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ECOLOGIC RACES OF SONG SPARROWS IN THE SAN FRANCISCO BAY REGION
PART I. HABITAT AND ABUNDANCE

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The Song Sparrow, *Passerella* (*Melospiza*) *melodia*, is a characteristic inhabitant of vegetation growing in wet places throughout North America from Alaska and eastern Canada south to central Mexico. The territory of a pair of Song Sparrows is small, roughly two-thirds of an acre (Nice, 1943:152); accordingly, wherever Song Sparrows exist they occur in dense populations, with the pairs close together. The species is highly variable geographically; there are thirty geographic races, counting all well differentiated forms (thus omitting *mailliardi* and *santaecrucis* of California) in the A. O. U. Check-list and its supplements (American Ornithologists' Union Committee, 1931:357-361; 1945:449) and adding three more from Mexico (Hellmayr, 1938:607-608).

The races in the northern and eastern parts of the range occupy large areas and are migratory, or at least partly so, in that individual migration occurs (Nice, 1937:29-42). On the west coast, the races in the Aleutians and along the coast of California, the race in the central valley of California, and all races farther south are considered highly sedentary, and they occupy smaller areas. There are eleven races breeding in California alone. Three of these are restricted to islands off the coast. Throughout the entire range of the species no two geographic races are known simultaneously to occupy an area when they are in breeding condition.

All races except one, to my knowledge, live in a niche characteristic for the whole species, consisting of vegetation of a certain configuration and spacing on moist ground along the edges of streams, sloughs and coastlines. This niche will be defined later on the basis of the totality of attributes shared in common by the subniches, which I shall call "habitats," occupied by Song Sparrows in the San Francisco Bay region. An exception is the habitat of the race on the Los Coronados Islands, Lower California, where according to Grinnell and Daggett (1903:34) there is no trace of fresh water and the birds occupy the sparse growth of shrubs on shaded northeast slopes.

Most of the races occupy the several habitats, such as stream-side vegetation and salt marsh, wherever they exist within the range of the race. However, on the eastern seaboard, *Passerella melodia atlantica* is limited to salt marshes along the coast and is morphologically distinct from its relative *P. m. euphonia* in the adjacent inland freshwater habitats (Wetmore, 1936 and 1941:529). In the San Francisco Bay region the spatial isolation of different habitats, particularly bay salt-marsh from upland freshwater growth, is correlated with a marked differentiation of very local races, no less than four of which exist in the counties surrounding the San Francisco, San Pablo and Suisun bays (fig. 42). These counties, exclusive of the Sacramento-San Joaquin river drainage to the east of Suisun Bay, constitute the area to which this study is limited.

The four races of the "bay region" are characterized by their possession of broader and more distinct black streaks in the plumage than in other races of *Passerella melodia*. Of these, the race *gouldii* of the upland fresh-water habitats is most like Song Sparrows elsewhere along the coast of California; it is, in fact, merely a series of populations falling in an intermediate position on a coastal gradient for reddish-brown dorsal "ground color" (the color prevailing over the dorsal surface excluding the black shaft streaks) which has its maximum development in the extremely reddish-brown race, *cleonensis*, to the north. It is worthy of a subspecific name because it is the most reddish-brown race which possesses in addition black shaft streaks. The other three races are confined to bay marshes. *P. m. samuelis*, of the salt marshes around San Pablo Bay, is blacker in ground color than any other Song Sparrow race. *Pusillula*, of the salt marshes around the border of San Francisco Bay, is one of the smallest races (in dimensions of bill, wing and tarsus); also, it is one of the lightest in dorsal ground color and is the only race of the species which possesses yellow coloration over the entire ventral surface. *Maxillaris*, of the Suisun Bay brackish marshes, is the darkest of all the Song Sparrows. Not only does it possess a great deal of black in the plumage, as in *samuelis*, but in addition the reddish-brown and yellow pigments are very heavy on the dorsal surface, the black streaks wider than in any other race, and the overall ground coloration is intense rich blackish-brown. *Maxillaris* is of larger size than the other three races and possesses by far the thickest bill of any race in the species. The sides of the maxilla are, in fact, swollen and bulged out laterally, hence the subspecific name. In bill depth, it averages 28 per cent larger than *pusillula*.

These San Francisco Bay region Song Sparrows are often mentioned in the ornithological literature dealing with the origin of species. Huxley (1942:272) cites them as "a case of ecotopic subspeciation in birds where the two forms are kept separate by their ecological preferences." Miller and McCabe (1935:145) regard the ecologic versatility of Song Sparrows as contributing to their racial differentiation. Miller (1947) suggests that non-adaptive variation, correlated with a small effective population size, is responsible for some of the local differentiation of Song Sparrows; and Mayr (1942:249) correctly (in my opinion) states that spatial isolation has probably been a necessary prelude to their present ecological differentiation. Grinnell (1913:194) maintains that there must be "a strong preferment on the part of individuals for the fresh-water conditions on the one hand or the salt-water on the other," which serves as an isolating mechanism in places where the two situations are confluent. The foregoing statements in the ornithological literature are of course based on data published in the brief original descriptions of these races, especially of those described by Grinnell. He has summarized accurately, but in general terms, the ecologic, distributional and morphologic facts for all the "bay region" Song Sparrows in two short taxonomic notices (Grinnell, 1901 and 1909).

The purpose of my study is to furnish more complete information than is present in Grinnell's two papers on the habitat requirements, spatial isolation and morphologic attributes not only of the four races but of the several populations into which each race is subdivided by geographic barriers. This will facilitate an evaluation of the various factors which restrict free interbreeding between populations, thus preventing the obliteration of the racial differences. Because of the limiting of my method to field observations on habitat occurrence, censuses of individuals, and the examination of museum study skins, the factors considered will be mainly habitat restriction and geographic isolation. At least we shall see to what extent the boundaries of visibly distinct populations coincide with the boundaries between different habitats and with the limits of geographic barriers. Thus, the paper cannot furnish a final answer to the question of how geographic races arise and are perpetuated. That problem requires for its solution

(not to mention breeding experiments) knowledge of the seasonal and yearly movements, if any, of individual birds and particularly the extent of such movements across habitat and geographic barriers, in addition to a determination of the distance from the nest at which young birds settle down eventually to breed, all of which can be studied only by marking individuals on a large scale. The substance of this paper might furnish a necessary foundation for such studies.

Only the portion of this study dealing with ecology of Song Sparrows is included in the present article. The rest, concerned with an analysis of geographic variation, the coincidence of changes in gradients of geographically variable characters with certain zones of transition from bay marsh to fresh-water types of habitat and an attempt at interpreting this situation in terms of isolating mechanisms is scheduled for a later issue of The Condor.

The materials upon which the present ecologic portion is based consist of my censuses of Song Sparrows in the various habitats and my identifications of plants and of items in the stomach contents. For information concerning the unique ecologic situation at Palo Alto, from 1896 to 1908, I have consulted the field notes of Joseph Grinnell and Joseph S. Dixon, which are filed at the Museum of Vertebrate Zoology. Also, I rely upon correspondence with early observers at Palo Alto, whose kindness in replying to my questions I greatly appreciate. They are the following: John C. Brown, Joseph S. Dixon, Walter K. Fisher, Theodore J. Hoover, J. R. Pemberton and Robert E. Snodgrass. I am also indebted to William Longhurst, who piloted me around the bay region on a habitat inspection from the air and took me through the Napa River marshes in his scull boat. John E. Kesseli permitted me to examine his aerial photographs of Contra Costa County, and Emerson A. Stoner introduced me to the Suisun marsh area.

Joseph Grinnell's interest in this problem began in the period from 1900 to 1902 when he collected Song Sparrows in the salt marsh and an adjacent willow patch at the mouth of San Francisquito Creek, Palo Alto. He kept complete information in his field notebooks on the habitat occurrence of the individual specimens and called attention to the striking racial difference between the birds of the willow patch and the salt marsh (Grinnell, 1901).

From at least 1900 to 1908, there existed at the mouth of San Francisquito Creek an alluvium of several acres clothed with willows and containing about a dozen pairs of Song Sparrows distributed along its edge. The steepness of the alluvium brought about an abrupt change in habitat from willow growth to the surrounding *Salicornia-Grindelia* salt marsh, along a line several hundred yards long. Throughout this period the creek was populated with Song Sparrows for its entire length from the willow patch westward into the hills, and from there it was continuous with the upland population of the peninsula.

An examination of Grinnell's specimens taken beteen 1900 and 1902 reveals that interbreeding was definitely restricted between these representatives of two populations "a stone's throw" from each other. All but five of the twenty-six willow-patch birds are identical with specimens taken elsewhere in the uplands of the San Francisco peninsula; they have a brown back, white belly and large wing, tarsus and bill, whereas most of the twenty-eight salt marsh specimens are yellowish-gray on the back, yellow below and of small size. They are identical with specimens taken elsewhere in the salt marshes from Palo Alto north to San Bruno. The presence of one yellowish-gray and four yellowish-brown backs, and two yellow bellies in the willow patch series indicates that interbreeding must have taken place, although on a very small scale. A small collection taken by Dixon in 1908 reveals lack of mixing of the two racial populations equal to that in 1900-1902. The willow patch has since been obliterated and it is no longer possible to

study a similar situation at any point around the bay where races are well distinguished from each other morphologically. Grinnell (1901) suggested that the two races were behaving as incipient species at this habitat junction. With this in mind let us consider the habitat preference of the birds throughout the rest of the bay region, and especially their behavior at other junctions between habitats.

METHOD

Eighty-nine days were spent in the field and for each locality visited there was recorded the habitat, plant species, numbers of birds, their behavior and relations with other species. Where specimens were collected I have in addition recorded the plant association in which each specimen was taken, identified the stomach contents (of 233 birds collected in the fall) so far as hand lens will permit, and in critical areas have plotted each specimen on a map and identified members of breeding pairs. Fifty-four censuses (of birds not collected) were made in 36 localities during 37 days of the nesting season of 1947, March 29 to June 28. Each census record consists of a map, usually covering one to four miles along a habitat, with the vegetation identified and sketched in, and each Song Sparrow represented by a symbol. In critical areas I have added for each bird any outstanding morphological characteristics which could be discerned at close range with 6-power binoculars. All this is recorded in the field.

Preliminary intensive study for ten days at San Pablo revealed (as was confirmed by all subsequent observations) that pairs occupy territories arranged end-to-end in linear sequence, and always in single file. This is a consequence of the fact that the Song Sparrow habitats consist of narrow fringes of vegetation bounded on both sides by unfavorable habitat, whether it be the open water of a wide river or slough, or dry grassland adjoining the willow growth along a stream. Accordingly, most of the birds can be flushed by walking along a stream or slough bank, and it is therefore not necessary to map territories in order to count the birds. They flush at 10 or 15 yards, and those in likely-looking vegetation off the line of march can be attracted to a conspicuous perch or at least made to call loudly if the observed merely makes a squeaking sound, which to the Song Sparrow seems irresistable. A singing male, or two silent birds flushed together in an area in which no male is singing at the moment, I regard as representing pairs; a scale is furnished with the map so that the average distance between pairs can be computed in yards.

In particularly dense populations, ten or more pairs of birds within hearing distance of each other engage in universal singing or loud calling at times of particularly intense singing, fighting or alarm on the part of any one bird or pair. At such times they can be counted and thus a check is made of the census. Also I usually repeat each census hastily on the return trip. Not only does a carefully made census tally with a hasty return count, repeats on different days and times of day, and with numbers heard in periods of universal singing or calling, but it also agrees with censuses made along comparable habitats elsewhere. Therefore, it is felt that this census method yields a fairly accurate count in the nesting season.

GEOGRAPHY

The terrain of the "bay region" is mostly hilly; the only extensive flat areas border the three bays in a strip two to five miles wide, interrupted by hills reaching the bay shore at San Pablo Strait, Black Point, Carquinez Strait, South San Francisco and the Golden Gate. At the north side of San Pablo Bay, the Napa Valley constitutes an extension of the bay-side plain as far north as St. Helena; similarly at the south end of San Francisco Bay, the broad, flat valley of Coyote Creek extends far southward. These

plains peripheral to the three bays are of great importance in the distribution of Song Sparrows because they slope so gradually into the water that vast expanses of marsh vegetation can exist there. The hill systems consist of two parallel north-south chains, one along the coast, which is interrupted by the Golden Gate, the other along the east side of the Napa Valley, San Pablo and San Francisco bays, which is interrupted only at Carquinez Strait. The Pacific Ocean shore is mostly rugged and precipitous. It is irregular and cut by deep gorges so that north- and south-facing hill slopes alternate all along its length. Only at Bolinas Bay, Drakes Bay and Tomales Bay is the coastline relieved by estuaries which sufficient low-lying flat land to allow for the development of salt marshes.

CLIMATE

The climate of the San Francisco Bay region is cool and humid and because of proximity to the ocean is sufficiently uniform the year around so that the places inhabited by Song Sparrows differ little in the appearance of the vegetation through the seasons. The humidity allows the persistence of moist conditions the year around, except on the east slopes of the ranges, where the creeks dry up in summer. The source of moisture is rain clouds and fog which move toward the coast from the ocean and are caught by the ranges of hills. Accordingly the slope of the coast ranges rising from and facing the ocean shore is the most humid and has the most numerous streams, most of which are permanent. All north-facing hillsides there are moist enough to support Song Sparrows independently of actual riparian habitats. Fewer fog masses pass inland over the first range of hills, resulting in much drier conditions, particularly on the east slopes of hills and on the plains bordering the three bays. Thus the east side of the coastal range of hills is drier, with fewer streams than the side facing the ocean. The next rank of hills (bordering the east side of the San Francisco and San Pablo bays) is dry on its west slope except for an area directly east of the Golden Gate, where fog and clouds escape the dragnet of coastal hills and move across the bay to provide conditions moist enough for Song Sparrows on north-facing hillsides in Berkeley and Oakland. The east slopes of these hills and the territory beyond is still drier and much warmer than the east side of the coastal hills, and here one finds very few streams, few of which are permanent. Because of lower temperature and increase in humidity toward the north, moist conditions occur much farther inland in the northern part of the "bay region" than in the south. The most important influence of climate upon the distribution of Song Sparrows is the aridity of the plains surrounding the three bays. They are covered mostly with dry grassland, which constitutes a barrier between bay marsh Song Sparrows and those living in the adjacent uplands.

SALINITY OF THE BAYS

The major source of salt water for the three bays is, of course, the tidal flow through the Golden Gate from the ocean. Judging from the marsh vegetation, the saltiest bay is San Francisco, because the climate around it is hotter and drier so that only a few small streams enter it. There is little addition of fresh water, and evaporation concentrates the salt still more. Such streams as do reach this bay are too small and too steep to produce a zone of brackish water at their mouths. At low tide they contain running fresh water, at high tide salt water.

San Pablo Bay is salty, but less so than San Francisco Bay because it receives a large amount of fresh water from the San Joaquin and Sacramento rivers via Carquinez Strait. In addition it receives large rivers which drain the humid land to the north. The beds of these rivers (Petaluma Creek, Sonoma Creek, the Napa River) are more gradually sloping, broader, and contain more water than those emptying into San Francisco

Bay; accordingly they produce at their mouths a broad zone of brackish water which becomes slightly less salty in the rainy season but does not vary much with the tides.

Suisun Bay receives salt water from the tides which flow eastward through Carquinez Strait and fresh water from the Sacramento-San Joaquin River. It is entirely brackish, judging from the uniformity of its marsh vegetation.

HABITATS

Fresh-water marsh.—The vegetation of fresh-water marshes consists of *Typha latifolia* and *Scirpus californicus*. A marsh may have only one or the other species, or may have both in alternating pure patches. The configuration of vegetation (fig. 40*a*) is a mass of parallel vertical stems five to ten feet high, the individual stems being about two inches apart but deployed in clumps in such a way that at the ground level almost any point can be reached by a sparrow via six-inch wide passages. *Typha* growth provides more shade than *Scirpus* because of the several leaves ascending from each stem. Usually these plants grow in patches ten to twenty yards in diameter, and each growth is highest in the center, tapering off toward the circumference. Dense piles of dead prostrate stems of the previous year's growth are constant features. Between patches, or at the dry margin of the marsh, and at the bases of the stems not covered with water is bare cracked mud or wet ooze. The vegetation ceases at the dry margin of the marsh and in deep water. It can persist, because of its perennial rhizomes in places where the water dries up for part of the year.

There are several small fresh-water marshes near the coast, especially along the peninsula from Lake Merced south to Tunitas Creek and along the San Andreas fault. Others occur near the mouth of the Napa River and there was once a vast marsh at the mouth of Walnut Creek, Contra Costa County, which is no longer in existence. Otherwise, in the interior, these marshes exist only at artificial lakes. The total area of fresh-water marshes is slight compared to other Song Sparrow habitats. Near the coast, they are connected to soft chaparral where bounded by humid, north-facing slopes, and to the riparian habitat where streams enter them. Inland, they are usually surrounded by dry grassland and their only connection with other Song Sparrow habitats is a narrow one at the stream entrance. However, there is ălways some connection between fresh-water marshes and other Song Sparrow habitats, whether they be riparian, soft chaparral or brackish marsh. There is generally a gradual change in habitat at the connections, and in all cases the sparrows show no preference for one or the other habitat and form a continuous population across such boundaries.

I have no counts of pairs in fresh-water habitats, but my impression is that the birds are as abundant there as in brackish or salt marshes of similar vegetational configuration. This growth always constitutes a narrow band of vegetation whose width is greater, the more gradually sloping the shore of the pond concerned. There is never more than a single row of pairs in this band, and I should guess that pairs are about 30 yards apart where the width is forty yards, and about 80 yards apart where it is 10-15 yards.

Song Sparrows sing from the highest stems in the center of patches of vegetation, hide in the dense piles of prostrate stems and forage on the mud at the base of the stems or on the lake margin, obtaining their food of seeds and small insects. I have never seen them eating seeds from the plants themselves; apparently they must wait for them to fall to the ground. However, I once saw an individual climbing the stems of *Scirpus californicus* like a nuthatch, picking off tiny insects.

Song Sparrows are less tolerant of drying than *Typha* and *Scirpus californicus* and are further limited within the most permanently moist marshes to the portions where bare ground is available for foraging. Thus, the distribution of the birds is much more

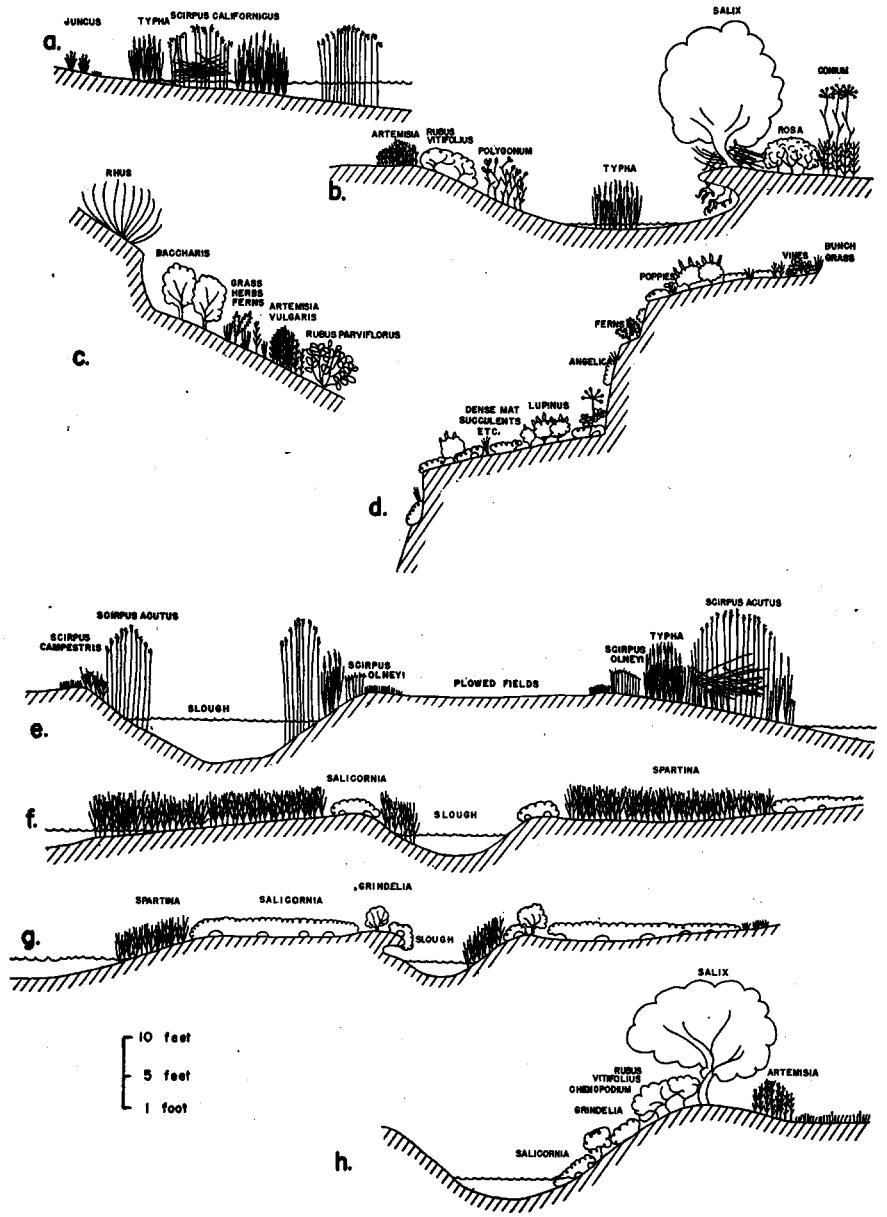

Fig. 40. Song Sparrow habitats in diagrammatic cross-section: (a) *fresh-water marsh,* mouth of Olema Creek, Marin County; (b) *riparian,* San Leandro Creek, Alameda County; (c) *soft chaparral,* Strawberry Canyon, Alameda County; (d) *seaside chaparral,* Point Reyes, Marin County; (e) *brackish marsh,* Grizzly Island, Solano County; (f) *Spartina marsh,* San Pablo, Contra Costa County; (g) *Salicornia-Grindelia marsh,* Corte Madera, Marin County; (h) intermediate zone at mouth of Guadalupe River, Santa Clara County.

circumscribed than the distribution of the vegetation. Further, the birds are absent from fresh-water marshes where the growth is sparse, with stems a foot or so apart; such growth offers no concealment.

Marsh Wrens, Yellow-throats and Red-winged Blackbirds are fairly constant associates of the Song Sparrow in fresh-water marshes, but the only birds which have somewhat similar foraging requirements are, in winter, the Lincoln Sparrow and the Savannah Sparrow. These birds are seldom found in the actual marsh vegetation and forage mostly in moist grassland around the edges of the marsh. The Song Sparrow is the most abundant and most characteristic avian inhabitant and probably has no effective competitors for food, nesting sites, song perches and hiding-places among the other birds.

Stream and river margins.—Willow trees are the characteristic and predominant growth along streams, but smaller plants, *Rubus vitifolius, Rosa californica* and *Artemisia vulgaris,* are constantly associated with them. In addition, other trees, in order of their frequency, are often associated with the willow: *Acer negundo, Aesculus californica, Populus fremontii, Fraxinus oregona* and *Acer macrophyllum*; and the following plants may add to the low growth: *Conium maculatum, Polygonum acer, Urtica gracilis, Rumex crispus* and *Symphoricarpos albus. Typha latifolia* and *Scirpus californicus* occur in the stream itself where light is sufficient.

The configuration or growth form of this vegetation (fig. 40*b*) consists of the willow stems dividing into many branches at the ground level and ascending outward 10 to 25 feet to form a hemispherical crown. With closely-spaced trees these stems retain a loose pile of dead twigs on the ground, but under more open stands which are occasionally washed by the stream, the ground is bare or littered with dead leaves. Bare mud occurs at the water's edge and the root systems may be undercut by the stream, providing many dark labyrinths where Song Sparrows forage. Around the edges of the willows and between widely spaced trees grow the dense vine tangles of rose and blackberry and compact masses of the erect stems of *Artemisia* and *Polygonum* 3 to 5 feet high. These plants usually occur in alternating pure patches 5 to 15 yards long.

The limiting factors for this particular kind of riparian growth appear to be water and light. This vegetation disappears in canyons whose steep walls or coniferous timber shade the stream, and it is absent from streams with beds cut so low that the roots of the plants cannot reach water. However, it can persist along streams which are dry for part of the year. Riparian habitats are most prevalent near the coast, where every little gully on the north-facing slopes is lined with willows. Inland, streams become fewer, losing this type of riparian growth where they pass through heavy forests, but some provide continuous environment suitable for Song Sparrows through gaps in the hills, and they become more numerous again in the east bay hills opposite the Golden Gate. In the arid eastern part of the bay region, streams become fewer and are not permanent. Nevertheless, this habitat forms a vast branching network which connects all the other Song Sparrow habitats to each other and which provides the principal environment for upland Song Sparrows.

With two exceptions (mouth of San Francisquito Creek and mouth of Mill Creek, Marin County) riparian habitat grades smoothly through a zone of intermediate or mixed vegetation into all the other habitats and at no such zone have I observed any interruption in the linear continuity of Song Sparrow territories, nor any marked preference for one or the other habitat by birds in the intermediate zones. There is a marked difference in the form of this junction with salt marshes in San Francisco Bay as opposed to northern San Pablo Bay. There is no area of brackish water at the mouths of the small streams entering San Francisco Bay. Accordingly the salt-water vegetation extends upstream as far as the tides reach and grows low on the banks. The fresh-water

vegetation grows above it on the top of the bank and thins out toward the marsh. Thus, there is a zone several hundred yards long where the two habitats overlap (fig. 40*h*), and both are included in the territory of each pair of sparrows there. Neither habitat is wide enough to support Song Sparrows by itself. Sparrows are observed foraging in both types of vegetation, which is proven by the stomach contents; for instance, *Conium* seeds and snail shells are to be found in the same stomach. The large streams which enter northern San Pablo Bay form brackish marshes at their mouths, and the transition from riparian to salt vegetation is thus much more gradual.

Other factors being equal, the distance between pairs of Song Sparrows (that is, the density of the riparian population) along streams crossing the bayside plains depends on the width of the band of stream-side vegetation. Pairs are farther apart in narrow than wide zones of riparian vegetation. Most streams in the bay area have been banked off so that this growth is restricted to a 5- to 10-yard fringe on steep banks. Under natural conditions the vegetation may extend out 25 yards. Each Song Sparrow pair has the headquarters of its territory at the bank of the stream, so that there is never more than a single row of pairs along one bank. Triple rows are found only under natural conditions, such as the mouth of Walnut Creek, where there is a row of pairs along each bank of the main creek and a third row along an accessory creek 50 to 100 yards to the side. Pairs are 50 yards apart here, where the vegetation is about 25 yards wide.

At the Napa River (south side of Napa) the vegetation is only 5 to 15 yards wide but the river is broad (60 yards), and I saw no birds crossing it, even when chased around in their territories. Here we have two rows of territories, one row on each side of the river, with 60 yards between pairs. Sonoma Creek, at Glen Ellen, is only 3 or 4 yards wide and the vegetation grows out 10 to 20 yards on each side. Birds fly back and forth across the creek and we find a pair every 33 yards but in a staggered arrangement, permitting a telescoping of territories because of the wide habitat. At the mouth of San Pablo Creek, which is narrow, the growth is restricted to a 10-yard band on each bank, and a single file of pairs is found, one pair every 57 yards. In canyons, the riparian growth becomes more or less shaded out of existence by laurels and live oaks, and at Wildcat Canyon there is a pair only every 110 yards. At Miller Creek, with still more laurels, pairs are 280 yards apart, on the average. Song Sparrows sing from the upper parts of the willows, find concealment in the dense shrubbery and usually forage on the ground. (I once saw some birds feeding on caterpillars high in the willows.) In foraging, they hop rapidly over the mud of the stream margin and work under the patches of blackberry and *Artemisia*. They are particularly attracted to the piles of willow twigs and the dark recesses under the stream banks where they resemble Canyon Wrens in their activity, slipping among the roots in very dark crannies. Food consists mostly of seeds, although small insects are also taken.

The factors of moisture and light seem to exert more stringent limitations upon the Song Sparrow than upon the willow. Sparrows respond to dry conditions in the eastern part of the "bay region" by moving or possibly migrating in the fall. At Muir Woods, the general configuration of streamside vegetation is similar, both inside and outside of the redwoods. But Song Sparrows are very common (pair every 40 to 50 yards) downstream from the redwoods and are entirely absent from that part which is roofed over by the trees. (The last pair is just 50 yards inside the main entrance to the park.) Absence of the vine and shrub growth along streams is another serious limitation to Song Sparrows. Places such as Huichica Creek, Napa County, where all this growth is grazed and trampled by cattle, are devoid of Song Sparrows. Even the willow itself limits sparrows when it grows in a continuous dense canopy. At the south end of Lake

Merced, San Francisco, there is a veritable "woodland" of dense tall willow growth, the dark interior of which is avoided by the birds.

Song Sparrows are the most abundant and characteristic avian inhabitants of riparian habitat, at least along streams crossing the bayside plains. They have the habitat pretty much to themselves and so do not have competitors with similar requirements at least in summer. In winter, riparian growth is shared with winter visitant races of Song Sparrows, White-crowned Sparrows and Lincoln Sparrows. However, the Lincoln Sparrows prefer moist grassland or more open weed growth away from the willows, the White-crowns and *Passerella m. fisherella* forage in drier brush and weeds near the stream, and *Passerella m. morphna* is thus the only form which competes with the local race for food, but it is outnumbered about 10 to 1.

Soft chaparral.—Baccharis pilularis, Rubus parviflorus, Rubus vitifolius, Rhus diversiloba, Conium maculatum, Heracleum lanatum and *Artemisia vulgaris* are but a few of the multitude of plants, including ferns, grasses and sedges, which compose the soft chaparral. These plants tend to form a continuous, dense cover 4 to 8 feet high, but Song Sparrows frequent them only in places where the growth is divided into small clumps of bushes and separate tangles of vines bordered by small grasses, ferns and flowers, and separated from each other by bare ground which is actually wet. In this form (fig. 40*c*) soft chaparral is limited by moisture conditions to north-facing slopes along the coast (but not within 100 yards of the ocean) and to those interior north-facing slopes which are near or east of the Golden Gate. Accordingly its distribution embraces only that part of the coastal hills where coniferous or oak-madrone woodland is absent, small patches along the southern border of Richardson Bay salt marsh and Corte Madera salt marsh in Marin County, the Richmond Hills, and the Berkeley Hills from two miles southeast of Redwood Peak to Wildcat Canyon.

Within 100 to 200 yards of the ocean, soft chaparral blends gradually into seaside chaparral, and it is penetrated by riparian habitat along every moist gully. Inland, it is invariably linked to riparian habitat, but only at Drake Bay, Richardson Bay and Corte Madera do we find it contiguous both with salt marshes and streamside growth. At Richmond Hills it is joined to the San Pablo Bay salt marsh. These junctions with salt marsh vegetation are of course abrupt, but do not involve a radical change in vegetational growth form; *Baccharis* grades into *Grindelia* and the low grasses and weeds into the *Salicornia* mat of the salt marsh. Song Sparrow territories there appear to include both habitats within their boundaries. Birds continually fly back and forth from *Salicornia* to poison oak thickets, and I have seen at Richardson Bay a female which repeatedly carried food from the salt marsh to its young in a nest in poison oak.

The abundance of Song Sparrows in soft chaparral depends upon the amount of "edge" and moisture provided. At Richmond Hills, where the *Baccharis* bushes are far apart and where the ground is so wet that there is a growth of *Juncus,* pairs average 50 yards apart. At Frank Valley, Marin County, pairs average 87 yards apart; the drier Montara Mountains, San Mateo County, have pairs 200 yards apart; and at Strawberry Canyon, Alameda County, pairs are separated by 225 yards, occurring only where the continuous cover of vegetation is broken by steep gullies or slides. (*Conium maculatum* in Strawberry and Wildcat canyons forms pure stands in which a singing male can be found every 25 yards.)

Song Sparrows utilize the dense tangle of vegetation for concealment, sing from the tops of the highest bushes, and forage almost exclusively on the bare ground under and around the edges of the clumps of bushes for their food of seeds and small insects. Light is a limiting factor which seems to work directly on the birds, for they are absent from chaparral which forms a continuous high canopy and from that portion of the soft

chaparral, even though it is composed of the same species, which penetrates woodland and there forms the understory vegetation. Only at the summit of Inverness Ridge, Marin County, and Redwood Peak, Alameda County, are there any Song Sparrows in patches of soft chaparral within the forest; in both these places the trees (bishop pine and redwood, respectively) are small and widely spaced and the sparrows are found only in the widest clearings. Elsewhere, for instance along the Tunitas Creek and Kings Mountain roads in San Mateo County, they are totally absent even from the wide clearings, moist swales, and poison-oak thickets both in the redwood forest and the oak-madrone forest.

White-crowned Sparrows share this habitat with the Song Sparrow only at the Richmond Hills and close to the sea coast. Their interrelations will be discussed under the next habitat, seaside chaparral.

Seaside chaparral.—On the north slope of Point Reyes there is a band of vegetation growing between the edge of the cliff and the 500-foot contour in exceedingly moist conditions resulting from almost constant fog and a high rainfall. The ground is everywhere wet, although there is no standing water. Predominant plants are hemispherical shrubs of *Lupinus arboreus* 2 to 4 feet high, growing in short rows with stems three feet apart or as solitary bushes nine feet apart. The ground between the lupines is densely clothed with a mat a foot or more high of succulents, grasses, vines, flowers and ferns (fig. 40*d*). Some of the plants which contribute to this mat are *Eriogonum nudum, Echinocystis fabacea, Pteridium aquilinum, Orthocarpus,* a small *Rubus, Eschscholtzia californica, Grindelia robusta, Ligusticum apiodorum* and various grasses. Other solitary plants, such as *Angelica hendersonii* (22 inches) and a bunch grass (12 inches) stand by themselves or extend above the general level of the turf and *Achillea millefolium* and *Stachys californica* recline against or grow up through the lupine. There is space under the lupines where Song Sparrows can forage on bare ground; also, the vegetational mat is permeated by channels made by rainwater and perhaps small mammals. Rocks, steep bare banks and cliffs divide the vegetation into patches so that plenty of "edges" are provided for foraging. There is room in this seaside chaparral habitat for a single or staggered row of Song Sparrow territories, and a pair is found every 43 yards.

A little patch of seaside chaparral is found at Montara Point, San Mateo County. Here the configuration of vegetation is a solid mat two feet tall, bounded by rocks and steep banks. The predominant plants are *Eriophyllum staechadifolium,* prostrate *Baccharis pilularis, Angelica hendersonii, Ericameria ericoides, Castilleia, Rubus, Equisetum, Juncus* and several kinds of grass. Song Sparrow pairs here are 30 yards apart, all within 50 yards of the beach. At the mouth of Tunitas Creek, San Mateo County, pairs are 150 yards apart because the shoreline faces west and the patches of *Eriophyllum staechadifolium* (4 to 5 feet tall) and their associates (*Eriogonum, Heracleum, Rubus vitifolius* and *Chlorogalum*) are restricted to the north-facing sides of gullies which must alternate with drier exposures. Pairs here are within 25 yards of the ocean.

Seaside chaparral is limited apparently by its demands for constant moisture (short of standing water) to north-facing slopes within 100 yards of the ocean. It is bounded by the steep bank or cliffs at the shore and is lost inland where grassland or drier chaparral begins. Its distribution in the bay region consists of patches at the mouth of Tunitas Creek, Montara Point, a belt along the ocean base of Montara Mountain, a continuous belt around the north end of the San Francisco peninsula from Point Lobos east to the Golden Gate Bridge, along the coast of southern Marin County, Point Reyes, and from Tomales Point to the Russian River. In a few places it grades gradually into soft chaparral, but it is mostly connected to other Song Sparrow habitats by willow

growth along streams which reach the coast. In such places the birds form continuous breeding series across the habitat boundaries.

Song Sparrows utilize the tops of the lupine bushes for song perches and can find concealment anywhere in the vegetation. They forage on the ground under the lupines and along the mammal trails and other passageways under the low dense growth. They also feed among rocks and in each tiny patch of vegetation clinging to the steepest cliffs. Thus, they must expend much energy flying vertically, to say nothing of countering the constant strong winds which buffet them. Food consists mostly of seeds of *Eriophyllum*.

There is no discernible limitation restricting the birds to any portion of seaside chaparral, and the range of the sparrow coincides with that of the vegetation. They are totally absent from grazed areas on the Point Reyes peninsula, where the mat of succulent vegetation between the lupines is lacking and where White-crowned Sparrows persist. At Point Reyes, the seaside chaparral is interdigitated with grassland, which becomes predominant on the top of this headland. Thus, the Savannah Sparrow is brought into close contact with the Song Sparrow and the two can be found singing, foraging and hiding in identical situations, although the Savannah Sparrow appears not to forage under vegetation. They do not affect each other, as each Savannah Sparrow has a very large forage area most of which is in the grassland.

The resident race of White-crowned Sparrow, *Zonotrichia leucophrys nuttalli*, comes into closer association with Song Sparrows than does *Passerculus*. In all seaside chaparral and on the very wet north-facing slopes of the Richmond Hills, the two species occupy common ground, and in equal numbers. Cursory observations reveal no territorial accommodation one for the other, so that we find for the Song Sparrow at least, normal-sized territories bordering upon each other in continuous chains, with the territories of White-crowns seemingly superimposed upon them. The two species pay no attention to each other, nor does it appear that they compete in any way for food or nesting or singing sites. It is my impression that although the White-crowned Sparrow forages on the ground under large bushes, it does not go under the mat of succulents; it also picks seeds from the upper portions of the plants.

Brackish marsh.—Scirpus acutus and *Typha latifolia* are the predominant plant species in brackish marshes. Associated with them are *Scirpus olneyi, Scirpus campestris* and *Scirpus californicus*. At the gradually sloping bay shore this growth is fairly homogeneous, consisting of a belt 100 to 200 yards wide of mixed *Typha* and *Scirpus olneyi* 6 to 8 feet high and widely spaced large patches of *Scirpus acutus* 8 to 12 feet high. Their stems are 4 to 6 inches apart. In addition, there are large patches of pure *Scirpus campestris* 2 to 3 feet high with stems 1 to 2 inches apart. On the steeper banks of large sloughs this growth is more zonal, with stands of pure *S. acutus* growing in deep water, either in a continuous belt or in patches 50 to 75 yards apart, followed by a fairly continuous band of *Typha* higher on the bank, then large masses of pure *S. olneyi* alternating with *S. campestris*. These plants, especially *S. acutus*, retain masses of dead stems of the previous year, sometimes in piles six feet high; there is exposed mud at the bases of the stems and along the slough margins. This habitat (fig. 40*e*) is limited to that portion of the land which is covered at high tide and drained by sloughs at low tide.

Brackish marsh is the prevailing habitat of Suisun Bay. Elsewhere, it occurs on the lower half of Southampton Bay, and in a zone bridging the gap between fresh and saltwater habitats along the Napa River (three miles long), Sonoma Creek (two miles long), Petaluma Creek (no longer connected to riparian growth) and at the head of Tomales Bay. The connection between brackish marsh and riparian habitat is very gradual because *Scirpus californicus* and *Typha* carry the growth form (identical with *Scirpus acutus*) far up-stream beyond the limit of tidal flow. Similarly, *Scirpus acutus*, with its

greater tolerance for salt, continues from the brackish zone far into the salt marsh area at the mouths of large rivers, so that it grades finally into *Spartina* stands of roughly equivalent growth form, as far as sparrows are concerned. There is no interruption of the linear sequence of breeding Song Sparrows through these transitions and the birds at any intermediate zone do not sort out into different plant associations. Song Sparrow pairs are about 48 yards apart along the broad band of vegetation at the bay shore and are separated by 52 to 70 yards along slough banks, depending upon the width of the fringe of plants (15 to 5 yards, respectively). They use the tallest *Scirpus acutus* in the centers of patches of that species for song and calling perches and find concealment in the piles of dead stems, where their presence is announced by continual rattling of the stems as the birds hop from one to another.

Foraging takes place on the bare surface of the ooze at the bases of stems and along the slough margin at low tide. They feed principally on *Scirpus* seeds, but take insects, especially mosquito larvae. Here these energetic birds pick the *Scirpus* seeds from the ground after they fall, to be carried away by each tide, while only six feet over their heads exists the vast untapped supply on the flowering stems. Song Sparrows are limited to the area covered by the tides, where the flow is unimpeded by man-made levees. The height of these levees has permitted the appearance of upland plants requiring fresh water, namely *Baccharis pilularis*, *Rosa californica* and some *Salix*; Song Sparrows do not avoid them, but their territorial headquarters are always at the slough margin.

In the fall, both adults and juveniles may wander over the levees to forage and even sing in the adjoining hayfields. Artificial levees in many parts of Suisun Bay have caused the development of salt marsh vegetation in low places which are flooded by extremely high tides, following which the salt is concentrated by evaporation. *Salicornia* and *Grindelia* grow in these areas, but they are consistently avoided by the sparrows. This is not because the birds are intolerant of salt vegetation but rather because the tidal flow is impeded and the water is stagnant and red in color. (The same condition is found even in the salt marshes of San Francisco Bay, where the birds avoid stagnant situations.) On the east side of Cordelia, Solano County, there is a little marsh which has a considerable expanse of pure *Salicornia* resulting from a restricted tidal flow through a railroad culvert. Nevertheless, the marsh is drained at low tide, has no stagnant water, and Song Sparrows utilize the *Salicornia* for foraging and sing there as if their territories included that vegetation in addition to the adjacent *Scirpus*. Therefore, it cannot be argued that Suisun Bay Song Sparrows are strictly intolerant of *Salicornia-Grindelia* growth. Of course, under natural conditions such vegetation is entirely lacking from their domain.

Within typical brackish marsh each pair is limited to a territory which contains a patch of *Scirpus acutus* standing above the surrounding vegetation. Apparently such high song perches are necessary for the birds, and their absence might constitute a limiting factor in Song Sparrow distribution. The birds generally avoid *Scirpus campestris* where it grows in low patches with closely packed stems.

Song Sparrows in brackish marshes are, as in most of the other habitats, the sole ground-foraging birds and the predominant avian species. Marsh Wrens, Yellow-throats and Red-winged Blackbirds are also prominant in brackish marshes, but the two former appear to forage mostly in the upper parts of the plants, and the Red-wings forage in adjacent fields, so that the Song Sparrow probably has no serious competition for food.

Salt-marsh.—Spartina foliosa, *Salicornia ambigua* and *Grindelia cuneifolia* compose the vegetation of salt marshes. (*Distichlis spicata* and *Frankenia grandifolia* are relatively inconspicuous associates of *Salicornia*. Occasionally they form little circular

patches with closely packed stems permitting no entrance for foraging by the birds.) These plants grow in successive altitudinal strata with *Spartina* lowest and *Grindelia* highest. Thus, in a marsh which slopes gradually into the bay we find (inland from the mud flats which are exposed only at low tides) first a broad zone of *Spartina,* whose stems are partly covered at high tide, then inland on higher ground, a broad zone of *Salicornia* which is covered only by the highest tides. Beyond the *Salicornia* comes grassland, which is above the high-tide mark, and we thus find no zone of *Grindelia* on the inner border of the marsh. *Grindelia* occurs on the elevated banks of sloughs in the *Salicornia* zone.

The belt of *Spartina* is traversed by straight sloughs with gradually sloping banks, too deep for vegetation to grow, and not emptied at low tide. The tops of the banks of these sloughs, under natural conditions, are higher than the surrounding *Spartina* marsh and have a band of *Salicornia* along them. Upon reaching the inner zone of *Salicornia,* the sloughs branch and begin to wind in intricate convolutions. They are shallow enough to permit the growth of *Spartina* in their beds, and the raised tops of the banks support a band of *Grindelia.* Because of the ability of the *Salicornia* to hold soil with its roots, the banks of sloughs in the *Salicornia* zone are deeply undercut. Accordingly the configuration of the habitat in the *Spartina* belt (fig. 40*f*) consists between sloughs of the continuous solid growth of vertical *Spartina* stems 2 to 4 inches apart and with mud at their bases exposed at low tide, giving way to a band six feet wide of *Salicornia* on the top of the slough banks (growing two feet high in the middle of the band), then *Spartina* again on the descending slope of the slough, below which a mud area is exposed at low tide.

For the *Salicornia* belt (fig. 40*g*), the growth between sloughs consists of a solid mass of radial *Salicornia* bushes 12 to 18 inches high and growing close together so that their branches interlock. This mat is permeated at the ground level by the runways of large *Microtus,* and other spaces between bushes at the ground level, apparently formed by a raising of the lateral branches of *Salicornia* with the tides. At the raised part of the slough bank grow *Grindelia* bushes of spherical shape, 3 to 4 feet high, either in chains or as individual plants, forming a belt 1 to 10 yards wide bordering each slough. At the very brink of the slough the *Salicornia* turf projects 1 to 3 feet out over the steep bank, and the bottom of the slough is choked with *Spartina.*

Old, high marshes lack the *Spartina* zone, and at such places as the mouth of Alviso Slough, the *Salicornia* growth ends at an abrupt six-foot bank fronting on the mud flats. In younger, low marshes, such as San Pablo Marsh, the *Spartina* zone is predominant, 400 yards wide, and *Grindelia* is just beginning to appear on some of the highest slough banks. At Pinole, the level of the marsh is raised so high that the *Spartina, Salicornia* and *Grindelia* zones are condensed at the steep bank facing the bay, interior to which grasses and weeds such as *Rumex* and *Chenopodium* are already gaining a foothold and suggesting the fate of all salt marshes which continue to rise without extending their boundaries farther out into the bay.

It can be seen, therefore, that the limiting factors affecting the salt-marsh vegetation are deep water (lacking wave action) and dry land, and the growth is thus limited to approximately the upper two-thirds of the intertidal zone. Its distribution includes all the bay marshes of San Francisco and San Pablo bays, the upper half of Southampton Bay marsh, the lower half of the marsh at Tomales Bay on the coast, and a small patch at Drakes Bay on the Point Reyes peninsula.

Song Sparrow pairs in *Spartina* portions of salt marshes are spaced at 76 yards along the edges of the sloughs, in single file along each bank. In the *Salicornia-Grindelia* portion pairs are 30 to 100 yards apart. They are closer together where the *Grindelia*

band is widest. In the *Spartina* type of marsh, Song Sparrows sing from the tallest *Spartina* stalks and feed on the mud either at the gradually sloping bank of the slough or among the *Spartina* stems, or in the *Salicornia* of the raised banks. Only at high tide do they forage more than 30 yards from the sloughs. Their food is mostly snails, small nereid polychaete worms, insects and other small invertebrates, but in fall they eat quantities of green *Spartina* flowers which they reach by alighting in the stems.

In *Salicornia-Grindelia* marsh the birds utilize the tops of the *Grindelia* bushes for song perches and find concealment under the vegetation or under the overhanging slough banks. When alarmed, they cannot reach the undercut slough bank without flying and so revealing themselves; however, they make the best of it by looping into the slough as fast and low as possible, then streaking off in headlong flight a few inches above the water to a point under the bank often 50 yards away, all the while admirably following the tortuous course of the slough.

They forage under the overhanging banks at low tide. The forage behavior here consists of very rapid progression by a smooth series of hops with head and tail held low, apparently when they are pursuing flying insects. At other times they progress more slowly and in jerky manner with head up, the tail constantly jerked upward at a high angle, and pick up objects from the mud. When foraging in the vegetation, they fly to the top of a *Grindelia* bush, hop down through it to the ground, then creep along through the mammal trails far out into the pure *Salicornia* mat. They progress exceedingly rapidly under the *Salicornia,* for it is possible, if the observer runs fast enough and in the right direction, to flush a sparrow 25 or 30 yards away from his *Grindelia* bush only a few seconds after it reached the ground level. The food consists of small nereids, snails and a variety of insects and other invertebrates. On one occasion I saw a bird feeding on *Grindelia* seeds in the manner of a finch, from the top of the flowering stalk; collected it and found carefully peeled *Grindelia* seeds in its stomach and bill. At Pinole, I collected a bird which had made several fly-catching flights from a fixed perch, a three-foot stake. It had an adult mosquito in its bill and another in its stomach.

Song Sparrows are limited by the height of the salt vegetation. At Alviso, they are absent from *Spartina* 18 inches or less in height and from a great area where the *Spartina* has from unknown causes been flattened. At another point where the *Spartina* is only 2 to 3 feet high, pairs are 100 yards apart. Song Sparrows are also absent from a broad belt of *Salicornia* growth less than a foot tall which is normally found on the highest portion of a marsh (inland), and which is occupied only by Savannah Sparrows. Territories invariably are restricted to a single row along one or both banks of the sloughs (depending on the width of the slough and the width of the *Grindelia* band bordering it). Song Sparrows are absent from all areas where the tidal flow is cut off by man-made dykes. Such places have vegetation similar to a natural marsh, but the water there is stagnant and foul.

In the inner parts of the marshes where the *Salicornia* growth becomes progressively lower, the ranges of the Song and Savannah sparrows overlap. Savannah Sparrows extend inland to and including moist grassland surrounding the marsh. Owing to the exceedingly long flights made by this species to forage ground, we find it at low tide feeding on slough banks well within the Song Sparrow's domain.

DISTRIBUTION OF HABITATS AND OF SONG SPARROW POPULATIONS

Figure 41 shows the distribution of the kinds of environment occupied by Song Sparrows in the Bay region. Of primary importance is the fact that under natural conditions each kind of habitat, wherever it exists, is at some point connected to another kind by a zone of intermediate vegetation forming a gradual transition between them

(except at San Francisquito Creek and Southampton Bay). Such zones of transition invariably involve a long row of Song Sparrow pairs at the opposite ends of which free interbreeding takes place with the birds of the respective divergent habitats. Figure 41 is of course equivalent to a map of the occurrence of Song Sparrows. Using the areas of

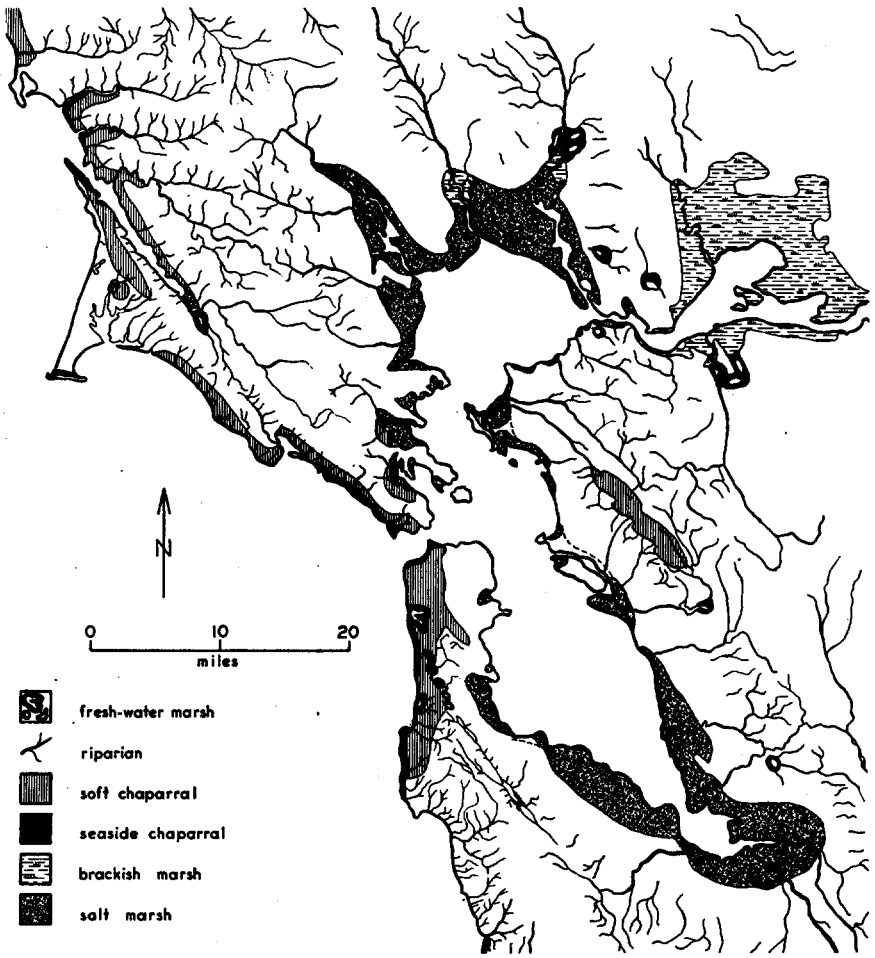

Fig. 41. Distribution of Song Sparrow habitats in the San Francisco Bay region. No attempt has been made to indicate the limitation of soft chaparral to each north-facing slope within the areas allotted to that habitat. The width of the seaside chaparral belt along the coast has been greatly exaggerated, to make it show on the map. The distribution of the bay marshes and the riparian avenues connecting them to the uplands follow U. S. G. S. maps made around 1900, and are intended to show the probable distribution of these habitats under natural conditions prior to the drastic reduction in their areas brought about by civilization.

absence or sparse occurrence of Song Sparrows as boundaries, we can divide the birds into populations as shown in figure 42. This reveals that the dense bay marsh populations are separated from each other by open water or by ranges of hills jutting into the bay and are separated from upland populations by the width of the arid bayside plain. In the uplands we find sparse populations which become denser toward the coast, consisting mostly of single rows of pairs along streams.

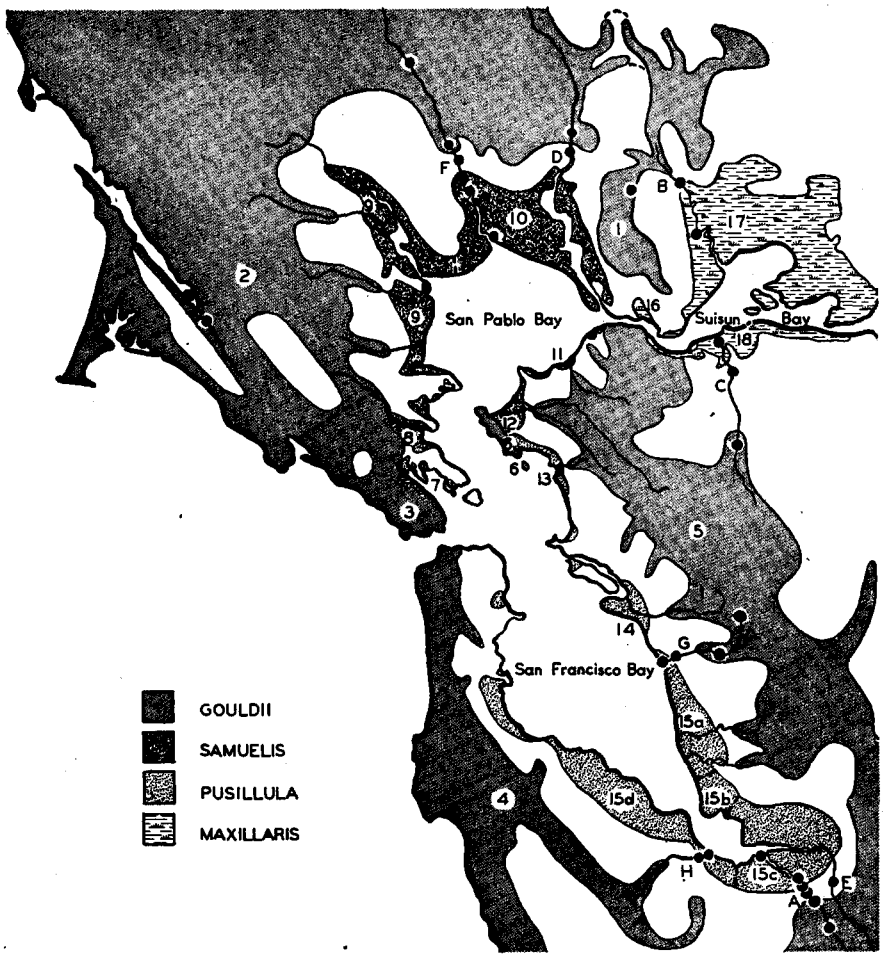

Fig. 42. Distribution of Song Sparrow populations in the San Francisco Bay region (same scale as fig. 41). Dots indicate points along the following connecting avenues from which samples will be described: (A) Guadalupe River, (B) Green Valley Creek, (C) Walnut Creek, (D) Napa River, (E) Coyote Creek, (F) Sonoma Creek, (G) San Lorenzo Creek, and (H) San Francisquito Creek. The two dots at the extreme left of the map, at Tomales Bay, refer to two samples which will be mentioned in the text, one from a salt marsh, the other from a fresh-water marsh.

Populations are numbered as follows: (1) Solano, (2) Marin, (3) Elk Valley, (4) Peninsula, (5) East Bay, (6) Richmond Hills, (7) Richardson Bay, (8) Corte Madera, (9) Petaluma, (10) Napa, (11) Pinole, (12) San Pablo, (13) Stege, (14) San Leandro and (15) San Francisco Bay. The last is divided into four sections as follows: (a) San Lorenzo Creek south to Patterson Creek, (b) Dumbarton Point, (c) Alviso and (d) Palo Alto north to San Bruno. Number (16) is Southampton Bay, (17) North Suisun and (18) South Suisun.

Connecting avenues are shown as they probably existed under natural conditions. At present the only ones which still provide continuity, though narrower than formerly, are the following streams, in order around the bay clockwise from the Golden Gate (numbers not entered on map): Corte Madera Creek (2d), Miller Creek (3rd), Novato Creek (4th), Sonoma Creek (7th), Napa River (8th), Green Valley Creek (9th), Walnut Creek (10th), San Pablo Creek (12th), Wildcat Creek (13th), San Leandro Creek (15th), Patterson Creek (18th) a recent connection not shown in figure 41, and Guadalupe River (20th).

Running between the upland and the bay marsh populations are the narrow connecting avenues, the rows of Song Sparrows along streams crossing the bayside plain. Remembering that Song Sparrow pairs occur in continuous linear sequence along banks of sloughs, streams and the seacoast, and that soft chaparral carries them over the summits of the ranges into proximity with headwaters of riparian habitat beyond, and that the sequence of territories laid end-to-end is unaffected by transition from one habitat to another (except at the mouth of San Francisquito Creek), it is at once evident that all populations are connected to each other by continuous series of breeding pairs except that at the Golden Gate, Carquinez Strait, and the dry hills surrounding Southampton Bay, there is a break in this continuity amounting to complete spatial separation.

VEGETATIONAL SUCCESSION AND THE FATE OF POPULATIONS

Fresh-water habitats.—It is possible to regard the seaside chaparral as a permanent habitat configuration which persists along the coast because it is outside the tolerance ranges of coniferous forest, which is limited here by soil and wind conditions. It provides a permanent source of Song Sparrows existing in the maximum concentration possible for the species, and it provides a reservoir for colonization of the other less stable habitats. The connecting avenues for such colonization always are present in the form of young riparian habitats, although any one stream is liable to pass into a stage where it is no longer inhabitable by Song Sparrows.

Soft chaparral is apparently a stage in the succession culminating in deciduous or coniferous forest, as it now grows in several areas where such forests once occurred and were logged off. Their regrowth will eliminate Song Sparrows from these areas. Concerning the fresh-water marshes, such as the marsh at the mouth of Olema Creek, we can see from the altitudinal progression of vegetation inland from the water's edge (*Typha-Scirpus, Salix-Juncus, Salix,* a fringe of soft chaparral, then madrone-laurel woodland) that with the filling of the body of water by deposition of soil, the *Typha-Scirpus* portion will eventually become *Salix,* which in turn will give way to moist chaparral and finally woodland. Therefore, the Song Sparrow populations in fresh-water marshes are destined to become limited to whatever narrow streams may persist there after the marshes or lakes fill up. New fresh-water marshes are populated from the birds along the streams which flow into them.

Concerning the fate of Song Sparrow populations along streams, it is obvious that the stream itself will cause the ultimate eradication of the birds because of continued deepening of the channel and consequent elimination of moisture-loving vegetation from its banks and its replacement by laurel, maple, and live oak, the culmination of which is observed at Carneros Creek, Napa County. However, there will always be riparian habitat available at the mouths of streams where sedimentation keeps filling up the channel and at inland localities where the vegetation is not sufficient to prevent erosional breakdown of the stream banks in flood times. Therefore, one can envisage the continuance of avenues of connection between (ultimately) the seaside chaparral populations and the bay marsh populations along such streams.

The requirement for forming an abrupt demarcation between riparian and contiguous salt marsh habitats is the presence of a steep alluvium at the mouth of a stream. Evidently such a situation once existed at the mouth of San Francisquito Creek, and until 1942 at the mouth of Mill Creek, which empties into the Richardson Bay salt marsh. The latter spot was at the time deemed not suitable for studies in ecologic isolation inasmuch as the bay marsh and upland birds there are practially indistinguishable and show little evidence of any kind of isolation, being continuous through soft chaparral. Considering the topography of the bay region as a whole, it seems unlikely that such an abrupt demarcation of the two habitats would ever come into being at the

mouths of most of the streams, in view of the gentleness of the slope of the bay-side plain. (There is some evidence that the alluvium at the mouth of San Francisquito Creek was started by man's activities.) It is even less likely that such a boundary would endure long enough to play a decisive role in the differentiation of races.

Brackish habitats.—We are here interested in the relative permanence of brackish habitats because of their importance in providing a blending continuity (at the mouths of streams) between upland and bay marsh Song Sparrow populations in the area surrounding Suisun and northern San Pablo bays. This intermediate zone will be pushed farther toward the bay as sediment builds up, counteracted by the deepening of the rivers permitting tides to flow farther upstream, thus carrying the brackish vegetation with them. As long as these opposing processes maintain any sort of balance, we can expect the brackish zone to persist.

Salt-marsh habitats.—The absence of wave action at the edge of the gradually sloping bay-side plain permits the growth of the marsh vegetation. As deposition continues the vegetation of the intertidal zone disappears inland as the land there is raised above the high-tide mark, and advances bayward as soil is added to the mud flats. Thus, the marsh may advance into the bay until proximity to some main tidal channel provides for the sediment to be carried away as fast as it is deposited. It must then suffer oblivion as the shore steepens, and eventually be converted into grassland, soft chaparral or oak-laurel woodland. The sucessional types are usually all represented to varying extents on a single marsh, proceeding in orderly sequence from low- to high-tide levels.

We can postulate that San Pablo marsh is young, has recently emerged from bare mud flats and is now in the *Spartina* stage of development, the lowest plant form in the altitudinal sense. This marsh is of such low elevation generally that *Spartina* covers most of it. *Salicornia* is limited to higher ground, namely the raised banks of all the sloughs and the inland belt on the periphery of the marsh, and the total area it occupies is insignificant compared to that of *Spartina*. *Grindelia,* the next higher type, is only beginning to pioneer on this marsh and is found (in my study area) in only two isolated patches and a couple of lone bushes on the highest banks available. With further raising of the level of the marsh by deposition, providing the shore-line remained stationary, we would expect *Salicornia* to encroach upon *Spartina*, which would become limited to a fringe at the shore and in the bottoms of the deepest sloughs; *Grindelia* would take over the raised banks of the sloughs, which would now be too high for *Salicornia*. This is precisely the situation found at Corte Madera and Dumbarton Point. (The marsh at Stege, Contra Costa County, has changed from pure *Spartina* to the *Salicornia-Grindelia* stage since 1940. Deposition here has been speeded up by man and his dump-trucks.) With still further deposition, the area would no longer be covered by tides; grasses and weeds such as *Chenopodium* and *Rumex* would replace *Salicornia,* and *Baccharis pilularis* would replace *Grindelia* on the slough banks and Song Sparrows would no longer dwell there. This process has progressed half-way to completion at Pinole, where the whole series, *Spartina* to *Grindelia,* is condensed into a narrow belt at the bay shore, inland from which *Chenopodium* and other weeds hold sway, although with some admixture of *Salicornia*.

Concerning the fate of a population of Song Sparrows on a salt marsh, the point of interest is that throughout the history of sucessional stages of vegetation, the marsh will continually provide "edge environments" on the raised slough banks with their floral differentiation. Furthermore, we can at least postulate that processes are at work which, barring compensatory geological events, might eventually wipe out a given salt-marsh population entirely. However, as far as I can determine, there has been no such reduction of populations through natural events in the time since Song Sparrows were

first collected in the bay region. Whole marshes have, of course, been wiped out by the activities of man. Such reclamation generally consists of halting the flow of tides and rivers by the construction of levees on the banks of rivers and sloughs, with the result that the marsh is replaced by grassland, weeds or *Baccharis*.

LIMITING FACTORS APPLYING TO SONG SPARROW ENVIRONMENT OF THE BAY REGION AS A WHOLE

From the foregoing outline of the limitations imposed on Song Sparrows in each habitat, we can conclude that the species, in the bay area at least, is limited in its distribution by appropriate extremes of vegetation, water, light and accessibility of the ground for foraging.

The Song Sparrow requires vegetation for its existence, in particular, for nesting sites, hiding places, song perches, and for concealment during the major part of its foraging. Only in rare instances does a Song Sparrow wander more than ten yards from cover, as when foraging on beaches and flying across wide sloughs and rivers. It is further dependent on this vegetation for a large part of its food, which consists, except in salt marshes, mostly of seeds picked up on the ground.

Fresh water in the form of dew is provided in all the habitats in the early morning. But the Song Sparrow requires at least some permanent water or moisture in its own territory. In fresh-water habitats this can be standing or running water, or in the case of seaside and soft chaparral, merely condensation of fog or seepage. In salt or brackish habitats the water must be tidal, that is, it must ebb and flow. This water requirement coupled with the disposition of territories in single rows along narrow bands of vegetation is somewhat different from the condition described by Nice (1937:70-71) as her maps of territories show them three or four deep along the bank of the Olentangy River. (However, the maps for central Interpont in 1934 and 1935, pp. 72-73, show territories in a single rank along the river and along various widely separated dikes.) Nice mentions (1937:12) that "The birds must leave their territories several times a day to procure water for drinking and bathing purposes." She regards this situation as not typical for the species, however.

It seems likely that Song Sparrows are limited to moist situations not as a direct consequence of particular food or plant growth provided by the water. Rather, the species manifests an instinctive preference for the moisture plus a certain configuration of vegetation, which is a psychological adaptation insuring that the individual will find suitable cover and food in such areas. In other words, food appears not to be a direct limiting factor. There are many moist situations probably providing adequate food which are not occupied by Song Sparrows. There is, moreover, a marked difference in the food of salt marsh birds from the food of those in other habitats. The former eat mostly invertebrates, the latter mostly seeds, in the non-nesting season at least.

Although Song Sparrows "delight" in foraging in dark crevices under overhanging stream and slough banks, and hide in piles of twigs or dead *Scirpus* stems which are very dark inside, yet any continuous high leafy canopy, such as coniferous forest, deciduous woodland or even tall dense willow growth is a barrier past which they never trespass, regardless of the moisture conditions that may prevail there, or the attractive appearance of the understory vegetation, even when it is composed of the identical plant species inhabited outside of the forest canopy. This suggests that the light factor operates directly on the Song Sparrow through its psychological responses, rather than indirectly by imposing limits on particular plant species which the birds inhabit. It should be noted that the leafless stems of *Scirpus acutus* and *Scirpus californicus* cast very small shadows, consequently the interior of such stands is well lighted.

The densest vegetation which Song Sparrows can tolerate is the continuous mat of foliage and stems found in *Salicornia* marshes and seaside chaparral; presumably they are able to get about in it only because it is opened up by the flow of water and the runways of small mammals. (Grassland, also permeated by *Microtus* trails, is too dry for them, does not furnish cover the year around, and offers no suitable song perches.) The densest growth in which Song Sparrows can exist without such openings at the ground level is *Scirpus campestris*. In this species, the stems generally grow one or two inches apart, and this is the lower limit at which it is physically possible for the sparrows to make their way. *Spartina,* the other *Scirpus* and *Typha* all grow farther apart. There is a species of *Juncus* in pure stands around the edge of Southampton Bay which illustrates the next stage in closeness of stems which is prohibitive to Song Sparrows. It is really a miniature of *S. acutus*; it grows on wet ground and has a round stem which ascends vertically and unbranched for 18 inches. The stems, however, are only one-half inch or less apart.

Closeness of stems is an environmental limiting factor which is tied up with the availability of the ground for foraging. As noted under the account of the several habitats, bare ground is a feature of each, and is apparently a necessity for occupancy of soft chaparral. In the other habitats, the ground must be available at least under a large part of the vegetation, either in mammal runways or by reason of separation of stems at an appropriate distance.

In summary, I might list the attributes that are common to all the Song Sparrow habitats in this area: (1) plenty of water; (2) plenty of light, furnished by low though dense growth as in *Salicornia,* or if higher, by absence of leaves as in *Scirpus acutus,* or if still higher and very leafy, by scattering of the trees in widely spaced patches separated by low vegetation; (3) plenty of vegetation which can be continuous and 4 to 10 feet high if not too leafy (*Scirpus, Spartina, Typha*), or if leafy so as to cut out light, it must be separated into patches (soft chaparral) or narrow ranks (*Salix*), or be differentiated into low and high elements (*Salicornia-Grindelia* marsh and seaside chaparral), or be widely spaced (continuous stands of *Grindelia* at Tomales Bay salt marsh, and some continuous stands of *Salix* around lake margins); (4) exposed ground or leaf litter for foraging; and (5) piles of twigs or dense shrubs for concealed foraging and for hiding. Such features common to the several kinds of Song Sparrow environments are sought as a background for a discussion of whether or not some of the "ecologic races" in the bay region are adapted to environments unique for the species, and which other Song Sparrows cannot endure. In other words, does the occupancy of salt marshes, for instance, by the races *pusillula* and *samuelis* involve a successful pioneering into a new environment, such that we could say that these races represent incipient species in the process of diverging from the rest of *Passerella melodia*?

INFRASPECIFIC ADAPTATION

Over the rest of its range *Passerella melodia,* to my knowledge, inhabits all the types of environment described here for the bay region and others, such as willow thickets in mountain meadows of the Sierra Nevada and beach vegetation in Alaska, wherever they provide the necessities outlined in the preceding statement. Each race usually occupies the several different kinds of habitat wherever they occur within its area. For instance, *cooperi* of the California coast south of San Mateo County breeds in freshwater marshes, riparian growth, soft chaparral, brackish marsh and suitable portions of *Salicornia* marshes (personal observation). *Cleonensis* (Grinnell and Miller, 1944:547) and *morphna* to the north are likewise not restricted to any one kind of habitat, although seaside chaparral is the most extensive one in their ranges.

The virtual absence of Song Sparrows (of the race *cooperi*) from the great salt marshes of coastal southern California has long been thought to be due either to their lack of adaptation to that environment or to the adverse competition with the Savannah Sparrows, which abound there. However, I found that the vegetation, although consisting of species similar to those around San Francisco Bay, is too low for Song Sparrows and is just what one would expect, from study in the "bay region," to be ideal for Savannah Sparrows. *Salicornia* grows as single erect stems six inches tall and usually unbranched; so does *Frankenia, Jaumea* and *Distichlis. Spartina* there is only 18 inches tall at the most. I have found Song Sparrows in the few spots on those marshes where man-made changes have permitted the development of patches of *Salicornia* two to three feet high, and the birds appear to be successfully established in spite of being hemmed in by the densest imaginable population of Savannah Sparrows.

At Elkhorn Slough, Monterey County, although most of the marsh is not visited by *cooperi* either because of the shortness of the *Grindelia* or possibly because of unfavorable action of tides, yet there is one spot where I found Song Sparrows foraging under the *Salicornia* and singing from tall *Grindelia* bushes. When chased, they returned to a little fresh-water marsh 100 yards away, which was the territorial headquarters for a half-dozen pairs. At least at low tide, these birds recognized the marsh as a place to forage.

Much more instructive is the occurrence of individuals of *gouldii,* the race of the San Francisco Bay region upland fresh-water environments, in *Salicornia-Grindelia* marshes at Drake Bay and Tomales Bay on the coast of Marin County. These marshes are of course far removed spatially from identical environments around San Francisco and San Pablo bays, and because of humid conditions near the coast are surrounded by fresh-water habitats. As a result the populations in them are not isolated spatially and in fact are in broad breeding continuity with typical individuals of *gouldii.* At Tomales Bay this continuity is provided not only by riparian growth and soft chaparral all along the southwest border of the marsh and much of the northeastern border, but by a gradual transition through a brackish marsh to a fresh-water marsh at the head of the bay, at the mouth of Olema Creek. Birds collected on this marsh are identical morphologically (and are undoubtedly identical genetically also) with *gouldii* which surrounds them and interbreeds with them. In summer they nest and have territories staked out all over this salt marsh; they feed under the overhanging slough banks on the same food (snails, other invertebrates, and *Grindelia* seeds) and occur in the same density as do members of the race *pusillula* in the most favorable *Salicornia-Grindelia* areas around San Francisco Bay. Fall specimens show the characteristic plumage abrasion attending life in *Salicornia* beds; therefore, these individuals are successful full-time residents on the marsh.

It is not intended in this discussion to minimize the fact that bay marsh races are superior to *gouldii* in their adaptation to salt marsh existence. Rather, it is desired to suggest that this adaptive divergence is of small magnitude compared to differences in ecology between species of the genus *Passerella*; it is a difference in degree rather than quality, and does not suggest the kind of adaptation which permits two forms to occupy simultaneously the same general area. It has not been accompanied by any noticeable difference in song, mating behavior, and particularly foraging behavior among the bay region races. They are all primarily ground foragers; the few instances of other kinds of foraging under the accounts of each habitat are regarded as very unusual, but they show that in each habitat, some birds are likely to carry on some strange kind of foraging above the ground level.

There is no evident aversion on the part of Song Sparrows of upland habitat affini-

ties to life in salt marshes, providing they are not chased out by individuals already living there and providing they dwell close enough to the marsh to become familiar with the attractive conditions which prevail. There is as much difference in vegetational configuration within bay marsh and upland categories of habitats as between them. It is suggested, therefore, that the species *Passerella melodia* is adapted to the entire range of environmental limiting factors mentioned in the preceding section, which we might call the species niche. The kinds of habitats discussed for the various populations and races in the bay region are then subniches, potentially habitable by any individual of the species. Factors such as proximity and familiarity with the subniche will determine which individuals will occupy it.

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