct are the San Francisco Bay marsh populations that were studied intensively by Marshall (1948). They are the smallest in all linear measurements except bill length, which is almost the smallest, but the bills are of medium stoutness. The wing is very rounded, being exceeded only by Gila Mountains and Mexican Shrub Steppe birds, and the ratio of tarsus to wing length is almost the greatest. The adjoining population of the California Chaparral, of which the marshes are a seral stage, although they act as a distinctive Life Belt, is similar in size and proportions to the marsh population but larger in linear measurements. In the ratio of tarsus to wing, the chaparral population has the highest value of all populations. The small size adapts the chaparral and San Francisco Bay salt marsh birds to mild winters in accordance with Bergmann's rule, the rounded wings to a sedentary habit, and the long tarsi to a ground inhabiting existence.

The Atlantic Coastal Marsh population has the stoutest bill of all, although it is approached in this character by the population of the adjoining deciduous forest of which the salt marsh is a seral stage. Very stout bills should adapt those birds to winter diets composed largely of seeds, possibly of varieties with harder coats than varieties which are consumed by other populations that winter in less rigorous weather.

Boreal and Laurentian Forest Song Sparrows have the most pointed wings although closely approached by Short-grass Prairie birds in this respect. This character presumably is adaptive for stronger and more sustained flight in these birds of more northern and more open habitats. The prairie and prairie parkland populations are also characterized by shorter tarsi in proportion to wing length than other populations. This characteristic may indicate adaptation for perching and flying rather than running on the ground, although such habits are not known to be especially characteristic of those birds.

Upper Gila Mountains Forest and Mexican Shrub Steppe populations have the most rounded wings, which presumably are an adaptation to more sedentary flight habits. The Gila Mountains birds also have the longest tails as compared to wing length, although southern desert birds approach them in this respect. Possible adaptive value of relatively long tails compared to wings in populations in dryer climates is not obvious.

At this point we are confronted with the old question of which is the most important influence in causing the interpopulation variation which has been noted: ecological adaptation or random variation resulting from geographic separation which retards gene flow. Presumably, both have effects in most cases, which is the reason for using both ecological (Life Area) and a combination of ecological and geographical (Ecoregion) units as strata for analysis of data. It has been shown above that many significant differences exist between populations of the same Life Areas within different Ecoregion Sections. These may represent Life Belts of Ecoregion Sections. However, those Life Area segments that differ from each other, such as California Grassland and Short-grass Prairie, and Central Boreal and Newfoundland Boreal, to some extent are different from each other ecologically, probably on the scale of the Associations of Weaver and Clements (1938) or the more finely subdivided climax vegetation units of Küchler (1964). As has been pointed out by Marshall (1948), Mayr (1951) and Miller (1956), it is impossible to have variation between populations of animals without their being separated geographically to some degree. Probably geographical separation is minimized and ecological effect maximized in the cases of Life Belt differences noted in Ecoregion Section/Life Area units. In the California Chaparral Ecoregion Section, the true Chaparral-Oak Woodland Life Belt population includes birds with longer wings and tails than birds of the Grassland or San Francisco Bay Marsh Life Belts, but shorter wings than birds of the Pine-Oak Life Belt in Baja California. Song Sparrows in the Chaparral-Oak have longer and stouter bills than birds in the San Francisco Bay Marsh; birds in the Grassland also have stouter bills than those of the San Francisco Bay Marsh Life Belt. In both the Grassland and Chaparral Life Belts Song Sparrows have longer tarsi than birds in the San Francisco Bay Marsh; Chaparral birds also have relatively shorter tarsi as compared to wings than birds of the bay marsh. The ratio of tarsus to wing is greater in the Chaparral population than that of the Pine-Oak Life Belt. In the Sagebrush-Wheatgrass Ecoregion Section, birds of the Piñon-Juniper Life Belt have a higher and wider maxilla and a longer tarsus, both actual and in proportion to wing, than those of the Northern Desert Scrub (sagebrush) Life Belt. In the Rocky Mountains (Douglas-fir) Ecoregion Section the population of the Montane Woodland-Brush has a longer wing-tip and bill, but smaller tarsus to wing ratio than that of the Northern Desert Scrub (sagebrush) Life Belt. In the Appalachian Oak Ecoregion Section the population of the Northern Hardwood-Conifer Life Belt has a more pointed wing than that of the Atlantic Coastal Marsh (north); and the population of the Deciduous Forest Life Belt has a stouter bill and longer tarsus than that of the Northern Hardwood-Conifer Life Belt; it also has a longer tarsus than the population of the Atlantic Coastal Marsh (north).

Most of the birds of the above ecogeographical areas, in addition to the distinctive characteristics mentioned, have more than five mensural characters that differ significantly from the same characters in adjoining populations. Other populations, besides those mentioned, that also have more than five characters differing significantly from those of their immediate neighbors, are the populations of the Alaska Pacific Forest, Sitka Spruce-Cedar-Hemlock, Redwood Forest, Sierran Forest, California Grassland (valley), Lahontan Saltbush-Greasewood, Columbia Forest (moist), Southeastern Mixed Forest, and Palouse Grassland. Those Ecogeographic Sections, if substantiated by similar variations in other representative species, would probably be suitable candidates for designation as "centers of differentiation" (Oberholser 1932; Miller 1941). The significant differences between characters representative of Sagebrush-Wheatgrass and Lahontan Saltbush-Greasewood Ecoregion Sections seem to support Miller's (1941) recognition of northern and southwestern Great Basin centers of differentiation.

The morphological differences associated with Life Belts within Ecoregion Sections shown in the treatment of Ecoregion Section/Life Areas are probably about as close to the "ecotypical" variation in plants (McMillan 1960) as we can come with birds. Fretwell (1969) described intraspecific variation in tarsal length among wintering populations of emberizid species, that he called ecotypic, but the evidence seems questionable (Banks 1970).

Considering all evidence in the present study, it is my opinion that the ecological forces selecting adaptive genetic differences have a greater effect on morphological change or microevolution than do geographical separation or isolation. This opinion is based primarily on the fact that significant morphological variation is noted between populations with no apparent impediment to exchange of genes other than marked ecological differences in their habitats, whereas little or no morphological change is noted between some populations with ecologically similar habitats that are separated by long stretches of inhospitable environment.

I have demonstrated ecogeographical variation in morphological characters of Song Sparrows, and a number of probable adaptive relationships have been suggested. However, we are a long way from isolating the critical factors within each of the Life Areas and Ecoregions to which their included populations are exposed, that select the genotypic variation on which the noted phenotypic characters are based. It will require much study of the tolerance of birds to the different climates, soils, vegetation, and other physical and biological factors of each Life Area and Ecoregion to answer those questions. The considerable amount of information on such environmental factors in the ecological literature should be used in assessing adaptive evolutionary changes in bird morphology.

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SUMMARY

Climax ecological communities are the products of the ultimate adaptive development of their included organisms in response to the total environment of the area in which they occur, including physiographic, climatic, and biotic elements. Those ecological factors act to select morphological, as well as physiological, characteristics that best adapt genetically varying populations to particular situations. Life Areas, based on climax vegetation, and Ecoregions, based on all environmental factors including climax vegetation, are used in this study to stratify populations of Song Sparrows for analysis of variation in their mensural characters.

Comparisons of mean measurements and ratios of measurements of Song Sparrows, stratified by Life Areas, Ecoregions, and combinations of the two, show differences apparently correlated with the ecological differences characterizing those strata. Lengths of wing and wing-tip are correlated with variations in latitude and elevation, being greater in more northern and higher regions in conformance with Bergmann's rule. These measurements are also correlated with life form and density of the vegetation, and atmospheric moisture in the breeding areas; longer wings are found in birds of more open, dryer situations. Ratios of wing-tip to total wing length, indicating more pointed or more rounded wings, appear related to migratory habits of the birds and life form of the vegetation in their environment, with more pointed wings in more migratory populations and in more open habitats. Bill linear measurements are correlated to some extent with overall size of the birds and, thus, are in accord with Bergmann's rule, but there are exceptions to this trend, particularly in the east where local factors seem to disrupt it. There is little evidence of conformance of bill length with Allen's rule. Ratios of bill height and bill width to length of bill (stoutness) vary, with more slender bills in the humid Pacific Northwest, as well as southern deserts, and stouter bills in eastern coastal marshes, forests, and grasslands. Also bill stoutness appears to be related to proportions of plant and animal food eaten during the winter. Birds with stouter bills eat more seeds, and those with more slender bills eat more invertebrates. Tarsus length conforms in general to variation in body size, and, thus, with Bergmann's rather than Allen's rule, although it may be modified to some degree by local environmental conditions. Ratios of tarsus to wing length (relatively long-leggedness) show an ecological correlation with environmental factors similar to that of stoutness of bill, suggesting a similar relationship to feeding on varying proportions of plant and animal food. Relatively long-legged birds may also be adapted for spending a greater amount of time on the ground, in contrast to short-legged individuals that have more arboreal habits.

Sexual dimorphism appears in all linear measurements and in both bill shape and relative leg length. Males average longer in all linear measurements, and females average stouter-billed and relatively longer-legged than males. The stouter bills suggest that females are adapted to more seed-eating during critical winter periods. The relatively longer legs suggest that females are adapted to spending more time on the ground foraging, and carrying out nesting activities, in contrast to males that perch in trees and fly about in defense of the breeding territory. Toe lengths vary with the same pattern as tarsus length both ecogeographically and sexually and probably are influenced by the same adaptive factors. Tail lengths vary, in general, like wings, in accordance with Bergmann's rule, but there is an additional tendency for longer-tailed birds to occupy arid regions, and for shorter-tailed birds to occupy areas of moist climate.

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APPENDIX I

SONG SPARROW BREEDING HABITATS

The following notes on breeding habitats of Song Sparrows, with abundance data when available, were derived from the literature cited. Abundance data are all from Breeding Bird Population Reports published in *Audubon Field Notes* and *American Birds,* and are given as numbers of singing males per 100 hectares. The habitat descriptions and abundance notations are classified by the particular Ecoregion Section/Life Area units in which the habitats occur.

1-M1310 Alaska Range (Aleutians).—Beach grass just above high tide line; grassy slopes near beach; boulders and drift-wood along beach (Gabrielson and Lincoln 1959; Murie 1959; Claudia Wilds, pers. comm.); tidal mud flats for winter feeding (Sutton and Wilson 1946).

3-1320A Yukon Forest (Newfoundland Boreal).—Thickets, preferably bushes along streams or near ponds, swampy land near a spring or ditch, or along bush-bordered rivers (Peters and Burleigh 1951).

3-1320B Yukon Forest (Central Boreal).—Shrubby field, Fort Resolution, N.W.T. (Preble 1908); willow-aspen, shrubs and hedges in residential area, Senneterre, Quebec (13/100 ha) (Loery 1970).

6-M2111 Douglas-fir Forest (Columbia Forest, montane).—Brushy places near water, hawthorn brush bordering clearings; tangled willows and cottonwoods, dogwoods and alders along streams (Jewett et al. 1953).

4-2112 Northern Hardwoods-Fir Forest (Upper Peninsula, Michigan).—Aspen (first year after clear-cut), scattered patches of aspen shoots, slash and bare ground (33/100 ha); Aspen (4th year after clear-cut) average 3.5 m tall (33/100 ha) (Van Velzen 1981); Aspen (2 years after clear-cut) height 1.2 m, herbaceous ground cover, Song Sparrow most abundant species (158/100 ha) (Van Velzen 1979); semi-open black spruce bog, ground cover sphagnum, leatherleaf, Labrador Tea, *Kalmia,* and bog rosemary, scattered spruces and tamaracks (60/100 ha) (Van Velzen 1977).

7-M2112 Cedar-Hemlock-Douglas-fir (Columbia Forest, moist).—Bulrush-cattail marsh in conifer forest (27/100 ha) (Van Velzen 1981); river and falls (40%), forest (60%) of western red cedar, Douglas-fir, western larch, chokecherry, alder, quaking aspen, and shrubs (8/100 ha) (Van Velzen 1979).

4-2113 Northern Hardwoods Forest (New York-Wisconsin).—Upland mixed pine-spruce-hardwood plantation (9/100 ha); upland Scotch pine plantation (193/100 ha); marsh with brushy field (36/100 ha) (Van Velzen 1981); abandoned field 57% forbs, 8% tree seedlings, 9% shrubs, goldenrod and grasses predominant (67/100 ha); transmission line right of way, grasses 20%, forbs 30%, shrubs 20%, trees 20% (white ash, gray birch, pincherry, red maple, and quaking aspen) (84/100 ha); fresh water marsh with silky dogwood, blackberry, speckled alder, and cattail (97/100 ha) (Van Velzen 1979).

4-2114 Northern Hardwood-Spruce (New England).—Preferred habitat brushy field borders and wood margins (Stewart and Aldrich 1952); also common along country roads in bushes (Palmer 1949); mixed forest, old field, homesite (73/100 ha); abandoned pasture-young mixed forest (29/100 ha); young red maple-gray birch forest (37/100 ha) (Van Velzen 1979); young white ash-basswood forest (17/100 ha) (Van Velzen 1978); deciduous-coniferous second growth (12/100 ha) (Van Velzen 1977).

6-M2120 Intermontane (British Columbia).—Black cottonwood flood plain forest with subcanopy of willows and mountain alder (9/100 ha); disturbed spruce stand with willow swales and undergrowth of black twinberry, rose, and squashberry, all overgrown with purple pea (17/100 ha) (Van Velzen 1975).

4-2214A Northern Hardwoods-Spruce (Maritime).—Birch forest (5 years after clear-cutting) (55/100 ha) (Van Velzen 1981); residential habitat (71/100 ha) (Van Velzen 1980); open bog with sphagnum and low hummocks of spruce and ericaceous bog shrubs (11/100 ha) (Van Velzen 1974).

8-2211 Mixed Mesophytic Forest (deciduous).—Pasture, marsh, shrubs, brambles, and mature trees mixed (49/100 ha) (Van Velzen 1981); grassland with scattered shrubs and 9-m wide clump of speckled alder (33/100 ha) (Van Velzen 1980); deciduous clear-cut (5/100 ha) (Van Velzen 1977).

8-2212 Beech-Maple Forest.—Wooded city ravine with boxelder, willow and bog shrubs (9/100 ha); mature mixed hardwood forest (38/100 ha); button bush swamp (20/100 ha); abandoned field with brome grass, scattered shrubs, and small trees (51/100 ha); dune pond with sedge and tamaracks (10/100 ha) (Van Velzen 1979); residential habitat (25/100 ha) (Van Velzen 1980).

8-2213 Maple-Basswood Forest.—Mixed wetland with tamarack and aspen groves, shrubland, and fen (41/100 ha); 4-row shelterbelt (287/100 ha); grass fields in which woody vegetation is limited to narrow row of honeysuckle, small willows, and cottonwoods (12/100 ha) (Van Velzen 1980); brushy sedge meadow, Song Sparrow most abundant species (78/100 ha) (Van Velzen 1972); clear-cut, aspen with understory of raspberry, bracken, hazel, and round-leaf dogwood (10/100 ha) (Van Velzen 1979).

4-2214 Appalachian Oak (N. Hardwood-Conifer).—Habitat above 1829 m in Great Smoky Mountains, brushy openings in moist situations (Stupka 1963); in Georgia mountains in thickets and underbrush in valleys, not in thick woods, mountainsides or ravines (Odum and Burleigh 1946; Burleigh 1958); meadows with young hemlock, red spruce, and alder (Stewart and Robbins 1958); old field, meadow (10/100 ha); field abandoned 10 years with blackberries, shrubs, a few saplings, ground cover of herbs (139/100 ha) (Van Velzen 1981).

8-2214 Appalachian Oak (deciduous).—Nests usually on moist land near swamp, spring, brook or ditch where water is at hand, or in thickets near margins of ponds, lakes or rivers (Forbush 1929); brushy fields and homesites with steeplebush, narrow-leaf dogwood, smooth sumac, blackberry, goldenrod and invading trees of black willow and Scotch pine (190/100 ha) (Van Velzen 1974); abandoned nursery with hedgerows (70/100 ha) (Van Velzen 1979); second growth hardwood trees (10/100 ha); hardwood sprouts 3 years after removal of red pine plantation (35/100 ha); mature upland forest and swamp shrubs (16/100 ha); deciduous forest with pond and brook (6/100 ha); old field with shrubs, herbs, and scattered red cedars (177/100 ha); brushy field and wooded edge (96/100 ha); cleared area after 3 years, covered with grass and herbs with some trees and shrubs (116/100 ha); shrubby swamp with sedge hummocks (37/100 ha) (Van Velzen 1981).

8A-2214A Atlantic Coastal Marsh (north).—Salt marsh grasses interspersed with marsh elder, poison ivy, and bayberry on raised island along ditch banks (16/100 ha) (Loery 1970).

9-2215 Oak-Hickory Forest.—River flood plain with rank growth of weeds, patches of elderberry, and scattered trees (Nice 1937); wide variety of brushy situations at forest edges, shrub-bordered fence rows, residential yards and gardens (Mengel 1965).

8-2320 Southeastern Mixed Forest.—Mixed agricultural habitat including hedgerows and wood margins, field edge habitat, flood plain forest, brushy fields (Stewart and Robbins 1958); moist thickets, gardens in towns, shrubbery along woods edge (Stone 1937); mature deciduous flood plain forest (7/100 ha); mixed upland city park habitat (7/100 ha) (Van Velzen 1981).

8A-2320A Atlantic Coastal Marsh (south).—Rarely, if ever, found far from salt water, nests in myrtle thickets and willows at edge of salt marsh (Burleigh 1958); along a narrow strip of natural vegetation of a scrubby life form on the dunes bordering Atlantic coastal salt marshes (Odum and Burleigh 1946).

7-2410 Willamette-Puget Forest.—Oak-ash-Douglas-fir with shrub understory and ground-cover of grasses (107/100 ha) (Van Velzen 1979); riparian forest of medium to large-sized black cottonwoods, big-leaf maple, and red alder with scattered coniferous species, and dense understory of salmonberry and other shrubs, Song Sparrows second commonest species (206/100 ha) (Van Velzen 1981); oak-ash-Douglas-fir, shrub understory, ground-cover grasses (107/100 ha) (Van Velzen 1979); common in all successional stages of alder forest (Stiles 1980).

7-M2416 Alaska Pacific Forest.—On beaches, nesting and feeding within a few meters of the beach; nests in brush and grassland on islands and along shore (Willett 1928); in southeastern Alaska sometimes found in bushy habitats like those frequented by more southern Song Sparrows (Gabrielson and Lincoln 1959).

7-M2411 Sitka Spruce-Cedar-Hemlock Forest (Pacific Forest, coast).—Dredged island in Columbia River, with shore pine, scotch broom, beach grass, red alder, and Pacific willow (83/100 ha) (Van Velzen 1977); distinctly a ground bird in brush along creek banks, generally in wet places, but sometimes in dry brushy locations, weedy lots, about dooryards in towns, on tide flats and beaches among stranded logs (Jewett et al. 1953); nesting habitat grassy meadows with some trees and shrubbery chiefly grand fir, Douglas-fir and Pacific madrone with rich undergrowth of willows, ocean spray, and English hawthorns; breeding territories in shrubby growth mixed with grassland; forage in tidal zone as common feeding ground (Tompa 1962).

7-M2412 Redwood Forest.—Low dense cover on fog-drenched slopes such as blackberry patches, *Ceanothus* clumps, bracken, weeds, brush piles, willow thickets, fresh and salt water marshes (Grinnell and Miller 1944); coastal salt marsh with brush (31/100 ha); diked coastal brackish marsh with coyote bush brush and ground cover of rush (*Juncus*) (170/100 ha) (Van Velzen 1981); diked coastal salt and fresh water marsh with alder and willow patches surrounded by redwood forest and pastureland (89/100 ha) (Van Velzen 1980).

7-M2413 Cedar-Hemlock-Douglas-fir (Pacific Forest, inland).—Willow thickets and brush patches along streams, and even blackberry patches on hillsides considerably distant from water (Gabrielson and Jewett 1940); open brushy situations, usually near water, but often in dry brushy localities some distance from water (Jewett et al. 1953).

7-M2414 California Mixed Evergreen.—Seaside chaparral which is limited by its demands for constant moisture to north-facing slopes within 91 m of the ocean, consisting of shrubs of *Lupinus* 0.6 to 1.2 m high in rows with stems 0.9 m apart, or as solitary bushes 2.7 m apart, with ground cover a dense mat of succulent grasses, vines, and herbs, characterized by exceedingly moist conditions from almost constant fog and high rainfall, a pair of Song Sparrows occurs every 39 m; soft chaparral consisting of *Baccharis, Rubus, Rhus, Conium, Heracleum,* and *Artemisia,* including ferns and grasses, forms a continuous dense cover 1.2 to 2.4 m high along the coast, Song Sparrows frequent this only in places where growth is divided into small clumps of bushes and vines bordered by grasses and ferns and separated by wet bare ground (Marshall 1948); Coastal scrub (58/100 ha); disturbed coastal scrub, Song Sparrow commonest species (128/100 ha) (Van Velzen 1981); Bishop pine-mixed forest (9/100 ha); logged Douglas fir reseeded to Monterey pine (12/100 ha) (Van Velzen 1978).

5-2530E Aspen Parkland (east).—White-top meadow (prairie marsh) (7/100 ha); green ash-boxelder forest (7/100 ha) (Van Velzen 1981).

9-2532 Tall-grass Prairie (west).—Fresh water lake with cattail and *Phragmites* (1/100 ha); cattail-bulrush (1/100 ha, and 1/100 ha) (Van Velzen 1979); three-row shelterbelt (125/100 ha); six-row shelterbelt (63/100 ha) (Loery 1967).

9-2610 California Grassland (valley).—Fresh water marshes with growth of tules and cattails, riparian thickets of willow and nettle (Grinnell and Miller 1944); mixed shrubs, trees, and marsh (10/100 ha) (Van Velzen 1979); disturbed riparian stream border of cottonwood, willow, black walnut, elderberry, and boxelder (31/100 ha) (Van Velzen 1977).

6-M2610 Sierran Forest.—Riparian vegetation, marshes and lake borders with willow thickets, cattails, bulrushes, and rose thickets; combination of dense low cover and surface water with wet ground essential (Grinnell and Miller 1944).

15-M2620 California Chaparral.—River-bottom thickets of nettle, blackberry, and willows, fresh water marshes, margins of salt marshes, coastal fog-swept chaparral, garden shrubbery, dense tangled vegetation and moist ground essential (Grinnell and Miller 1944); natural riparian habitat (422/100 ha) (Van Velzen 1978); live oak woodland (91/100 ha); urban nature center (52/100 ha); beach residential (439/100 ha); cattail-tule marsh with willow edge, Song Sparrow commonest species (502/100 ha) (Van Velzen 1981); Sycamore-coast live oak riparian woodland (15/100 ha); undisturbed coastal sage scrub with stream in canyon (45/100 ha); disturbed coastal salt marsh (35/100 ha) (Van Velzen 1978); wax myrtle forest with understory mainly willow and tree tobacco, Song Sparrow commonest species (305/100 ha) (Van Velzen 1975).

9-M2620 California Chaparral (grassland).—Song Sparrows the most abundant and characteristic avian inhabitants of riparian habitat along streams crossing the San Francisco bayside plane where they have the habitat nearly to themselves, density dependent on width of streamside vegetation, willows with dense tangles of rose, blackberries, and herbaceous plants predominate; Song Sparrows occur only where vegetation is not too dense to exclude light but dense enough for cover, and where moist bare ground is available for foraging (Marshall 1948).

9-M2620A San Francisco Bay Marsh (north).—Salt and brackish marshes with cordgrass (*Spartina*), pickleweed (*Salicornia*) and gumplant (*Grindelia*); brackish marshes with cattails, tules, sedges, and *Salicornia* (Grinnell and Miller 1944); cattails and rushes on brackish water mudflats in Suisun Bay and a few places on river mouths entering San Pablo Bay between salt and fresh marshes. Song Sparrows forage on the mud (Marshall 1948).

9-M2620B San Francisco Bay Marsh (south).—Salt marshes on south arm of San Francisco Bay with pickleweed (*Salicornia*) and low bushes (*Grindelia*) (Grinnell and Miller 1944); *Spartina, Salicornia* and *Grindelia* compose the dominant vegetation, growing primarily in that order in zones from wetter to dryer situations; grassland above the high tide mark; Song Sparrow pairs occur in all three zones but most numerously where the *Grindelia* belt is widest (Marshall 1948); diked bay marsh (286/100 ha) (Van Velzen 1981).

9-3111 and 3113 Short-grass Prairie (west).—Willows and alders along permanent streams (McCrearey 1939); brushy draws containing water, and river bottoms with rose bush and willow, wooded river valleys, brush along woodland roads and streams (Salt and Wilk 1966); preferred habitat a spring grown with cattails, tules, watercress, and willows, also along willow-bordered streams (Bailey and Niedrach 1965); flood plain cottonwoods (77/100 ha) (Van Velzen 1979); cottonwood-willow creek bottom (74/100 ha) (Van Velzen 1981).

9-3112 Short-grass Prairie (east).—Green ash and elm growth along draw with understory of choke-cherry and Juneberry, and ground cover of long-beaked sedge and bedstraw (10/100 ha, 12/100 ha, and 7/100 ha); cottonwood flood plain (6/100 ha) (Van Velzen 1981).

6-M3112 and M3111 Douglas-fir Forest (Montane Woodland-Brush, Northern Rockies) and Grand Fir-Douglas-fir Forest (Montane Woodland-Brush, Oregon).—Dense thickets along open water (Salt 1957); flood-plain cottonwoods with understory of willows, dogwood, and alders (130/100 ha); alder creek bottom in montane forest (25/100 ha) (Linehan 1968).

14-M3113 Ponderosa Pine-Douglas-fir (Piñon-Juniper, S. Rockies).—Clumps of dead tules and sage-brush fringing lake (Wetmore, 1920); willows along rivers and around reservoirs (Bailey 1928).

9-3120 Palouse Grassland.—Tangles of willow, cottonwood, and alder, open sedge-grown brushy meadows, hawthorn brush bordering clearings, lakeside marshy situations (Jewett et al. 1953).

11-3131 Sagebrush-Wheatgrass (Northern Desert Scrub).—Brush bordering marshes and lakes, feeding from floating leaves of water plants (Jewett et al. 1953); streamside willows (Peck 1911); riparian vegetation, marshes, and lake borders with dense low cover and wet ground (Grinnell and Miller 1944); standard woodland riparian species (Johnson 1978).

12-3221 Creosote Bush (Southern Desert Scrub, Mojave).—Breeds in vicinity of cattail swamps with standing water and with brushy thickets such as mesquite or rose in immediate dry land surroundings; both thickets and cattails used (Marshall and Behle 1942); desert riparian, woodland, and mesquite thickets, freshwater bulrush-cattail marsh and ponds (19/100 ha) (Van Velzen 1979); riparian wood-land willow thickets (12/100 ha) (Van Velzen 1975).

12-3222 Creosote Bush-Bur Sage (Southern Desert Scrub, Sonoran).—Riparian habitat, notably dom-inated by arrowweed, *Baccharis,* young willows, and tule beds, along irrigation ditches (Grinnell and Miller 1944); reed-sedge-brush types along major permanent rivers (Phillips et al. 1964); breed in streamside grass and brush, around reservoirs, in marshy areas along Santa Cruz River near Tucson, Arizona, vegetation consists of heavy clumps of tamarisk, cattails, various small grasses and sedges in marsh proper, with dense tumbleweed and dock along edges, a few mesquites and paloverdes also in places along edge (Crossin 1965); freshwater marsh with cattails, tamarisk, phragmites and saltbush (20/100 ha) (Van Velzen 1980).

13-3140S Mexican Highlands Shrub Steppe (south).—Marshes on lake shores with willows and other trees bordered on the water side by low sedge grading to tall stands of cattail and bulrushes; also marshes in poorly drained areas near springs; riparian situations (Dickerman 1963).

17S Mexican Pine-Oak (south).—Stream-side associations (Dickerman 1963).

Discussion

Except for the Aleutian Islands and Alaska Pacific populations, Song Sparrows use remarkably similar habitat types throughout the range of the species. The Alaskan habitats differ, for the most part, in consisting merely of grassy growth close to the ocean beaches instead of the usual shrubby or marshy situations in the rest of the species' range. Although broadly overlapping in types of habitat, populations of more arid regions tend to occupy wetter and more open habitats than those of more humid regions. Most habitats used in the eastern and northwestern forested regions involve brush in wet or moist situations, but some are rather dry brushland or forest border. Habitats used in the deserts are invariably in wet, brushy streamside situations, or even in fairly open marshes. One characteristic of all Song Sparrow habitats, except coastal Alaskan, is the proximity of low, not too dense woody vegetation of shrubs or small trees, with fairly thick ground cover of herbs, grasses, or vines, interspersed with open grassy, weedy, or marshy areas. Habitats with demonstrated dense breeding populations of Song Sparrows (more than 100 singing males per 100 hectares) are: Northern Hardwood-Conifer in early stages of succession after clear-cutting, abandoned agricultural fields grown to brush and brambles, and swamp shrub situations; Willamette-Puget Forest in riparian oak-ash-

Douglas-fir, and cottonwood-maple-red alder forests; California Mixed Evergreen Forest in disturbed coastal scrub; Tall-grass Prairie shelterbelts; California Chaparral in cattail-tule marshes with willows, natural riparian habitat, wax myrtle forest with willows, and San Francisco Bay marshes.

APPENDIX II

Song Sparrow Migration

Song Sparrows are migratory in certain ecoregions, sedentary in others, and in a number of regions some individuals are migratory and others sedentary or nearly so. The literature on bird species distribution gives a general idea of the migratory status of Song Sparrow populations but, for the most part, considerable question exists as to whether individual birds seen in winter are the same as those that were there in summer. Published reports of the movements of banded individuals are very scarce. In the absence of identified specimen or banding evidence, comments about Song Sparrows being permanent residents in more southern regions are meaningless because of the impossibility of distinguishing residents from northern migrants. The most meaningful general statement about Song Sparrow migration is probably that of Nolan (1968), that some birds winter fairly far north, but most withdraw from Canada and northern New England and move southward as far as Florida.

Banding records show that some individuals are resident in regions where most of their kind are migratory (Nice 1937). In a study area in Columbus, Ohio about half of the resident males and about 20 percent of the females proved to be permanent residents (Nice 1937). It is probably safe to consider Song Sparrows of the Aleutian Islands and Alaska Peninsula permanent residents, but those of coastal Alaska farther east are partially migratory, with some individuals wintering as far south as the Washington and Oregon coasts (Gabrielson and Lincoln 1959). Grinnell and Miller (1944) considered Song Sparrows of the northern interior and eastern sections of California as partially migratory and those of all the rest of the state as permanent residents. Birds of the Washington coast were considered permanent residents by Jewett et al. (1953), although joined in winter by individuals from the north. Most authors consider Song Sparrows east of the Cascades and Sierra Nevada as partially resident and partially migratory, with records of wintering, but not necessarily the same individuals that breed there, as far north as intermontane British Columbia (Munro and Cowan 1947), northern Idaho (Burleigh 1972), western Montana (Saunders 1921), southern South Dakota (Whitney 1978), southern Wisconsin (Cory 1909), southern Michigan (Wood 1951), western Pennsylvania (Todd 1940), eastern Maine (Palmer 1949), Nova Scotia (Tufts 1961), and Newfoundland (Peters and Burleigh 1951).

I attempted in the present study to determine, by examination of the banding data, the migratory movement, if any, of individual Song Sparrows representative of particular Ecoregion Section/Life Area units. M. K. Klimkiewicz of the Bird Banding Laboratory, U.S. Fish and Wildlife Service, Laurel, Maryland, provided a computer printout of all recoveries of the 16,215 Song Sparrows banded in North America during the winter months of January and February since 1955. The 800 recoveries, which represent 5 percent of all winter bandings, include 149 recovered during the breeding season (May-August inclusive) at the locality of banding; nine were recovered during the breeding season away from the banding locality, and 26 were recovered in the non-breeding season away from the banding locality (Appendix III). These recoveries provide data of a more definite nature than that in the literature on the migratory or sedentary behavior of the birds. The remaining 616 recovered during the non-breeding season at the wintering locality of banding have no value in showing migratory or sedentary behavior because there is no way of telling where the birds went during the time between the two winter periods of capture. They do, however, indicate a high degree of affinity of individual Song Sparrows for a particular wintering locality.

Specific instances of sedentary behavior and migratory movements of individual Song Sparrows representative of different Ecoregion Section/Life Areas that may be deduced from the banding data (Appendix III) are:

4-2111 Spruce-Fir Forest (N. Hardwood-Conifer, Minnesota).—There were no winter banding records; one breeding season recovery from this area was of a bird banded in winter in 10-2511 Oak-Hickory-Bluestem Parkland (Oak-Savannah).

4-2113 N. Hardwoods Forest (N. Hardwood-Conifer, New York-Wisconsin).—Of the birds banded in that ecogeographical area, three were permanent residents; one was taken in the breeding season in 4-2114 (A) Northern Hardwoods-Spruce (N. Hardwood-Conifer, Maritime); one taken in the non-breeding season in 4-2113 was in winter in 4-2114 N. Hardwoods-Spruce (N. Hardwood-Conifer, New England).

4-2114 N. Hardwoods-Spruce (N. Hardwood-Conifer, New England).—Of birds banded, none was a permanent resident; one was taken in the non-breeding season in 4-2113 N. Hardwoods Forest (N. Hardwood-Conifer, New York-Wisconsin); one was recovered in the non-breeding season in 16-2320 S. E. Mixed Forest (Southeast Evergreen); one breeding in 4-2114 wintered in 8-2320 S. E. Mixed Forest (Deciduous) where 714 birds were banded; three taken in the non-breeding season wintered in 8-2214 Appalachian Oak Forest (Deciduous); one taken in non-breeding season was banded in 8-2212 Beech-Maple Forest (Deciduous).

4-2114 (A) Northern Hardwoods-Spruce (N. Hardwood-Conifer, Maritime).—No birds banded there in winter were recovered; one breeding bird migrated to 4-2113 N. Hardwoods Forest (N. Hardwood-Conifer, New York-Wisconsin); one breeding bird wintered in 8-2320 S. E. Mixed Forest (S. E. Evergreen); one breeding bird migrated to 8-2214 Appalachian Oak Forest (Deciduous).

8-2211 Mixed Mesophytic Forest (Deciduous).—Five were permanent residents; one was recovered in breeding season in 4-2214 Appalachian Oak Forest (N. Hardwood-Conifer).

8-2212 Beech-Maple Forest (Deciduous).—Fourteen were permanent residents; one taken in the non-breeding season moved a short distance in the same Beech-Maple region; one was recovered in the non-breeding season in 4-2114 N. Hardwoods-Spruce (N. Hardwood-Conifer, New England), one recovered in non-breeding season in 16-2320 S. E. Mixed Forest (S. E. Evergreen).

8-2213 Maple-Basswood Forest (Deciduous).—One bird banded was a permanent resident.

4-2214 Appalachian Oak Forest (N. Hardwood-Conifer).—Seven were permanent residents; one breeding bird migrated to 8-2211 Mixed Mesophytic Forest (Deciduous); one taken in non-breeding season wintered in 8-2214 Appalachian Oak Forest (Deciduous).

8-2214 Appalachian Oak Forest (Deciduous).—Forty-five were permanent residents; one was taken in the breeding season in 4-2114A Northern Hardwoods-Spruce (N. Hardwood-Conifer, Maritime); two bred in the same ecogeographical area where banded; four appeared in the non-breeding season in the same area where banded; three occurred in the non-breeding season in 4-2114 N. Hardwoods-Spruce (N. Hardwood-Conifer, New England); one was found in the non-breeding season in 4-2214 Appalachian Oak Forest (N. Hardwood-Conifer); one breeding season bird had been banded in winter in 8-2320 S. E. Mixed Forest (Deciduous).

8-2215 Oak-Hickory Forest (Deciduous).—Five were permanent residents.

8-2320 S.E. Mixed Forest (Deciduous).—Twenty-eight were permanent residents; four birds taken in the non-breeding season, moved only within the same area of banding; one was taken in the breeding season in 4-2114A Northern Hardwoods-Spruce (N. Hardwood-Conifer, Maritime); one breeding bird was found in 8-2214 Appalachian Oak Forest (Deciduous); another bred in 4-2114 Northern Hardwoods-Spruce (N. Hardwood-Conifer, New England).

16-2320 S. E. Mixed Forest (S. E. Evergreen).—None was a permanent resident; one was taken in the non-breeding season in the same area where banded; one taken during the non-breeding season wintered in 4-2114 N. Hardwoods-Spruce (N. Hardwood-Conifer, New England); one non-breeding bird wintered in 8-2212 Beech-Maple Forest (Deciduous).

7-2410 Willamette-Puget Forest (Pacific Rain Forest).—Ten were permanent residents; three of those banded, which were taken in the non-breeding season in this area, moved within the ecoregion of banding; one taken in the non-breeding season in this area had wintered in 15-M2620 California Chaparral (Chaparral-Oak Woodland).

10-2511 Oak-Hickory-Bluestem Parkland (Oak-Savannah).—Four were permanent residents; one of those banded bred in 4-2111 Spruce-Fir Forest (N. Hardwood-Conifer, Minnesota).

15-M2620 California Chaparral (Chaparral-Oak Woodland).—Twenty-five were permanent residents; four taken in the non-breeding season moved within the same ecogeographical area where banded; one was recovered in the non-breeding season in 7-2410 Willamette-Puget Forest (Pacific Rain Forest).

6- and 9-M3111 Grand Fir-Douglas-fir (Montane Woodland-Brush-Grassland.).—One was a permanent resident.

11-M3113 Ponderosa Pine-Douglas-fir (N. Desert Scrub, Montane Woodland-Brush).—One was a permanent resident.

Following is an ecogeographical classification of Song Sparrow populations with respect to migratory or sedentary behavior based on all available evidence.

Primarily Migratory

3-1320B Yukon Forest (Central Boreal)
3-1320A Yukon Forest (Newfoundland Boreal)
4-2111 Spruce-Fir Forest (Minnesota)
4-2112 N. Hardwoods-Fir (Upper Peninsula, Michigan)
4-2114 N. Hardwoods-Spruce (New England)
4-2114A N. Hardwoods-Spruce (Maritime)
6-M2112 Intermontane (British Columbia)
5-2530W Tall-grass Prairie (Aspen Parkland, west)
5-2530E Tall-grass Prairie (Aspen Parkland, east)
9-3111 Grama-Needlegrass (Short-grass Prairie, west)
9-3112 Grama Wheatgrass-Needlegrass (Short-grass Prairie, east)

Primarily Sedentary

1-M1310 Alaska Range (Aleutians)
8-2211 Mixed Mesophytic Forest (Deciduous)
8-2215 Oak-Hickory Forest (Deciduous)
8-2320 S. E. Mixed Forest (Deciduous)
8A-2320A S. E. Mixed Forest (Atlantic Coastal Marsh)
16A-2320A S. E. Mixed Forest (Atlantic Coastal Marsh, S. E. Evergreen)
7-2410 Willamette-Puget Forest (Pacific Rain Forest)
7-M2411 Sitka Spruce-Cedar-Hemlock (Pacific Rain Forest)
7-M2412 Redwood Forest (Pacific Rain Forest)
7-M2413 Cedar-Hemlock-Douglas-fir (Pacific Forest, inland)
9-M2414 California Mixed Evergreen (Pacific Rain Forest)
10-2511 Oak-Hickory-Bluestem Parkland (Oak-Savannah)
9-2610 California Grassland (Valley)
9-M2620 California Chaparral (Coastal Grassland)
9-M2620A California Chaparral (San Francisco Bay Marsh north)
9-M2620B California Chaparral (San Francisco Bay Marsh south)
15-M2620 California Chaparral (Chaparral-Oak Woodland)
14-M3120 Upper Gila Mountains Forest (Piñon-Juniper-Oak)
13-3140 Mexican Highlands Shrub Steppe (Mesquite-Grassland)
13-3211 Grama-Tobosa (Mesquite-Grassland)
12-3222 Creosote Bush-Bur Sage (S. Desert Scrub, Sonoran)

Both Migratory and Sedentary

6-M2111 Douglas-fir Forest (Columbia Forest, montane)
7-M2112 Cedar-Hemlock-Douglas-fir (Columbia Forest, moist)
4-2113 N. Hardwoods (New York-Wisconsin)
8-2212 Beech-Maple Forest (Deciduous)
8-2213 Maple-Basswood Forest (Deciduous)
4-2214 Appalachian Oak Forest (N. Hardwood-Conifer)
8-2214 Appalachian Oak Forest (Deciduous)
7-M2416 Alaska Pacific Forest (Pacific Rain Forest)
9-2531 Bluestem Prairie (Tall-grass Prairie east)
9-2532 Wheatgrass-Bluestem-Needlegrass (Tall-grass Prairie west)
6-M2610 Sierran Forest (Montane)
9-M2610 Sierran Forest (Grassland)
6-M3112 Douglas-fir Forest (N. Rockies, Montane)
9-3120 Palouse Grassland
11-3131 Sagebrush-Wheatgrass (N. Desert Scrub)
11-3132 Lahontan Saltbush-Greasewood (N. Desert Scrub)

APPENDIX III

RECOVERIES OF WINTER-BANDED (JANUARY–FEBRUARY) SONG SPARROWS.

	Ecoregion section/life area where banded	No. banded	Recovered during the breeding season: At banding site	Recovered during the breeding season: Away from banding site		Recovered non-breeding season away from banding site	
4-2113	N. Hardwoods Forest (New York–Wisconsin)	97	3	4-2114A	N. Hardwoods-Spruce (Maritime)-1		0
4-2214	N. Hardwoods-Spruce (New England)	4	0		0	4-2113	N. Hardwoods (New York–Wisconsin)-1
						16-2320	S.E. Mixed Forest (S.E. Evergreen)-1
8-2211	Mixed Mesophytic Forest (Deciduous)	23	5	4-2214	Appalachian Oak (N. Hardwood-Conifer)-1		0
8-2212	Beech-Maple Forest (Deciduous)	323	14		0	4-2114	N. Hardwoods-Spruce (New England)-1
						16-2320	S.E. Mixed Forest (S.E. Evergreen)-1
						8-2212	Beech-Maple Forest (Deciduous)-1
8-2213	Maple-Basswood (Deciduous)	1	1		0		0
4-2214	Appalachian Oak (N. Hardwood-Conifer)	88	7		0		0
8-2214	Appalachian Oak (Deciduous)	1691	45	4-2114A	N. Hardwoods-Spruce (Maritime)-1	8-2214	Appalachian Oak (Deciduous)-4
				8-2214	Appalachian Oak (Deciduous)-2	4-2114	N. Hardwoods-Spruce (New England)-3
						4-2214	Appalachian Oak (N. Hardwood-Conifer)-1

APPENDIX III: CONTINUED.

	Ecoregion section/life area where banded	No. banded	Recovered during the breeding season: At banding site		Recovered during the breeding season: Away from banding site		Recovered non-breeding season away from banding site
8-2215	Oak-Hickory	54	5		0		0
8-2320	S.E. Mixed Forest (Deciduous)	714	28	4-2114A	N. Hardwoods-Spruce (Maritime)-1	8-2320	S.E. Mixed Forest (Deciduous)-4
				8-2214	Appalachian Oak (Deciduous)-1		
				4-2114	N. Hardwoods-Spruce (New England)-1		
16-2320	S.E. Mixed Forest (S.E. Evergreen)	135	0		0	16-2320	S.E. Mixed Forest (S.E. Evergreen)-1
7-2410	Willamette-Puget Forest (Pacific Rain Forest)	452	10		0	7-2410	Willamette-Puget Forest (Pacific Rain Forest)-3
10-2511	Oak-Hickory-Bluestem Parkland (Oak-Savannah)	47	4	4-2111	Spruce-Fir Forest (Minnesota)-1		0
15-M2620	California Chaparral (Chaparral-Oak)	146	25		0	7-2410	Willamette-Puget Forest (Pacific Rain Forest)-1
						15-M2620	California Chaparral (Chaparral-Oak)-4
6 & 9-M3111	Grand Fir-Douglas-fir (Montane Forest-Grassland)	1	1		0		0
11-M3113	Ponderosa Pine Douglas-fir (N. Desert Scrub, Southern Rockies)	8	1		0		0

APPENDIX IV
Food of Song Sparrows

Song Sparrows are adapted to a terrestrial life and spend most of their time foraging on the ground where they pick food from the surface or from the surface litter after kicking in it with both feet simultaneously (Harthill 1935; Stone 1937; Marshall 1948; Johnston 1968). Aleutian Island and Alaska coastal birds spend much of their time beachcombing, obtaining their food, including small marine life such as small mollusks and crustaceans, as well as seeds of wild rye grass and crowberries, chiefly from rocky beaches (Gabrielson and Lincoln 1951, 1959). In winter Aleutian birds also feed frequently on tidal mud flats along with sandpipers. The stomach of one Aleutian Song Sparrow contained several tiny snails (Sutton and Wilson 1946). In the Pacific Rain Forest area when feeding nestlings, Vancouver Island Song Sparrows search for food, mainly caterpillars, in brushy situations, but at other times frequent grassy areas for lacewings, and occasionally the tidal zone for marine life (Tompa 1962). The San Francisco Bay Song Sparrows scratch in the mud for small snails, catch flying salt marsh flies by making short jerky hops or runs, and even engage in aerial fly-catching occasionally (Johnston 1968). In the Northern Rocky Mountains, Nolan (1968) found plant food comprised 60 percent of the summer diet. In the Oak-Savannah area of Indiana, food of Song Sparrows is about 33 percent insects, and most of the remainder is grass and weed seeds (Butler 1897). In the Northern Hardwood-Conifer Life Area of northern New York State, nestlings in three nests received 74 pieces of animal matter, 56 pieces of plant food, and 41 pieces of unknown origin (Haldeman 1931). Animal food consisted of unrecognized insects 32, caterpillars 19, grasshoppers 17, lice 4, and butterflies 2. Plant food consisted of mulberries 47, barberries 8, and straw 1. Also in New York State in summer, more commonly than at other seasons, Song Sparrows sometimes forage for insects in foliage as high as 6 to 9 meters above the ground, although they usually stay among bushes and grass (Eaton 1914).

Analysis of foods in digestive tracts of Song Sparrows in many areas sampled over the entire year showed animal matter, chiefly small beetles, comprised 34 percent of the diet, and that the remainging 66 percent was composed of seeds of grasses and herbs, wild berries, and fruits (Judd 1901). An analysis by Martin et al. (1951), based on 199 specimens of Song Sparrow digestive tracts from a wide geographical area, showed 86 percent of the food to be plant and 14 percent animal matter in winter, 59 percent plant and 46 percent animal matter in spring, 60 percent plant and 40 percent animal matter in summer, and 92 percent plant and 8 percent animal matter in fall. The most important plant foods in the northeastern part of the country (10 to 25% of the diet) are smartweed, bristle grass, and ragweed seeds; less important (2 to 5% of diet) are crabgrass, oats, pigweed, dock, goosefoot, timothy, and sedge seeds. The order of importance in the Pacific region, mainly California, is pigweed seeds (10 to 25% of diet), knotweed seeds (5 to 10% of diet), and nightshade, miner's lettuce, oats, star thistle and chickweed seeds (2 to 5% of diet). The chief animal food items, not broken down by region or quantity, are: beetles, grasshoppers, crickets, caterpillars, ants and other hymenoptera, and hemiptera.

I tabulated percentages of animal and plant food identified in the digestive tracts in 222 Song Sparrows taken during the breeding season (May to August inclusive) and 99 taken in winter (December to February inclusive). The data are from the "Food Habits" files of the U.S. Fish and Wildlife Service housed at the Patuxent Wildlife Research Center, Laurel, Maryland. Most of the food items were identified by F. E. L. Beal of the U.S. Biological Survey, mainly in the late 1800's and early 1900's. Contents of a few stomachs were identified by E. R. Kalmback, E. A. Chapin, C. W. Leister, L. Kelso, C. Cottam, and R. T. Mitchell of the Biological Survey and Fish and Wildlife Service. In Appendix V, I present mean percentages of animal material (plant material comprises the remainder, totaling 100%) in breeding and winter season stomach contents of Song Sparrows from different Ecoregion Section/Life Area units, and in winter stomach contents of birds from Life Areas. Comparisons were made of only the Ecogeographical samples thought to be sufficiently large to be meaningful. No significant sex differences were found in relative amounts of animal and plant food eaten by Song Sparrows when arranged by either season or ecogeographic area, so the data for both sexes, as well as unsexed birds, were combined for analysis in those units and seasons. However, when all data for all seasons and all ecogeographic areas are combined into groups by sex, females consumed 42.27 percent animal food ($n = 86$), against 39.27 percent for males ($n = 115$; $P < 0.1$). The only significant differences between percentages of animal food consumed by Song Sparrows during the breeding season in any two ecogeographic units for which data are available are: greater percentage of animal food in the samples from Northern Hardwood Forest (New York-Wisconsin), Southeastern Mixed Forest and

Appalachian Oak (deciduous) than in California Chaparral (Chaparral-Oak) ($P < 0.001$). Winter food samples show a significantly greater amount of animal matter ($P < 0.01$) in the Willamette-Puget Forest samples than those from Southeastern Mixed Forest. The amount of animal matter is also greater in Willamette-Puget Forest than in California Chaparral, but not significantly so ($P < 0.2$). Organized by Life Area, animal food in the Pacific Rain Forest samples is significantly greater in winter than in both Eastern Deciduous Forest ($P < 0.001$) and Chaparral-Oak Woodland ($P < 0.01$). The deciduous forest and chaparral proportions of animal food are similar in winter.

APPENDIX V

Differences in Proportions of Animal Food of Song Sparrows During Breeding and Winter Seasons.[1]

		n	Mean % animal[2]	Probability[3]
	Ecoregion/Life Area, Breeding (May–August)			
15-M2620	California Chaparral (chaparral)	77	26.81	<0.001
8-2320	Southeastern Mixed Forest	27	71.04	0.4
8-2214	Appalachian Oak (deciduous)	33	60.97	0.001
15-M2620	California Chaparral (chaparral)	77	26.81	0.001
4-2113	N. Hardwood (New York–Wisconsin)	34	68.29	0.9
8-2320	Southeastern Mixed Forest	27	71.04	0.2
7-M2414	California Mixed Evergreen	7	49.14	0.2
15-M2620	California Chaparral (chaparral)	77	26.81	
	Ecoregion/Life Area, Winter (December–February)			
8-2320	Southeastern Mixed Forest	18	3.89	0.01
7-2410	Willamette-Puget forest	13	36.92	0.2
15-M2620	California Chaparral (chaparral)	8	10.00	0.4
8-2320	Southeastern Mixed Forest	18	3.89	
	Life Area, Winter (December–February)			
8-	Eastern Deciduous Forest	36	3.92	0.001
7-	Pacific Rain Forest	15	37.00	0.01
15-	Chaparral-Oak Woodland	16	5.56	0.9
9-	Grasslands	10	3.60	—
8-	Eastern Deciduous Forest	36	3.92	0.9
15-	Chaparral-Oak Woodland	16	5.56	

[1] Data for males and females combined.
[2] Proportion of plant food is the reciprocal of that of animal food to total 100%.
[3] Statistical significance of differences in means of successive ecogeographical units calculated by t-test.

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