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ECOLOGIC RACES OF SONG SPARROWS IN THE SAN FRANCISCO BAY REGION

PART II. GEOGRAPHIC VARIATION

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This is the second part of a study of variation in the Song Sparrow, *Passerella* (*Melospiza*) *melodia*, in the counties surrounding San Francisco, San Pablo and Suisun bays in west-central California. Within this small area four races are resident; they are more or less isolated spatially from one another, and the area of each presents a distinctive kind of environment either of fresh-water type, brackish marsh or salt marsh. These several "habitats" are equally characteristic of the niche utilized by individuals of the species as a whole, on the mainland at least. The present study is an outgrowth of Joseph Grinnell's interest in the problem and the resulting accumulation at the Museum of Vertebrate Zoology of a large collection of specimens from the bay region.

The previous section of this work (Marshall, 1948) was devoted to a discussion of the different kinds of habitats occupied by Song Sparrows and the distribution of these habitats such that a map was constructed showing the areal arrangement of actual populations of the birds in this area (*loc. cit.*: fig. 42). This map shows that each race is divided into several populations by geographic barriers, and it is to these populations that we now turn in presenting the ensuing information on morphologic variation. They represent the largest units within which no geographic variation can be found, and it is convenient therefore to combine all samples from any one population and present the color and size attributes of each in a form which will make it possible to detect gradients of change in these characters from one population to another and through linear series of populations. Data will also be presented, for coloration at least, from samples taken at various points along the avenues connecting bay marsh races with the upland race. These samples are located on the above-mentioned map by dots. Correlation of changes in gradients with differences in the ecologic situations and with spatial isolation are sought. Presuming that the color and size attributes of the birds are hereditary, we may then discuss possible explanations for the maintenance of the racial characters in the face of interbreeding between the races at their boundaries.

Study skins of resident races from the bay region totaling 2,015 comprise the series of specimens analyzed; these are limited to specimens in postjuvenal plumages, with reliable data on locality and habitat, from the following sources: California Academy of Sciences, Donald R. Dickey Collections, Museum of Vertebrate Zoology (including skins catalogued to November, 1947, 836 of which were collected by myself), Stanford University Natural History Museum, and the personal collection of Emerson A. Stoner. I am indebted to those in charge of these collections for the loan of specimens. I wish also to thank the following persons who collected large series of specimens (now in the Museum of Vertebrate Zoology) for my study: George A. Bartholomew, Jr., Seth B.

Benson, John Chattin, Wade Fox, Jr., Donald V. Hemphill, Malcolm Jollie, Mary R. Koford, William Longhurst, Charles G. Sibley, Ned W. Stone, and Albert Wolfson.

COLOR AND SIZE DIFFERENCES AMONG THE POPULATIONS

Dorsal color.—No color differences correlated with age (postjuvenal plumages only) and sex are found in bay region Song Sparrows, but the skins exhibit great differences in color due to artificial soiling, abrasion of feathers and fading. Specimens collected in *Salicornia* marshes have the greatest amount of feather abrasion because of constant rubbing against the *Salicornia* stems. Accordingly the backs of all the skins were wiped off with cotton soaked in carbon tetrachloride to remove dirt and smudge, and in all comparisons specimens were divided into the following groups: (1) those in fresh fall plumage (August to November, uplands; August to October, salt marshes) collected after 1929; (2) worn plumage since 1929; (3) fresh fall plumage, collected from 1880 to 1929; (4) worn plumage, collected from 1880 to 1929. Within the above groupings, samples from various populations were compared with each other in mass effect, then each specimen was assigned to one of eight arbitrary color categories for purposes of presenting the data in histograms. The color concerned is that which suffuses the entire dorsal surface exclusive of the black shaft spots. These two methods balanced each other in that the former emphasized the uniformity of mass effect of coloration prevailing in a given sample and the latter revealed the individual phenotypic variations.

Standards for the eight equivalent categories of dorsal coloration are named on a geographic basis as follows: *blackish-olive,* the color of 70 per cent of the Napa population, or what remains after removing the lightest and brownest specimens; *blackish-brown,* the color of 70 per cent of the North Suisun sample; *reddish-brown,* the reddest and lightest 70 per cent, lacking light gray edges, of the Marin population; *yellowish-gray,* 70 per cent of the San Francisco Bay population remaining after removing all dark specimens with obvious brown coloration; *yellowish-brown,* the predominating coloration found in the San Leandro population; *reddish-brown* with *conspicuous light gray edges on scapulars and interscapulars,* a common type in the Peninsula population; *dark olive-brown,* all birds which do not fall into any of the above categories which are as dark as any bird from the Napa population, found mostly in the northern part of the bay region; *light olive-brown,* often with gray edges, all birds not falling into one of the first six categories which are lighter than any birds from the Napa population, and which are found mostly in the southern part of the bay region. The results of color analysis for the four groups of age and wear are identical; accordingly the groups are combined by populations and the data presented in figures 48 and 49.

Specimens within any sample (usually ten specimens from a certain time and place) from the major populations are usually very uniform, varying within narrow limits of hue and somewhat wider limits of shade due to the greater visible effect of variation in black pigment. Accordingly it would be possible to represent this variability by a normal curve if the samples were divided into more categories. Within samples from zones of intermediate vegetation along the avenues connecting visibly distinct populations (Guadalupe River, 0.8 mi. SE Alviso; Green Valley Creek, mouth; Napa River, 3.5 mi. S Napa) and in the small Richardson Bay population, specimens fall into two approximately equal, radically different types of coloration as seen in mass effect, and they could be represented by bimodal curves of variability if more color categories were used. These two important considerations should be remembered in examining figures 48 and 49, upon which it was impossible to represent such fine points of variability inasmuch as the collection as a whole contains no two specimens exactly the same in the relative extent

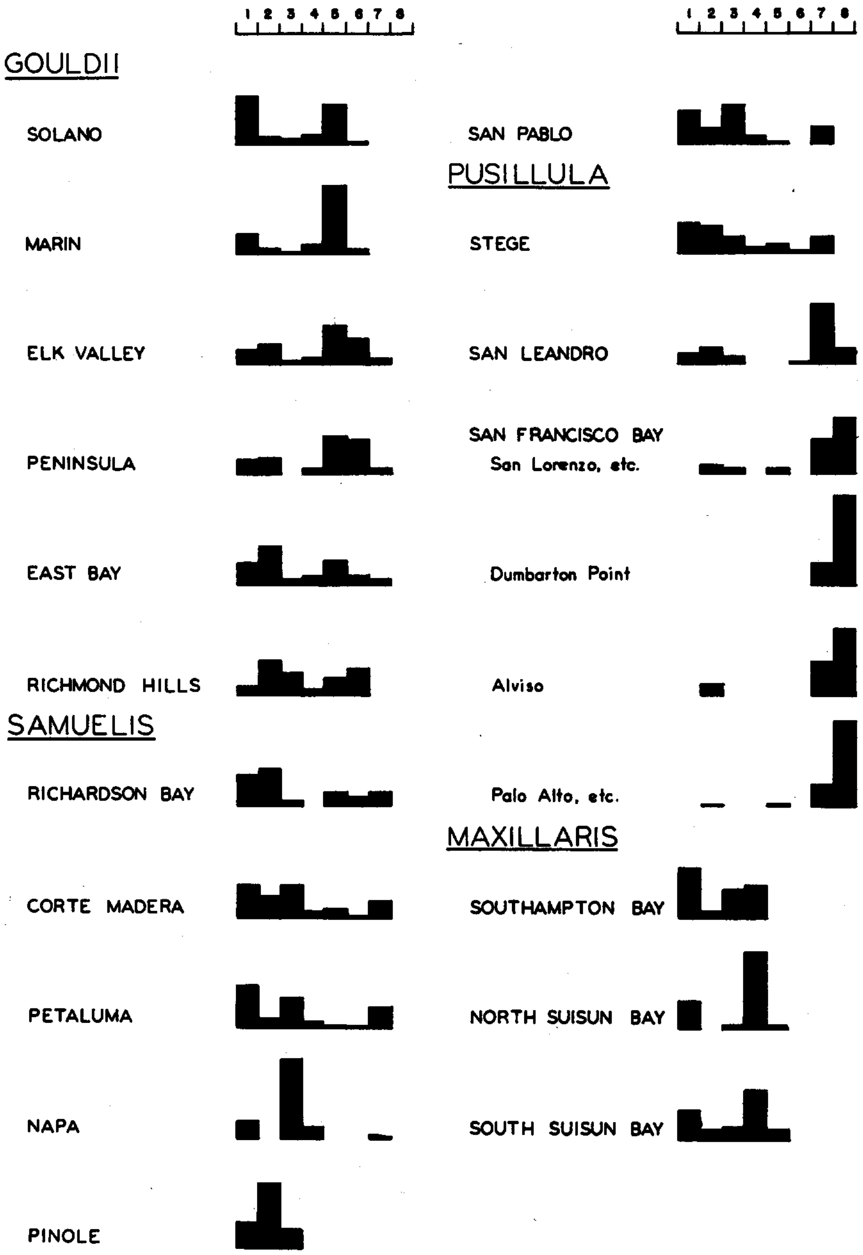

Fig. 48. Geographic variation in dorsal coloration by per cent for the population. Each segment of a histogram represents the same color as those in the same vertical column above and below it. Color categories are numbered as follows: (1) dark olive-brown, (2) light olive-brown, (3) blackish-olive, (4) blackish-brown, (5) reddish-brown, (6) reddish-brown with light gray edges, (7) yellowish-brown, (8) yellowish-gray. The distance from the bottom of one histogram to the bottom of the one just above it is 100 per cent. For number of specimens and habitat represented by each histogram see table 1.

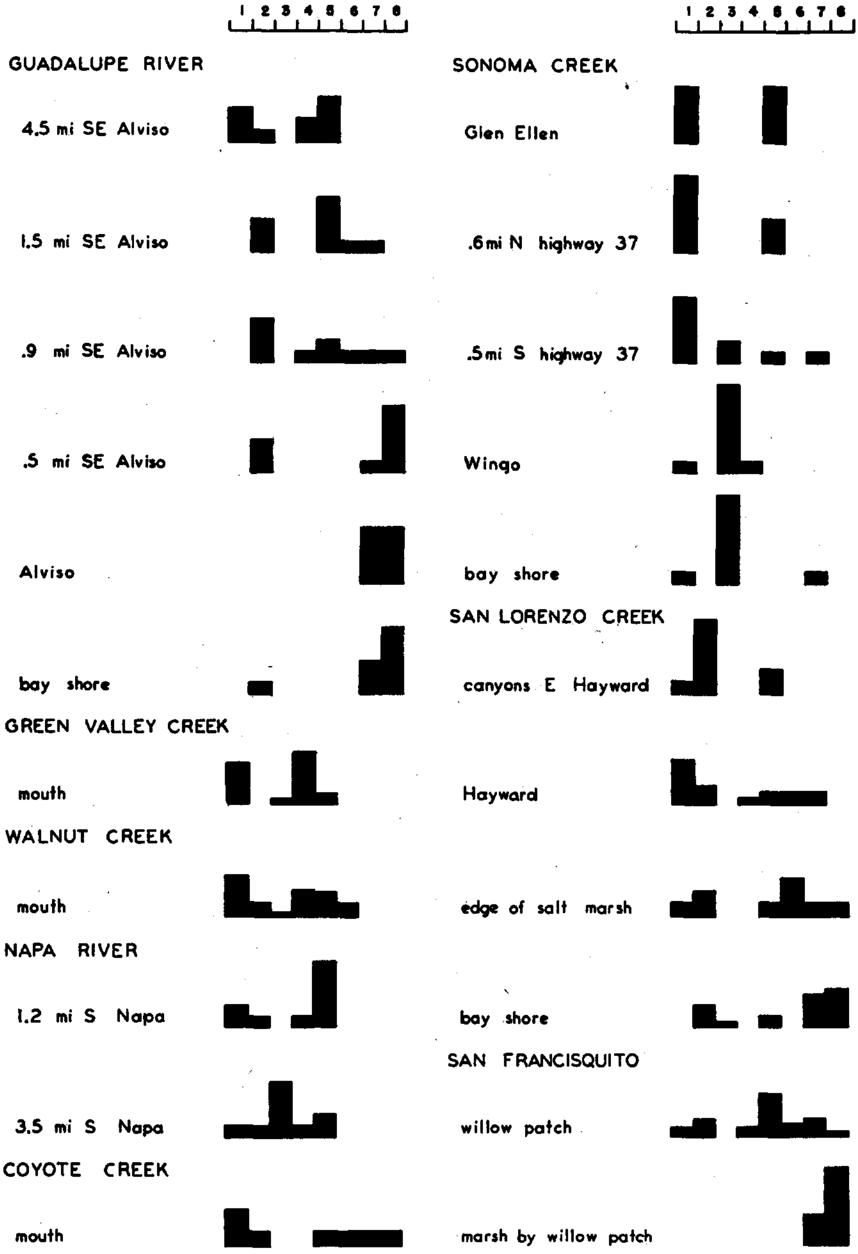

Fig. 49. Geographic variation in dorsal coloration by per cent for samples along the connecting avenues. Orientation and color designations are the same as in figure 48. For number of specimens, exact locality and habitat represented by each histogram, see table 2. Samples along these streams are in order from uplands to bay shore, and have been located by dots on the map of populations (Marshall, 1948: fig. 42).

of the black, yellow and red pigments. The figures do indicate, however, the proportion of specimens from a population which are easily discerned as unique and the proportion of those which are very difficult or impossible to distinguish from the same color category in an adjacent population.

There are four large populations where a color type is present in its extreme development in about 70 per cent of the specimens: reddish-brown (without gray edges) in the Marin population, blackish-olive in the Napa population, yellowish-gray in the San Francisco Bay population and blackish-brown in the North Suisun population. Accordingly we shall let these four populations represent the areas of maximum development of four color races *gouldii, samuelis, pusillula* and *maxillaris,* respectively, and shall extend the boundaries of each race to the half-way point on the gradient of color change connecting any two of these "typical" populations. Thus, the boundary of *gouldii* coincides with the habitat boundary between bay marsh and fresh-water habitats, and the boundaries of the three bay marsh color races with the geographic limits of their respective bays (see Marshall, 1948: fig. 42). The four racial designations are used for convenience in the following discussion; however, they are identifiable with and in area coincide with the subspecies denoted by trinomials in ornithological literature (Grinnell and Miller, 1944:547-551) except that the subspecies *santaecrucis* described from the Peninsula population is here combined with *gouldii* because less than 40 per cent of the birds from its range can be distinguished from typical *gouldii,* and its characteristic of reddish-brown back with light gray edges is an intermediate coloration between *gouldii* to the north and *cooperi* to the south.

Within the range of *gouldii,* there is a smooth gradient of decrease in frequency of the reddish-brown type (number 5, fig. 48), proceeding from the Marin population counterclockwise around the bay region. Reddish-brown is less frequent in the Elk Valley population (which is broadly continuous with Marin) by virtue of interbreeding of *gouldii* with *samuelis* around the edges of Richardson Bay and Corte Madera salt marshes. Thence the gradient jumps the San Pablo Strait to the Richmond Hills and across the Golden Gate to the Peninsula population. From the latter it proceeds to the East Bay population, which possesses the fewest reddish-brown backs. Eastward from Marin, reddish-brown decreases in the Solano population, and here we find the only hiatus in the gradient, namely between Solano and East Bay. These populations are separated not only by considerable distance, the Carquinez Strait and the dry hills on the north side of the strait, but by the interposing of two bay marsh populations between them. Reddish-brown backs occur as rare extreme variants in the three bay marsh races.

Within the range of *samuelis,* blackish-olive backs (number 3, fig. 48) gradually decrease in frequency in both directions away from the typical Napa population, showing no abrupt changes if the populations are spatially isolated, but showing gradual change even if the populations are broadly connected, as Petaluma is with Napa. A few extreme variants, somewhat difficult to recognize as different from the Napa blackish-olive type, occur in the areas of the other three races.

Within *pusillula,* a smooth gradient of decrease in frequency of yellowish-gray (number 8, fig. 48) begins in the part of the marsh from San Bruno to Palo Alto on the west side of San Francisco Bay. To the south, this gradient declines in the vicinity of the two connecting avenues near Alviso, then rises at Dumbarton Point, only to fall again to the northward (on the east side of San Francisco Bay) as more avenues of connection with *gouldii* again enter this vast and entirely continuous marsh population. Not a single example of yellowish-gray is found outside of the *pusillula* populations, but the yellowish-brown type, which represents a mixture of *pusillula, gouldii* and *samuelis* genetic attributes, carries the influence of *pusillula* on into the San Pablo, Richardson Bay and Corte Madera populations of *samuelis* despite some large spatial gaps between them.

The blackish-brown type (number 4, fig. 48) decreases in frequency in all directions from North Suisun Bay (*maxillaris*) and manifests itself in the adjoining range of *gouldii* much more than do the two salt marsh races. There are no blackish-brown examples in the San Francisco Bay population, which is farthest removed spatially from North Suisun. There are two irregularities to be noted in the otherwise smooth gradients for this color type. The first is a hiatus from the north to the south side of Suisun Bay (although they are separated at one point by only 900 yards), with a drop from 69½ per cent to 44½ per cent of blackish-brown backs. (The South Suisun Bay population has a much broader connection with *gouldii* than does North Suisun.) The second is the Southampton Bay population, which falls out of line of the gradient we would expect connecting Napa and North Suisun. Its samples are lighter than either of the latter populations. It is the only completely isolated population in the bay area and is small, containing an estimated 176 pairs of breeding Song Sparrows, based on a count made upon half the marsh.

The four dorsal color categories, dark and light olive-brown, reddish-brown with gray edges and yellowish-brown (numbers 1, 2, 6, 7, fig. 48) represent various intermediate conditions of the four extreme types; they further smooth out the gradients between typical populations of the four color races. The bay marsh and adjacent upland samples approach each other and are practically indistinguishable at the limits of the ranges of *samuelis* and *pusillula* where there is the greatest continuity in habitat from bay marsh to uplands and where the bay marsh populations are also the smallest. That is, the Richardson Bay and Corte Madera populations are practically indistinguishable from Elk Valley, and across the bay, Pinole, San Pablo and Stege are almost indistinguishable from the East Bay and Richmond Hills populations. Also, the South Suisun population is very close to East Bay in dorsal coloration. Accordingly, it is impossible to identify changes in gradient along connecting avenues at these points, where there is greatest ecologic and spatial continuity between bay marsh and adjacent upland populations.

Elsewhere, there is greater spatial separation of the two stocks, which are much more different from each other in color, and we find along the connecting avenues of the Guadalupe River, Sonoma Creek, the Napa River and Green Valley Creek miniature gradients exhibited along the single or double rows of Song Sparrow pairs (fig. 49). These gradients remain fairly uniform as long as the habitat is constant; at the zone of intermediate vegetation at the mouths of these creeks, a half-and-half mixture of bay marsh and upland color types is found, which constitutes an abrupt steepening of the color gradient in the ecologically intermediate zone. This transformation takes place within at most 3 miles on the Napa River, 2 miles on Sonoma Creek and one mile on the Guadalupe River and Green Valley Creek. The only connecting avenue which shows an actual hiatus is the gradient in San Francisquito Creek, where there is an abrupt change in vegetation from tall willows to *Salicornia-Grindelia* marsh without an intermediate zone.

No color difference is noted between the samples at Point Reyes Station (fresh-water marsh) and Tomales Bay (salt marsh) where the salt marsh population is almost entirely continuous with birds living in the soft chaparral, brackish marsh and fresh-water marsh around it.

Ventral coloration.—The character under consideration here is the color of the unspotted portion of the feathers of the ventral surface, which are either all pure white or all lemon yellow. Specimens were classified into pure white, light yellow, medium, and intense yellow categories but are represented in tables 1 and 2 only as yellow present or yellow absent. There is no sex or age (postjuvenal plumages) variation in this character. The greatest proportion of yellow bellies occurs in two segments of the San Francisco Bay population at Palo Alto and Dumbarton Point (91 and 95 per cent, respectively). Northward into San Pablo Bay this gradient, involving only salt marsh populations, decreases evenly the farther the samples are from these centers, becoming lowest at Napa, Pinole and San Pablo. In the uplands and Suisun Bay, ventral yellow turns up as an occasional variant and can be expected in any sample; generally it is of the palest yellow category. However, there are two bright yellow specimens from the uplands, one at Glen Ellen on Sonoma Creek, another at Lake Herman, Solano County.

Table 1
Ventral Coloration in Selected Populations

Race and habitat	Population	Number of specimens	Per cent yellow
Passerella m. gouldii	Solano	61	3½
(fresh-water)	Marin	273	2½
	Elk Valley	40	5
	Peninsula	135	½
	East Bay	253	3
	Richmond Hills	26	0
Passerella m. samuelis	Richardson Bay	24	25
(salt marsh)	Corte Madera	46	13
	Petaluma	124	21
	Napa	80	10
	Pinole	17	0
	San Pablo	73	2½
Passerella m. pusillula	Stege	51	25
(salt marsh)	San Leandro	74	67½
	San Francisco Bay:		
	San Lorenzo Creek to Patterson Creek	49	71½
	Dumbarton Point	21	95
	Alviso	42	81
	Palo Alto to San Bruno	110	91
Passerella m. maxillaris	Southampton Bay	21	0
(brackish marsh)	North Suisun Bay	181	3
	South Suisun Bay	45	2

The proportion of yellow birds drops abruptly at the intermediate zone between salt marsh and riparian habitat as one progresses up streams flowing into San Francisco Bay. The samples from Guadalupe River happen not to include yellow birds; however, in field observation it is common to see bright yellow birds at least a mile upstream. I have seen them at this distance at San Leandro Creek and the Guadalupe River, and have collected them at Coyote Creek, Santa Clara County.

There is only one pale yellow example out of ten specimens collected on the salt marsh at Tomales Bay. This is no more than is expected in any sample from the Marin population which surrounds Tomales Bay.

Wing.—Geographic variation in wing length of adult males, measured from the bend of the wrist to the tip of the longest primary (not straightened) shows (fig. 50) smooth gradients emanating with a decrement from the North Suisun Bay population and generally preserving an independence of upland from salt marsh populations. In the uplands

Table 2

Ventral Coloration in Populations Along Connecting Avenues

Stream and locality thereon	Habitat	Number of specimens	Per cent yellow
Guadalupe River			
4.5 mi SE Alviso	riparian	10	0
1.5 mi SE Alviso	riparian	10	0
.9 mi SE Alviso	mixed	10	10
.5 mi SE Alviso	salt marsh	10	50
Alviso	salt marsh	12	91½
Bay shore	salt marsh	10	90
Green Valley Creek			
Mouth	riparian	21	0
Walnut Creek			
Mouth	riparian	68	1½
Napa River			
1.2 mi S Napa	riparian	10	0
3.5 mi S Napa	brackish marsh	10	0
Coyote Creek			
Mouth	riparian	15	26½
Sonoma Creek			
Glen Ellen	riparian	10	10
.6 mi N Highway 37	riparian	10	0
.5 mi S Highway 37	brackish marsh	10	20
Wingo	salt marsh	10	10
Bay shore	salt marsh	10	40
San Lorenzo Creek			
Canyons E Hayward	riparian	9	0
Hayward	riparian	17	6
Edge salt marsh	edge of salt marsh	9	11
Bay shore	salt marsh	20	75
San Francisquito Creek			
Willow patch	riparian	26	11½
Marsh by willow patch	salt marsh	28	96½

it is maintained at a high level; in the salt marsh populations of San Francisco and San Pablo bays it remains low except that toward either side of San Pablo Strait it rises and approaches the dimensions of adjacent upland populations.

The only specimens in which age has been determined by skull examination are those collected in fresh fall plumage by Grinnell and by myself. Of these, the presence of a two-layered cranium with little pillars of bone connecting the layers is diagnostic of an adult until the middle of October, when the young begin to have completely two-layered skulls. All these specimens are plainly marked "ad" or "im" on the labels. I have not accepted similar marks on the labels of other collectors as meaning the same thing, except for birds collected by H. S. Swarth and by A. B. Howell. An intensive study of the molt of the above fall specimens revealed that adult wings are distinguishable from all other wings by the presence of a complete fall molt resulting in a new set of primaries which are broad, unabraded and heavily pigmented with black. All other birds, which are young of the year, retain the entire set of juvenal primaries, which are lightly pigmented and much frayed, or replace 4 or 5 outer ones or 2 or 3 inner ones. Only 2 or 3 specimens showed complete replacement. These new postjuvenal feathers look the same as adult feathers of the annual molt, are longer on the average than the juvenal primaries and shorter than adult primaries. Sexual dimorphism in wing length is pronounced, so that

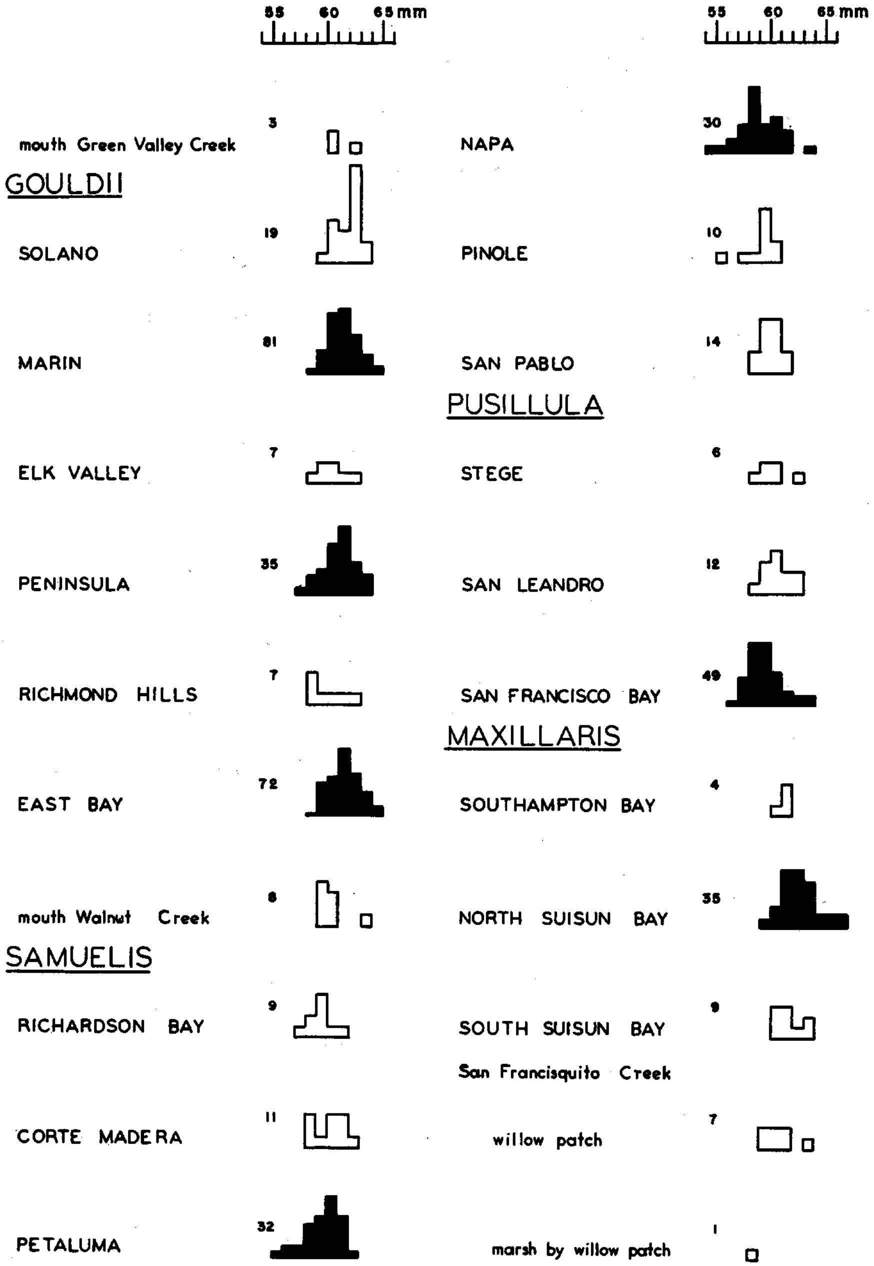

Fig. 50. Geographic variation in wing length by per cent. Populations are named in capitals, connecting avenues in lower-case letters. The distance between the bottom of one histogram and the bottom of the one just above or below it represents 50 per cent. Solid histograms are in per cent. Outlined ones, consisting of series of less than 20 specimens, represent actual specimens, each small square representing one bird. The figures at the side of each histogram refer to the number of specimens.

there are for each population six curves for wing length; those of the juvenal males and adult females coincide.

Table 3 gives the statistical constants for measurements of the four typical populations of the color races. At least the extremes of the gradients for measurements are thus seen to be significantly different from each other. For the few connecting avenues from which enough specimens are available, gradients for change in measurements are more gradual than those for color and involve more than the zone of intermediate habitat.

Table 3

Measurements of Typical Color-race Populations

Measurement and population	Number of specimens	Mean and standard error	Standard deviation
Wing length			
Marin (*gouldii*)	81	61.15 ± .14 mm.	1.30
Napa (*samuelis*)	30	58.77 ± .36	1.98
San Francisco Bay (*pusillula*)	49	59.16 ± .22	1.51
North Suisun (*maxillaris*)	35	62.47 ± .27	1.62
Tarsal length			
Marin	168	21.26 ± .04 mm.	.56
Napa	59	20.30 ± .09	.69
San Francisco Bay	134	20.33 ± .05	.60
North Suisun	116	21.56 ± .05	.58
Bill length			
Marin	265	8.57 ± .02 mm.	.39
Napa	102	9.03 ± .03	.37
San Francisco Bay	206	8.27 ± .03	.36
North Suisun	177	9.35 ± .03	.38
Bill depth			
Marin	230	6.60 ± .02 mm.	.25
Napa	81	6.82 ± .03	,26
San Francisco Bay	191	6.28 ± .02	.25
North Suisun	170	7.81 ± .02	.30
Weight			
Marin	39	19.96 ± .14 gr.	.89
Napa	17	18.79 ± .28	1.19
San Francisco Bay	37	18.60 ± .13	.80
North Suisun	27	20.76 ± .17	.91

Tarsus.—Tarsi were measured from the proximal end of the tibiotarsus (exposed at the lateral surface of the heel) to the distal margin of the last unfurrowed scute or its equivalent on the dorsal surface of the foot. Sexual dimorphism, but not age variation, is exhibited equally by all the populations; accordingly all males are combined for the histograms shown in figure 51. Gradients of decrease in tarsal length emanate from the North Suisun population, but pursue an independent course and at a higher level in the uplands than in the bay salt marshes.

Bill length.—Bill length, measured from the anterior edge of the nostril, shows no discernible difference correlated with sex or age. Geographically, it varies (fig. 52) purely as a function of distance from the North Suisun population, no matter what the habitat. It is greatest at that locality and decreases in an even gradient in all directions to a minimum in the San Francisco Bay and Peninsula populations.

Bill depth.—This measurement is from the highest part of the culmen to a point on the ventral border of the ramus in the same transverse plane. I have cut down inaccuracies (which amount to 0.1 mm.) by measuring as many bills as possible at a single sitting and by remeasuring a dozen or so bills before starting on a new batch. It is the

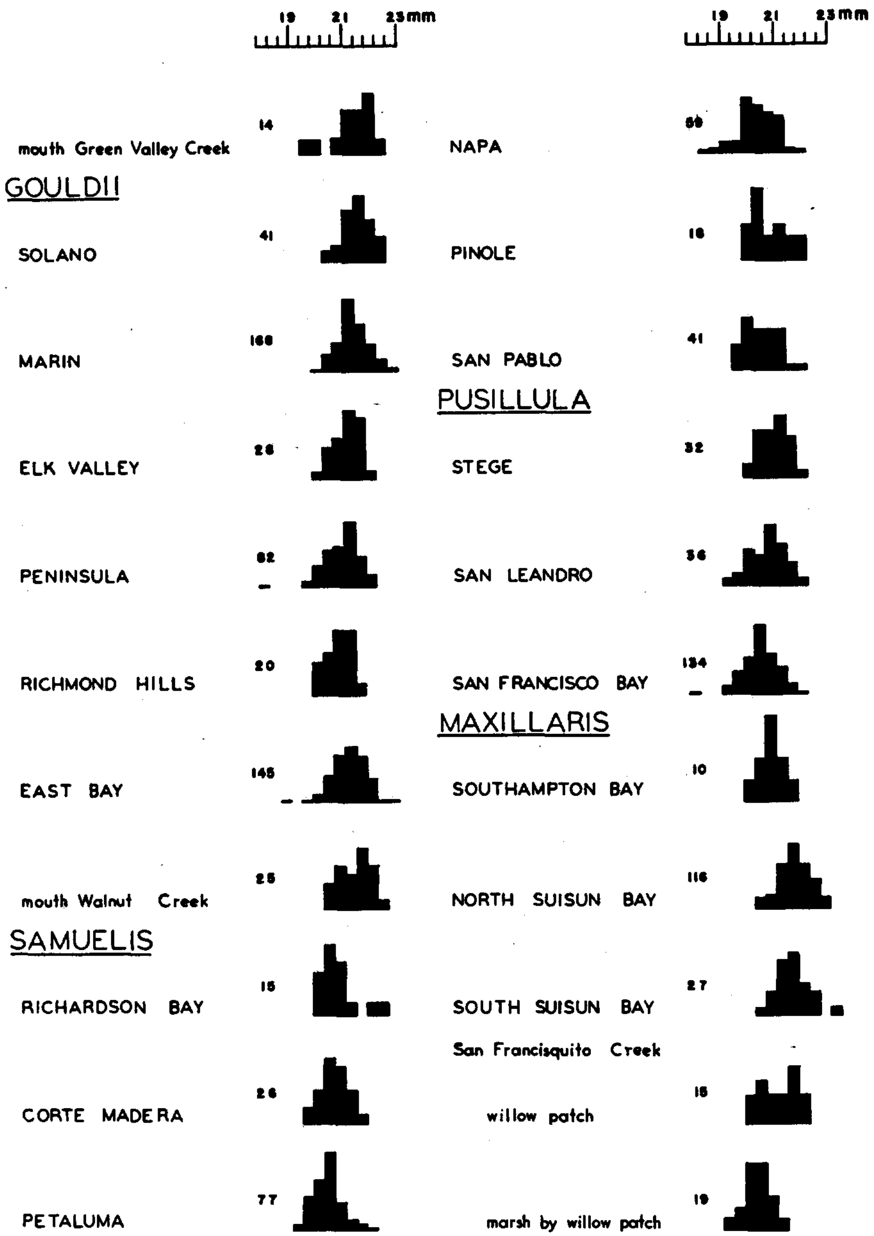

Fig. 51. Geographic variation in length of tarsus by per cent. The distance between the bottom of one histogram and the bottom of the one just above or below it represents 50 per cent. The figures at the side of each histogram refer to the number of specimens.

most revealing geographically variable measurement because of its small individual variation, absence of sexual and age variation, and the tremendous differences among populations. The North Suisun population (fig. 53), with the deepest bill, is 28 per cent greater in this dimension than the San Francisco Bay population, with the slenderest bill. As with the gradient for blackish-brown coloration, so with bill depth, there is a reduction

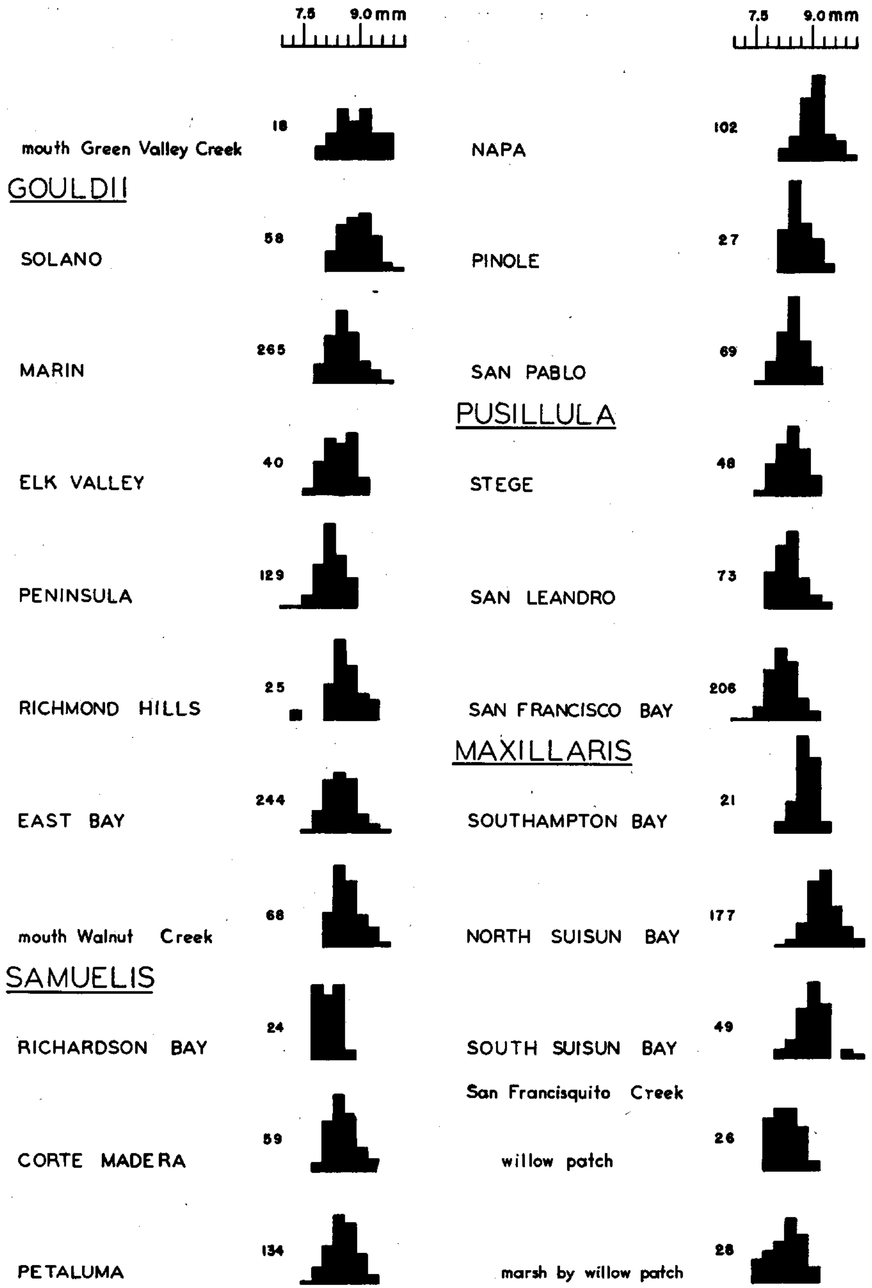

Fig. 52. Geographic variation in length of bill by per cent. Same vertical intervals as in figure 51.

from the maximum at North Suisun to the surrounding South Suisun, Southampton and Solano populations. From these localities the bills become smaller the farther the sample is from North Suisun Bay, but *gouldii* populations surrounding San Francisco Bay do

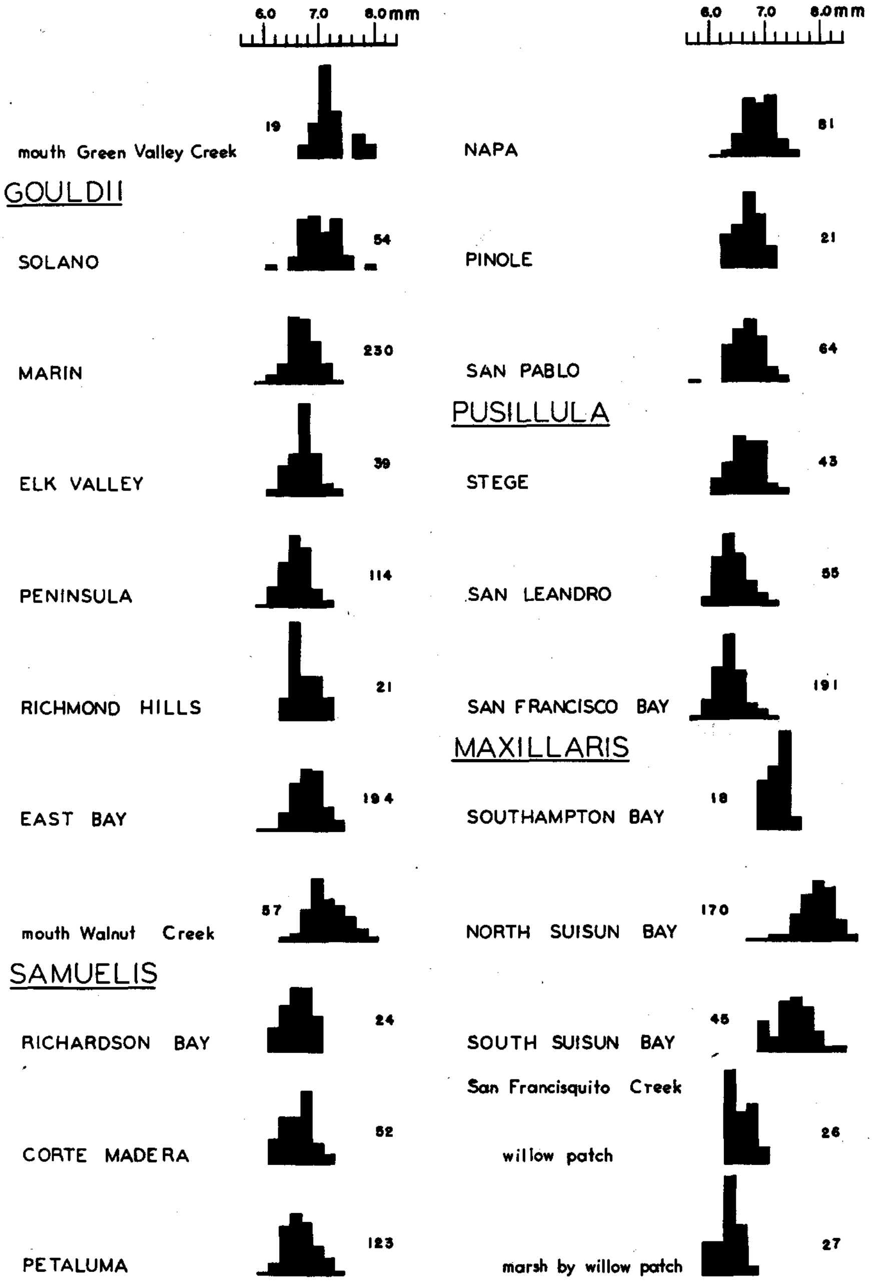

Fig. 53. Geographic variation in depth of bill by per cent. Same vertical intervals as in figure 51.

not keep pace with the decrease noticeable in the San Francisco Bay population, so that these adjacent samples show a significant difference from each other in bill depth.

Weight.—There is sexual dimorphism, but not age variation in weight, which was measured in grams. The males are heavier than the females. Geographic variation is revealed by a tabulation of weights of 289 recently collected fall males, including only those from the major populations. Table 3 presents the mean, standard error and standard deviation in weight for the four populations typical of the color races. Weight remains constant over the rest of the area occupied by the races; *maxillaris* is heaviest, *samuelis* and *pusillula* lightest and *gouldii* is intermediate. The following intergrading populations are exceptions: Southampton and South Suisun are slightly lighter than North Suisun, and Richardson Bay and Corte Madera are heavier than the rest of the *samuelis* populations. Body weight is correlated by populations rather closely with wing length and particularly the tarsus. The length of the tarsus, for which more examples are available than for weight, is therefore a good indication of the generally body size of birds of a population, but weight and tarsus are not correlated individually as was shown on scatter diagrams which were prepared. The greater constancy of weight than tarsus over populations having the same habitat, reveals the close correlation between this character and the environment. Salt marsh Song Sparrows are smallest in body size, fresh-water birds intermediate, and brackish marsh birds are largest.

DISCUSSION

POSSIBLE GENETIC CONTROL OF CHARACTERS

The coincidence of character and environmental gradients, particularly ventral yellow with salinity, does not necessarily indicate direct environmental determination of the character. I shall assume that these characters are largely determined genetically (Huxley, 1942:185), although experiments are needed to establish this for the Song Sparrow.

The several different dorsal colorations of Song Sparrows in the bay region are the result of different proportions of black, reddish-brown and yellow pigments. The important fact is that no specimen lacks any of these pigments in its feathers. Accordingly there is no qualitative difference between the back colors of different populations, no presence or absence of factors concerned. Taken as a whole, the specimens show every gradation between various conditions of predominance or sparseness of each color or each combination of colors. Individual differences are thus quantitative. Possibly their genetic determination involves many additive factors, cumulative genes as well as alternate alleles. Within a given population with a certain color predominating, the darker birds also are browner and yellower than the rest. Therefore, there may be genetic factors for intensity of general pigmentation as well as others which determine that in a given population one or the other pigments will be minimum or maximum in quantity. There is no discernible correlation in individuals between dorsal coloration and any size character.

Gradations of ventral yellow and the alternate condition of white belly are possibly determined by allelic factors. Yellow belly, if present at all, is usually correlated with yellow dorsal coloration; most of the yellow bellies occur with the yellowish-brown and yellowish-gray back categories. The relationship does not work in reverse, however, as most of the Marin reddish-brown and North Suisun blackish-brown backs have a great deal of yellow pigment which adds to the richness of the prevailing coloration, yet these specimens have pure white bellies. The absence of bright yellow from the Tomales Bay salt marsh specimens, the presence of yellow birds in riparian habitats a mile away from salt marshes (San Leandro Creek, Coyote Creek and Guadalupe River) and the occurrence of yellow variants in more remote uplands (Glen Ellen, Lake Herman) further points to the possibility that the character is hereditary. (These specimens are not wanderers from other populations, as will be shown later.)

Concerning the measurements, it is noteworthy that there is no individual correlation to be found between any two of them. This fact has come to light solely because of the refinement of my statistical data as a result of extensive efforts to determine correctly the age of each specimen. Scatter diagrams of correlation were prepared for all pairs of measurements, including tail length and weight. All apparent positive correlations vanished after the samples were purged of extraneous age groups.

CONSTANCY OF POPULATION CHARACTERS THROUGH TIME

The only instance of change through the years in any population or segment of a population is the appearance since 1940 of a few skins with the head and neck much darker than the back and rump. (One specimen from the East Bay from older collections, M.V.Z. no. 6553, may possess this character, but the skin is so shortened that it is difficult to tell.) Most Song Sparrows from the bay region show conformity of all parts of the dorsal surface (excluding the pure black areas) to a uniform hue and shade, although the relatively more prominent black spots on the crown make the head appear somewhat darker. Twenty-two recent specimens, out of a total of 2,015 both recent and old, have the new character, manifested by a differential increase in the light areas of the scapulars and interscapulars and their suppression on the head, combined with more black pigment on the hindneck than on the rump. Most of these show also a disproportionate increase of chestnut-brown color on the hindneck. The number of these apparent mutants in the samples is as follows: South Suisun 10, Southampton 3, North Suisun 2, East Bay 3, mouth of Walnut Creek 1, Marin 1, Elk Valley 1 and Richardson Bay 1.

Aside from this one very minor change, all series taken in different years from the same place are practically identical, in spite of many interruptions in connecting avenues (see explanation, Marshall, 1948: fig. 42) and obliteration of segments of bay marsh populations due to the activities of man. For instance, a series of 54 old specimens, 47 of them taken in 1916, from the mouth of Walnut Creek average the same in color and measurements as a series of 15 taken there from 1940 to 1942. At the time the earlier collection was made, Walnut Creek joined the South Suisun brackish marsh, in fact there was a large fresh-water marsh (where the specimens were taken) which was continuous both with the riparian and brackish marsh habitats. The recent sample was taken from the last willows at the mouth of Walnut Creek which at the time were separated from the brackish marsh by about two miles, as the fresh-water marsh had been drained and the last two miles of willows had been cut down. (A census in 1947 revealed a continuous connection of Song Sparrows along this avenue, as the willows had grown up again.)

Others examining the collection may wonder at differences in bill length between old and recent samples from the marshes around San Pablo Bay and differences in tarsus and coloration between old and recent samples from the Stege population. The old collections from San Pablo Bay contain many late summer specimens with long bills, which I believe have grown out due to changes in food utilized at that season. There are no specimens from that time of the year in recent collections, but old and recent fall specimens have the normal shorter bill. Concerning Stege, the old collection is from the portion of the marsh at the entrance of the connecting avenue, Cerrito Creek, and shows more characters of *gouldii* than *pusillula*. The recent birds are from a mile to the north. This population is a very narrow one, seldom more than two or three territories wide, and we can expect there miniature gradients similar to those found along connecting avenues.

FACTORS TENDING TO MAINTAIN THE DIFFERENCES AMONG POPULATIONS

Restriction in movements of individual Song Sparrows.—Several items of circumstantial evidence indicate that Song Sparrows here are highly sedentary:

1. Each pair stays within its limited territory during the nesting season. Rarely can they be chased more than 100 yards away from where they are flushed. In particularly violent aggressive behavior, birds may chase each other for more than 100 yards, sometimes out of their habitat, and even perch and sing in grassland at the edge of marshes; in both cases they invariably return to their territorial headquarters.
2. In all seasons, birds collected from riparian habitats within a few hundred yards of salt marshes have no mud on the crown and bill and are in relatively unabraded plumage. Those collected in salt marshes near or far from fresh-water habitats invariably have mud caked on their crown feathers, bill and feet and are in abraded plumage.
3. Specimens collected in a given population, provided it is not an intermediate population where one expects examples similar to an adjacent population, agree with each other in the totality of their variable characters; that is, wherever we find a specimen of coloration similar to some remote population, its measurements, especially bill depth, agree with the population where it was collected. Thus, extreme variants in dorsal color (for instance, two reddish-brown specimens from the Petaluma population, one at Palo Alto salt marsh and another at San Bruno salt marsh) as well as yellow-bellied birds from the uplands are not wanderers from a remote population. There is one exceptional specimen discussed below.
4. A comparison of summer and winter dorsal color types for each population reveals no significant seasonal differences except for the East Bay population. There is no increase of color types characteristic of bay marsh populations among upland populations and *vice versa* in fall and winter.

On the other hand, there is contrary evidence to show that under certain circumstances movements do take place:

1. One specimen agreeing in *both* color and measurements with the South Suisun population was collected by Grinnell at the mouth of San Francisquito Creek, Palo Alto, on January 19, 1901. It is evidently a wanderer 40 miles from home. A single example of the race *cleonensis,* a resident population continuous with Marin, was taken in the bay region at Olema, Marin County, September 17, 1909, a distance of 64 miles from the range of *cleonensis*. Out of 2,015 specimens examined from the bay region, these are the only ones which are definitely wanderers from a remote resident population.
2. In March, 1940, in the course of collecting specimens on a small salt marsh at Stege, Contra Costa County, I apparently frightened all six males off the marsh and found them singing from a barren rock breakwater 300 yards out in the bay!
3. A single specimen, resembling birds at the Richmond Hills, was collected on Red Rock Island 1,500 yards out in the bay by Ward C. Russell. There is no permanent population on the island, although there is soft chaparral there inhabited by several pairs of White-crowned Sparrows.
4. In late summer, adults and juveniles of dense bay marsh populations at Grizzly Island, Solano County, and Gallinas Station, Marin County, forage and even sing 200 yards out in hay fields and eucalyptus groves.
5. With the exception of the geographic barriers separating the North Suisun, South Suisun and Southampton populations from each other, there is in general a remarkable continuity of character gradients across geographic barriers. Particularly the samples on either side of the Golden Gate (Elk Valley and Peninsula), of San Pablo Strait (soft chaparral: Elk Valley and Richmond Hills; salt marsh: San Pablo and Corte Madera) and on either end of Dumbarton Bridge (Palo Alto and Dumbarton Point) resemble each other, indicating that birds may fly across these narrows from time to time.
6. Linsdale (1947:237) reports that Song Sparrows in the upper Carmel Valley, of

the race *cooperi,* continuous with the Peninsula population, are more numerous in summer than in winter.

7. There is a decrease in numbers of reddish-brown and dark olive-brown birds in summer in the East Bay population. Out of the collection of 253 skins, 50 are breeding birds taken from April to July, of which 12 per cent have reddish-brown backs, and 12 per cent have dark olive-brown backs. Of the remaining 203 fall and winter specimens, 23½ per cent are reddish-brown and 21 per cent are dark olive-brown. The Solano population is the logical area from which to expect possible migrants into the East Bay population, not only because it possesses a predominance of these two color categories in about equal numbers, but also because the streams there dry up in the fall. There were no Song Sparrows present in the fall of 1947 in the entire drainages of Green Valley Creek and Suisun Creek, which together compose the entire natural habitat of the Solano population, except that there were birds within the last mile of willows next to the bay marsh on both creeks. On April 18, 1948, Emerson A. Stoner and I retraced our path along these creeks and found pairs established and males singing every 50-60 yards along the entire stretch of suitable riparian habitat. Thus, it seems conclusive that these birds migrate, and it is likely that when they do so, they move only to riparian habitats, mostly in the East Bay. Migration is prevalent in many of the northern and northeastern races of the Song Sparrow; in Ohio, some individuals migrate and some do not (Nice, 1937:29-42). At any rate the impulse to migrate under certain conditions is common throughout the species.

It is evident, therefore, that although certain of the Song Sparrows of the bay region can make long flights or migratory movements, these movements are not into unfamiliar habitats, and that with the exception noted, these birds are remarkably sedentary. Especially, those in bay marshes, where the habitat never dries up, must move very seldom, and if at all, only to an adjacent marsh. Such movements as are made do not tend to break down the differences between bay marsh and upland populations.

Chance fixation of hereditary differences in a small, isolated population.—The only sample of specimens which falls out of line of a character gradient is the one from Southampton Bay marsh, Solano County, which appears to exemplify the role of accidental factors in differentiation (Wright, 1940:167). There are about 176 pairs on this marsh. They are cut off from communication with adjacent bay marsh populations by the steep banks of the north side of Carquinez Strait, which permit no marsh vegetation either east or west of Southampton Bay. They also lack connection with the upland Solano population because this marsh is surrounded by dry grassland on south-facing hills, and no riparian habitat crosses this arid expanse. As noted earlier, bay marsh birds, whose habitat is permanent and not subject to drying, are least likely to move; upland birds which move go only to habitats familiar to them. Therefore, Southampton Bay is the least likely of any population in the bay region to receive genetic influences, carried by wandering birds, from other populations. Conditions there would seem favorable for the accidental loss of genetic attributes and the perpetuation of those retained.

Huxley (1942:200) considers the chance factor in very small populations to be an important one in promoting local differentiation. Lack (1947) recognizes it as an important process promoting differentiation among Galapagos finches. However, the number of birds on the Southampton Bay marsh is greater than is usually regarded as readily permitting chance fixation of genetic factors (Wright, 1940:172). A further complication is the unique habitat at Southampton Bay. The lower half of the marsh is brackish and clothed with *Scirpus*; the upper half has predominantly salt vegetation, *Salicornia* and *Grindelia,* but mixed with a luxuriant array of other plants such as *Juncus* and

Achillea growing high on the slough banks and *Scirpus* in the bottoms of the sloughs. Selective factors may operate, not only within the unique habitat setting as a whole, but also between the birds at opposite ends of the marsh. On the other hand, this ecologic diversity may subdivide the population into small effective breeding units aided by a short distance of establishment of young birds from the nest, and together, these factors, coupled with the isolation of the marsh as a whole, may enhance the "Sewell Wright effect."

Further evidence that the Southampton Bay population is out of line of the gradient for dorsal color is furnished by three series of specimens, too worn for individual color analysis, taken from the Napa population near Sonoma Creek (14 specimens), the Napa population on the east side of the Napa River at Vallejo (14 specimens), and from the North Suisun (only 4 specimens but of same color as the average of all other North Suisun specimens). The Vallejo series is exactly intermediate between the other two, that is, it is uniformly dark olive-brown, much darker and browner than Southampton Bay specimens, although farther removed spatially from North Suisun. (These birds were among those taken by Joseph Grinnell on his bicycle trip around the bay in 1901. Each day he mailed his specimens to Stanford University where Robert E. Snodgrass prepared them as skins.)

Chance fixation within a continuous population.—Miller (1947) regards the chance loss of hereditary attributes as accounting for the differences between samples of California Song Sparrows taken within short distances of each other, because the size of the effective breeding population in this species is small. Using the data of Nice (1937) for banded Song Sparrows in Ohio, he arrives at a figure of about 400 meters for the median distance from the nest at which young birds settle in their first breeding season; consequently he sets the radius of the effective breeding unit at that distance also. It is to be remembered that many of Nice's birds are migratory, and the figure would be lower for Song Sparrows over most of the bay region because they are sedentary. Clearly this results in a slowing down of the spread of genetic characters between segments of the population and makes possible the loss of some characters in any small segment of the population in any one generation. In addition to a small effective breeding population, the distribution of these Song Sparrows is of a pattern exactly equivalent to what Wright (1940:172, 175) postulates as optimal for the expression of chance, non-adaptive change. Not only is their range divided into partly isolated segments, but within these segments (the populations), their distribution is essentially one dimensional, along shore-lines, rivers, etc. Therefore, we should find evidence for chance genetic change in the collection of bay region Song Sparrows. It seems to me that such evidence should consist of samples which fall out of line, more or less, with the prevailing character gradients passing through the populations. Miller (1947:190) appears to have such a criterion when he states that mainland populations of Song Sparrows "also show many local fluctuations of random sort, no two groups from a few miles apart showing evidence of just the same gene frequencies."

I have failed to find, with the exception of the Southampton Bay sample, an instance where, within a continuous population, a sample falls out of line of a character gradient even by as little difference as is shown in color between successive collections along just the riparian portions of the connecting avenues. Where differences in proportions of phenotypes do occur over short distances, they are predictable. For instance, the four segments of the San Francisco Bay population differ in color according to their respective proximity to connecting avenues; the difference between the Marin and Peninsula populations is exactly what is expected from their respective geographic positions in an overall, even gradient for dorsal coloration extending along the coast of California from *cleonensis* in the north to *cooperi* in the south. We do not find situations like the Big Pines colony of Oregon juncos, where a small isolated group of birds in the center of a rather homogeneous population presents a marked deviation in wing length (Miller, 1941:293-294). It can be argued that the collections, not obtained with the purpose of detecting differences between very small segments of populations, would not reflect such differences if they existed, because any one sample might be taken from several breeding units. On the other hand, the collection is rather unique compared with collections of other species inasmuch as it is composed mostly of series of ten or more specimens taken at the same spot on the same day. Unusual interest has attended the bay area races, and through the years many collectors have taken these large samples. They go to marshes, where sparrows are very abundant, and in an hour they can gather a series within a radius of a couple of hundred yards. The fact remains that these discrete series show remarkable uniformity not only over the years, but over distances within major populations. Almost all of my 836 skins are in series of ten taken the same day within the smallest radius in which it is convenient to collect them. From the Marin population alone I have five such samples of ten birds each in fall plumage, which are very much alike, also four samples from North Suisun and five from East Bay.

Spatial isolation.—It has been indicated that isolation by barriers of open water and unsuitable habitat is probably responsible for the maintenance of differences between the Southampton and adjacent populations, and between Solano and the East Bay. Also it is likely that the distance separating the Napa and San Francisco Bay populations is a decisive factor in preventing their direct admixture. But what of the role of spatial versus ecologic isolation in maintaining the distinctness of the typical populations of *samuelis* and *pusillula* from the upland populations adjacent to them? Stresemann (1943) has emphasized the importance of ecologic factors in differentiation of populations, but he appears to have slighted the role of spatial isolation in so doing. I wholeheartedly agree with Mayr (1942:196) and Lack (1947:131) that although ecologic differences can almost always be found between populations occupying different areas on the earth's surface, yet never can we find a case of differentiation on an infra-specific level definitely unaccompanied by spatial isolation. Without this isolation the Tomales Bay salt marsh birds are identical in morphological attributes with the birds in freshwater habitats surrounding them. Wherever it is lacking between bay marsh and upland populations as at Richardson Bay; Corte Madera and San Pablo, the respective populations become practically indistinguishable.

The San Francisco Bay population offers the most sensitive test of the possible *amount* of isolation (Mayr, 1947:268) sufficient to maintain population differences, because it is so highly differentiated from the adjacent upland birds that small amounts of "gene flow" from the connecting avenues register as visible differences in coloration. Neglecting for the moment the role of natural selection, we see that the presence of a single row of Song Sparrow pairs having *gouldii* coloration along each of the two rivers at the south end of San Francisco Bay and continuing into the salt marsh population at Alviso is sufficient to cause an increase in the intermediate dorsal color type, yellowish-brown, all the way to the bay shore, across four miles of continuous salt marsh. This influence of the upland birds is not enough to swamp out the typical salt marsh characters of the Alviso birds, however. Of course, this analysis breaks down because it is impossible to neglect natural selection in such considerations. At least it is true that in the bay region as a whole there is a direct correlation between magnitude of spatial continuity and similarity of bay marsh populations and respective upland populations, regardless of their ecologic differences. Perhaps we can also conclude that *at least* the amount of spatial isolation provided now by the arid bayside plain crossed by only a few connecting avenues was necessary for the formation of the races.

Natural selection.—The characters distinguishing the bay area races are certainly not obviously adaptive, nor do gradients of change in several characters align themselves along geographic or ecologic gradients; rather they appear to follow the line of least resistance through zones of maximum breeding continuity in several cases. Nevertheless, it is probable that decisive adaptational advantages accompany the racial characters, at least in the well differentiated populations. What other agency than natural selection can explain the halting of upland characters in the salt marsh populations, after they have penetrated considerable distances beyond the frontiers of the salt marsh races?

Mutation pressure could hardly be great enough to counteract the influx of "foreign" attributes coming not only from the connecting avenues but via the large intergrading populations as well. Only natural selection can account for the restriction of the area of major change in color characters along the connecting avenues to the intermediate habitat zone (Mayr, 1947:268). Huxley (1942:209) states: "Crosses between two harmoniously-stabilized gene-complexes will give relatively disharmonious gene-combinations. The zone of intergradation will constantly be renewed by intercrossing; but it will as constantly be prevented from spreading by selective elimination in favour of the better internal adaptations on either side, even though it may shift its position." Of especial importance is the fact that the zone of intergradation is not half-way along the connecting avenue nor at the portion of the avenue where the population is narrowest or least dense, but precisely at the zone of intermediate habitat. This is nicely demonstrated, for instance, at the Napa River, where the color of *gouldii* is fully established in birds at the first pure fresh-water vegetation. At this point (1.2 mi. S Napa) there is a row of pairs down each side of the river and many more pairs in some adjoining fresh-water marshes; thus, there is broad continuity of the birds with those in the brackish zone. Farther upstream, on the north side of Napa, laurels and oaks appear along the river, and the Song Sparrows are reduced to a very few, widely separated pairs, becoming abundant again farther up the Napa Valley where willows again predominate.

Habitat preference.—We return now to a consideration of the situation at the mouth of San Francisquito Creek, an exception to all the inferences that have been previously made. We seek the actual mode of operation of ecologic isolation at a habitat boundary between two contrasting vegetational growth forms. There was a marked restriction of pairing between birds of the two races at this junction. It is unlikely that preferential mating on the basis of the racial characters was involved, because I have collected and observed in the field many pairs near the mouths of the Guadalupe River, Coyote Creek and San Leandro Creek, both in the salt marshes and in the willows, one member of which was small and yellow-bellied, the other large, brown-backed and white-bellied. Natural selection could not have been so strict that the birds, upon attempting to settle in the foreign habitat, would have disappeared and so have escaped being collected. I would guess that the birds were not used to the habitat across the boundary, did not recognize it as a suitable growth form, avoided it, and so failed to have an opportunity to meet and mate with birds across the boundary. The interposition of a zone of mixed or brackish habitat, as is usual elsewhere around the bay, would have alleviated this difficulty.

Habitat preference, based merely on the impulse of the individual to stay in the kind of environment in which it has been raised and with which it is familiar, may well suffice to answer the questions arising from the unique situation at San Francisquito Creek.

It should be evident that such preference would be unlikely to be fixed genetically, as opposed to the view of Grinnell (1913:194) who regards it as a racial trait, in view of the wide tolerance range of the species as a whole, and particularly, the utilization of salt marshes by such predominantly fresh-water races as *cleonensis, gouldii* and *cooperi*. In other words, it is thought that a non-hereditary habitat preference operates *within* the limits of instinctive recognition of the niche for the species (Miller, 1942). The fact that topographic conditions are such as not to favor the long duration of such sharp habitat boundaries makes it impossible to believe that new species could gradually be differentiated under such circumstances in the San Francisco Bay region.

Habitat preference can also account for the absence of even a single specimen out of its habitat in places removed from the immediate vicinity of zones of contiguity. As we have seen, the birds which are principally involved in apparent migratory movements are those from streams which dry up in certain seasons or certain years. This does not include the birds at the mouths of those streams; for instance at Green Valley Creek, there was the same number of birds in the last mile at its mouth both in the spring and fall of 1947, but all had disappeared farther upstream in the fall. Accordingly, those which wander are those with the least chance of becoming familiar with a bay marsh habitat. They apparently move to places of like habitat; this accounts for the lack of mixture of birds in the two opposite habitats on either side of the bayside plain, as the actual distance involved here offers no obstacle to the movements of birds across barriers into familiar habitats.

CONCLUSIONS

The foregoing discussion may have obscured the one important fact that all the various agencies maintaining the racial differences, and probably other agencies not mentioned, are working together to produce the results seen. This is an hypothesis only, but it may be desirable to develop it, not with the aim of disagreeing with the views of other students of this problem, but rather with the intention of seeking an overall explanation for the great amount of racial differentiation exhibited by the Song Sparrows of the San Francisco Bay region. Other writers have stressed the importance of this or that isolating mechanism working in a particular situation.

Let us consider as a starting point the unusual combination of geographic and climatic factors which has produced simultaneously regions of qualitatively different Song Sparrow habitat and regions unfavorable for Song Sparrows separating these same habitats. There is a coincidence here; the areas most different from each other in the kind of environment which they provide for Song Sparrows are at the same time the areas which are the most isolated from each other spatially. It seems feasible to assign to the one factor, spatial isolation, the major responsibility for the racial differentiation. Without the amount of isolation by distance that exists between the various races, it is very unlikely that they could have become differentiated in the first place, let alone maintain those differences.

A further coincidence is worthy of note: those populations which are to the greatest degree differentiated morphologically, namely, the populations typical of the three bay marsh color races, are not only the most isolated populations but are also the largest and densest. By "most isolated" I mean that they have the narrowest and fewest avenues of continuity with adjacent, sparse upland populations of the race *gouldii*. Therefore, even without marked difference in habitat, we might expect these populations to preserve their characteristics if we assume that "gene flow" would be in the direction from dense to sparse populations, providing ecologic diversity were absent. In the absence of this ecologic diversification, we should expect at least some racial differentiation, but the populations would probably fall morphologically into predictable intermediate positions on clines connecting the race *gouldii* with the race *heermanni* of the San Joaquin Valley. A fairly good illustration of the single influence of spatial isolation is the difference between the races *pusillula* and *samuelis,* both of which live in salt marshes which appear to have no environmental differences.

If we accept spatial isolation as the most important factor, without which the origin of four races within this small area would have been impossible, then surely the presence of ecologic differences among the areas occupied by those races is the next most important factor. This ecologic diversity makes possible a differential between the selective values of hereditary characters in the different races resulting in the selection of different phenotypes in different habitats. It also provides the basis for the awareness and choice of appropriate habitat by the individual bird. This habitat preference together with the sedentary nature of Song Sparrows in the San Francisco Bay region, both tending still further to enhance the effect of spatial isolation, complete the hypothetical picture of the mechanism responsible for the striking racial differentiation exhibited by bay region Song Sparrows.

I have used the word "race" to represent the entities listed usually as "subspecies." I avoid the terms "geographic race" and "ecologic race" because these groups of populations are scarcely more "geographic" than "ecologic." They are in fact nothing but color races definable solely because they contain a population which is the culmination of some color gradient. Because of the lack of correspondence between the various gradients for color and measurements, entirely different races could be designated on the basis of some other character gradient. The presence in the bay region Song Sparrows of these independent, smooth gradients for the various characters, which Huxley (1942) calls "clines," emphasizes the fact that we look in vain for any group of individuals which have the attributes of miniature species. No race possesses stable characters over a fixed area, nowhere is fertility between strains known to be reduced, no population is denied access to at least an occasional source of genetic mixing with its neighbors. If one desires to make the conclusions from this analysis more general, he may state that the San Francisco Bay region Song Sparrows exhibit the same kind of infra-specific variation as do most continental polytypic species. They are perhaps more sedentary than most birds, but that is their only difference.

There are two ways in which populations within a species can evolve under the influence of natural selection the better to adapt themselves to local environments and so the better to adapt the species as a whole to its niche, with the result that it fills that niche in space and time to the limit. Neither necessarily has anything to do with the origin of new species. Either the population can develop the migratory habit and therefore utilize its niche in areas habitable only part of the year, or it can adapt, through innumerable, small genetic changes, to constant sedentary life in the particular sub-niche available. This does not involve pioneering into habitats new for the species; in continental Song Sparrows at least. It involves concentration upon some particular phase of the overall niche of the species. The two processes are to an extent mutually exclusive. The more migratory a species becomes the more are its populations subject to mixture with one another due to irregularities in migration and the less possibility will there be for local differentiation. The more highly adapted a population becomes to its certain sub-niche, the less area does it have available for its most efficient utilization of the habitat, and the more sedentary it becomes. This is climaxed in bay marsh Song Sparrows. In either case, such infra-specific evolution makes the species a "better species," makes it more able to withstand competition from other species, and could just as well be regarded as a program which perpetuates the species as it is, rather than one which leads to new species. To my mind, the pronounced geographic variation shown in local

Song Sparrows is but another example of this nicety of adjustment of the species to its local environments; nowhere do we find a suggestion of the gross differences in habitat preference or the qualitative differences in foraging, song and mating behavior, nor the overlap in distributions which differentiate Song Sparrows from Lincoln Sparrows and Fox Sparrows, the congeners of *Passerella melodia*.

APPENDIX

The distribution of races of Passerella melodia in west-central California.—In addition to the specimens studied in connection with the foregoing account of Song Sparrows in the immediate vicinity of San Francisco, San Pablo and Suisun bays, I have examined all skins catalogued under the subspecific names *gouldii* and *santaecrucis* in the Dickey Collection, all *cleonensis, gouldii* and *santaecrucis* in the California Academy of Sciences, and all specimens from the mainland of the western United States in the collections of the Museum of Vertebrate Zoology. This revealed, among other things, that the subspecific names *santaecrucis* and *mailliardi,* mentioned (the former by a footnote) in the A.O.U. Check-list (A.O.U. Committee, 1931:359) represent populations which possess no unique attributes and are in fact intermediate in all respects between other more strongly differentiated populations continuous with them. (There are some unexplained gaps in the distribution of Song Sparrows in the central valley of California, but the character gradients are nevertheless fairly uniform, at least from Suisun Bay to Fort Tejon, Kern County.) Accordingly, I suggest that the races *santaecrucis* and *mailliardi* be synonymized, respectively, with *gouldii* and *heermanni*; and I present the following synopsis of the distribution of races in or bordering upon the "bay region," patterned after the account by Grinnell and Miller (1944:546-553). All localities mentioned are represented by specimens.

Passerella melodia cleonensis McGregor

Northwest coastal strip of California from Del Norte County south to Gualala, Mendocino County. Record of vagrant: Olema, Marin County, September 17, 1909 (no. 10570 Mus. Vert. Zool.).

Passerella melodia gouldii Baird

Coast districts from Cazadero and the mouth of the Russian River, Sonoma County, south to Pescadero, San Mateo County; in valleys of the inner coast ranges from Laytonville, Mendocino County south to Paicines, San Benito County, but exclusive of bay marshes bordering San Francisco, San Pablo and Suisun bays; ranges from coast inland to Stonyford, Colusa County, Rumsey, Yolo County, Vacaville, Solano County, and Danville, Contra Costa County.

Passerella melodia samuelis (Baird)

Salt marshes along north side of San Francisco and San Pablo bays, from Richardson Bay east to Vallejo, Solano County; also on south side of San Pablo Bay southwest to San Pablo Point on Richmond headland.

Passerella melodia pusillula Ridgway

Salt marshes bordering south arm of San Francisco Bay, from San Francisco (formerly) and San Bruno on the west, south to Alviso, Santa Clara County, and thence north on east side of bay to Stege, Contra Costa County.

Passerella melodia maxillaris Grinnell

Brackish marshes surrounding Suisun Bay; on the north side, in Solano County from Southampton Bay east to Grizzly Island, on south side, in Contra Costa County from Port Costa (formerly) and Martinez east to Pittsburg. Record of vagrant: Palo Alto, Santa Clara County, January 19, 1901 (no. 36009 Mus. Vert. Zool.).

Passerella melodia heermanni Baird

Sacramento-San Joaquin Valley from Colusa County south to Fort Tejon, Kern County, west to Rio Vista, Solano County, Antioch, Contra Costa County, and Los Baños, Merced County.

Passerella melodia cooperi Ridgway

Coast districts from Santa Cruz,. Santa Cruz County, south to northwestern Lower California.

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